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Coroner cites algae in teen's death

Experts are uncertain about toxin's role

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After a yearlong investigation, the Dane County coroner has concluded that the mysterious death of a Cottage Grove teenager last summer likely was the first in the nation caused by exposure to a toxin released by algae. Dane Rogers Photo/File Scholarship Fund The Rogers family will award two \$1,000 scholarships in their son's name to members of the Monona Grove High School soccer team, one boy and one girl. A golf outing to raise money for the scholarship program is scheduled Sept. 21 at The Oaks Golf Course off Highway TT in Cottage Grove. For information or to register, contact Mike or Kim Rogers at Stillwaters Restaurant, 250 State St., Madison.

Two days after swallowing water while splashing and diving in a scum-covered pond at a Dane County golf facility in July 2002, Dane Rogers went into shock and suffered a seizure before his heart failed, according to Coroner John Stanley's report.

Another teen, unnamed in the report, also was in the pond with Rogers and later became sick, complaining of severe diarrhea and abdominal pain. He survived.

Tests of blood and stool samples from both boys found the common blue-green algae, known as *Anabaena flos-aquae*, and its toxin, Anatoxin-a.

"Never in a million years did we think something like this could happen," said his father, Mike Rogers.

Kim Rogers, his mother, still recalls the evening of July 14 last year.

"It was 97 degrees that day," she said. "It was just getting dark, and they decided to cool off in there. I can just picture them jumping in the water."

"Our one wish is that golf courses would be required to put a sign up at ponds, warning of toxins in the water," she said.

Dane Rogers was 17 at the time and looking forward to his senior year at Monona Grove High School. He was captain of the school's soccer team and honored as an all-conference goalie, and a member of both the National Honor Society and French Honor Society.

"He was an all-around good kid," said his mother. Public awareness Coroner Stanley said he decided to release the report to make the public aware of the potential dangers of algal toxins in small ponds anywhere, whether at golf courses, farms or parks.

"There are a lot of ponds out there with a lot more algae than was in this one," he said. "We

wanted the public to know that you should not go swimming in algae-covered ponds. Parents should even be cautious not to let children collect golf balls from golf course ponds."

Still, there is no reason for the public to panic about the presence of the toxins, according to Stanley and other investigators. While blue-green algae is common in surface water, toxins are released only after thick blooms occur in summer. The toxins are diluted significantly in lakes, rivers and reservoirs and are easily removed by conventional drinking water treatment plants.

One international algal toxin expert who participated in the investigation is not 100% convinced that Anatoxin-a caused Rogers death.

Wayne Carmichael, a professor of toxicology at Wright State University in Dayton, Ohio, has studied toxins released in algal blooms throughout the world. His laboratory received tissue, blood and other fluid samples from the two boys, which were tested for several algal toxins.

Based on animal studies, Carmichael said the amount of Anatoxin-a found in the samples could have caused the diarrhea and seizure followed by rapid death. There are no other cases of human deaths caused by Anatoxin-a for comparison, however, he said.

The reason that Carmichael doubts this explanation is the length of time that elapsed - 48 hours - between the boys frolicking in the pond and Rogers' sudden death.

"We're confident the toxin was present, but the time of death does not fit into what we know about this toxin from animal studies," he said in an interview Friday. "If it had been Anatoxin-a poisoning, he would have experienced those symptoms within a few hours. In animals, you see the effects within minutes to an hour or two."

"Otherwise, the evidence points to anatoxin," Carmichael said. "It's still puzzling to me."

Stanley, the coroner, defended his conclusion.

"The only thing that didn't fit was the time frame, but these kids may have had a stomachache or diarrhea before they told their parents," Stanley said.

"Anatoxin is the most reasonable cause of his death with the available information."

At the time, Rogers' sudden death confounded medical investigators.

An autopsy by Robert Huntington III of the University of Wisconsin-Madison Medical School offered no explanation. "This young person crashed and died after onset of nausea and vomiting," Huntington said in a report. "We see acute heart damage."

Huntington's conclusion: "This is a sad and vexing case."

A series of laboratory tests for pesticides, parasites and other illness-causing organisms found no clues. Analyses of brain tissue ruled out meningitis and encephalitis.

Subsequent interviews with the teenager's friends and fellow soccer teammates revealed that Rogers and four of his buddies - about 48 hours before his death - had jumped a fence at Vitense Golfland on the Beltline Highway in Madison so that they could cool off in the

pond.

"They were in there horsing around," Stanley said in an interview Friday. "Pushing each other around and wrestling in the water."

While wrestling and diving, Rogers and one of the other boys had their heads underwater for varying lengths of time, according to statements made by the teens.

"They both got a mouthful of water," Stanley said.

The other boy who had been fully submerged became ill with the same symptoms of acute diarrhea and abdominal pain, the coroner said. The remaining three developed only minor symptoms.

The four survivors described the small pond to investigators as "dirty" and "scummy."

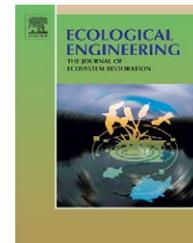
It was nearly two weeks after Rogers' death before researchers became aware of the pond as a potential source of a toxin or other cause of diarrhea.

Water samples were collected on July 26 that year, but studies were inconclusive. The samples were tested by the State Laboratory of Hygiene in Madison and the Madison Department of Public Health. The city laboratory found no illness-causing bacteria. The state laboratory found no algal toxins.

Nonetheless, Stanley concluded that the evidence linked Anabaena and anatoxin to Rogers death.

Diarrhea resulted from "incidental ingestion of the water from the pond," he says in an addendum to his original coroner's report.

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1 *Typha* × *glauca* dominance and extended hydroperiod 2 constrain restoration of wetland diversity

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6 ABSTRACT

Urban wetlands typically have few plant species. In wetlands designed to improve water quality, nutrient-rich water and highly variable water levels often favor aggressive, flood tolerant plants, such as *Typha* × *glauca* (hybrid cattail). At Des Plaines River Wetlands Demonstration Site (Lake Co., IL), we assessed *T. × glauca* dominance and plant community composition under varying hydroperiods in a complex of eight constructed wetlands. Plots flooded for more than 5 weeks during the growing season tended to be dominated by *T. × glauca*, while plots flooded fewer days did not. Plots with high cover of *T. × glauca* had low species richness (negative correlation, $R^2 = 0.72$, $p < 0.001$). However, overall species richness of the wetland complex was high (94 species), indicating that wetlands in urbanizing landscapes can support many plant species where *T. × glauca* is not dominant. *T. × glauca*-dominated areas resisted the establishment of a native plant community. Removing *T. × glauca* and introducing native species increased diversity initially, but did not prevent re-invasion. Although 12 of the 24 species we seeded became established in our cleared plots, *T. × glauca* rapidly re-invaded. In year 1, *T. × glauca* regained an average of 11 ramets m^{-2} , and its density doubled in year 2. The likelihood of planted species surviving decreased as duration of inundation increased, and in both seeded and planted plots, graminoids had greater survivorship through year 2 than forbs across a range of water levels. Within 4 years, however, *T. × glauca* was the most common plant, present in 92% of the cleared plots. Simply removing *T. × glauca* and adding propagules to an urban wetland is not sufficient to increase diversity.

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1. Introduction

22 The plant diversity of urban wetlands can be low because
23 of limited propagule availability, or because site conditions
24 are unfavorable. Propagules could be limited in an isolated
25 site that lacks dispersal corridors, or where only one species
26 is introduced to a constructed wetland (Kadlec and Knight,
27 1996; Bonilla-Warford and Zedler, 2002; Seabloom and van
28 der Valk, 2003). This suggests that introducing native species
29 through seeding or planting might be sufficient to promote

30 the development of a diverse community of native species.
31 However, limited propagule availability might not be the only
32 reason for low native species richness. The unnatural hydro-
33 logic regimes common to urban wetlands might discourage
34 some species and contribute to low diversity (Reinelt et al.,
35 1998; Galatowitsch et al., 2000; Kowalski and Wilcox, 2003).
36 Other stresses, such as sediment and nutrient inputs could
37 also hinder the growth of native plants and stimulate the
38 development of monotypic stands of aggressive species, such
as *Typha* spp. (cattail) (van der Valk and Davis, 1978; Maurer and

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Zedler, 2002; Werner and Zedler, 2002; Woo and Zedler, 2002). A better understanding of the relationship between hydrologic regime and plant species diversity would aid the restoration of wetland plant communities.

Urban wetlands are typically designed to store excess water and to improve water quality, but not to support biodiversity (Athanas, 1988; Livingston, 1989). Increasing the plant species diversity of urban wetlands could benefit both people and wildlife. Greater diversity could improve aesthetics, increase ability to attract migratory waterfowl and other animals, and offer greater recreational opportunities (e.g., bird watching; Duffield, 1986; Linz and Blixt, 1997; Linz et al., 1999). In addition, there is experimental evidence from shallow-water mesocosms that increasing species diversity could increase phosphorus removal (Engelhardt and Ritchie, 2001).

In the absence of plantings, *Typha* spp. are likely to colonize stormwater wetlands (Schueler, 1994), and species richness is likely to be low (Seabloom and van der Valk, 2003; Xiong et al., 2003; Baldwin, 2004). *T. latifolia* (broad-leaved cattail) is native to temperate North American wetlands, and *T. angustifolia* (narrow-leaved cattail) is an invasive species that is increasingly common in these wetland systems (Smith, 1987). The two species often produce an F1 hybrid, known as *T. × glauca* (Smith, 1967), which is highly invasive and tends to be more aggressive than its parents (Kuehn and White, 1999). *T. × glauca* tolerates a wider range of water levels than either parent species (from moist soil up to 1 m deep water), and exhibits competitive superiority over its parents at all water levels (Waters and Shay, 1991; Kuehn and White, 1999). *T. × glauca* is nearly sterile, however, it is capable of spreading rapidly via vegetative reproduction, and it readily establishes from vegetative propagules. Once established, rhizomes expand to create large monotypic stands.

In order to increase diversity in urban wetlands we need to know which native species are likely to tolerate the stresses found in urban wetlands, and if they can resist replacement by aggressive invasive species. We also need to know if urban wetland hydroperiods can be managed to favor native over invasive species. A community of native species can foster diversity, as additional species are likely to appear as volunteers. For example, a Maryland stormwater treatment wetland with plantings of *Schoenoplectus pungens*, *Saururus cernuus*, and *Sagittaria latifolia* formed a structural matrix that many other species appeared to exploit, despite invasion by *Typha* sp. (Schueler, 1994). However, a decrease in diversity of a restored native community is a likely outcome of colonization by invasive species. Oberts (1994) found that species planted in a stormwater treatment wetland (among them *Schoenoplectus* sp., *Nymphaea* sp., and *Iris* sp.) were largely supplanted after 10 years by invasive species, such as *Typha* sp., *Phalaris arundinacea*, and *Lythrum salicaria*.

We used eight wetland basins at the Des Plaines River Wetlands Demonstration Project (DPRWDP) to investigate patterns of *T. × glauca* dominance and plant diversity in relation to hydroperiod. These wetlands are located in an urbanizing landscape and are each dominated by *T. × glauca* at their lowest elevations. The wetlands have sloping sides, which allowed us to study sets of plots that are separated by a few meters but have very different hydroperiods. We hypothesized that plots that are flooded longer will have a greater density of

T. × glauca and will support fewer native species. To test this hypothesis, we measured species richness and cover of all species present in 96 1-m² plots with varying hydroperiods, over 4 years. We then conducted experiments to determine the effectiveness of removing *T. × glauca* followed by seeding or planting to restore species diversity to *T. × glauca*-dominated wetlands. Our objective was to determine if adding propagules would establish a native plant community that could resist reinvasion by *T. × glauca*. We analyzed *T. × glauca* re-invasion and planted species survival in 24 plots over 4 years, and re-invasion and seedling survival in 20 plots for 2 years.

2. Study site

The DPRWDP is a 223-ha wetland and prairie restoration along the Des Plaines River in Wadsworth, Lake County, Illinois. The site was developed by Wetlands Research Inc. in cooperation with the Lake County Forest Preserve District. DPRWDP functions as a mitigation wetland complex, research facility, and a public park. Eleven hectares are devoted to wetland research (Kadlec and Hey, 1994).

We studied *T. × glauca* dominance and plant community composition under different hydroperiods, and we experimentally planted native wetland plants in a set of eight-wetland cells at DPRWDP (Fig. 1). These wetland cells were constructed in 1991–1992 by excavating and removing topsoil and breaking subsurface drainage tiles. The eight cells are 160 m × 50 m (0.8 ha); each has a central channel and slopes up to narrow bands of wet meadow and prairie communities on either side. An additional 2 cells, #5 and #10, serve as holding basins. The channel contains emergent marsh species dominated by *T. × glauca*. The wetlands are above the natural water table and are supplied with water from Des Plaines River via a pump and irrigation lines. The river water has low nutrient concentrations in the summer and fall (Table 1). Four wetland

Table 1 – Water chemistry of the eight-wetland cells in 2001

	Minimum	Maximum	Mean
Dissolved phosphate (ppb)	55	140	–
Total phosphorus (ppb)	193	492	–
Dissolved phosphate removal (%)	27	90	–
Total phosphorus removal (%)	33	82	–
Ammonia (ppb)	–	–	25
Nitrate (ppb)	18	284	–
Total nitrogen (ppb)	44	112	–
Ammonia removal (%)	31	64	–
Nitrate removal (%)	0	100	–
Total nitrogen removal (%)	68	94	–
Turbidity (NTU)	5	150	30
Turbidity decrease (%)	70	95	–

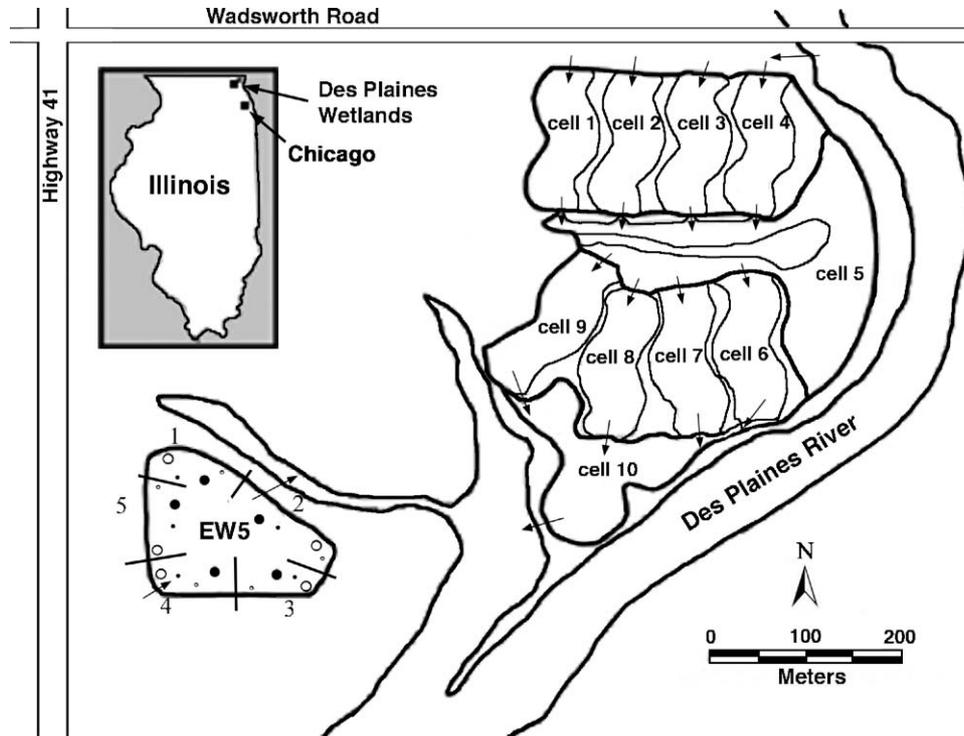


Fig. 1 – Map of DPRWDP. Arrows indicate direction of water flow. In the upper right are the eight cells (cells 1–4 and 6–9) where we sampled vegetation and planted native species. We experimentally seeded in EW5. Small and large circles indicate locations of small and large plots. Black circles indicate deeper water plots, and white circles indicate shallower plots. Numbers 1–5 surrounding EW5 indicate the blocks of plots.

131 cells receive water directly from the irrigation lines (cells 1–4).
 132 A fifth basin (cell 5) receives water that flows from cells 1–4,
 133 and conveys the water to the second set of four wetland cells
 134 (cells 6–9). A final basin, cell 10, receives the water from cells
 135 6–9 and conveys the water back to the Des Plaines River. Water
 136 flow out of the wetland cells is controlled by horizontal concrete
 137 weirs, which have removable stop boards that allow the water levels
 138 to be manipulated.

139 The experimental wetlands have been actively managed
 140 since their construction. An initial seed mix was applied in
 141 1992, and seeds of several native species were added in sub-
 142 sequent years. Managers have applied herbicides to control *P.*
 143 *arundinacea* and *L. salicaria* and hand-pulled aggressive shrubs
 144 and trees (*Salix* spp. and *Populus deltoides*; K. Paap, Wetlands
 145 Research Inc., personal communication). No management
 146 activities occurred during this study (2000–2004). Earlier stud-
 147 ies of sedge (*Carex* spp.) establishment and soil development
 148 (redoximorphic features) have taken place in these wetlands
 149 (Brenholm and van der Valk, 1993; Vepraskas et al., 1995).

150 Our seeding study was conducted in Experimental Wetland
 151 #5 (EW5) of DPRWDP; it is a 1.8-ha wetland created in 1989
 152 (Fig. 1). EW5 is hydrologically separated from the previously
 153 described wetland cells. Water is pumped into EW5 from a
 154 pipe near the southwestern edge, and a weir on the north-
 155 eastern edge controls the outflow. The wetland is supplied
 156 with both river water (from the Des Plaines River) and ground
 157 water. Nearly all of EW5 is a *T. × glauca* monotype that is dense
 158 and tall (45 ± 2.3 ramets m^{-2} and maximum height >2.5 m). A
 159 thick layer of *T. × glauca* litter has formed throughout the wet-

land. The invasive *P. arundinacea* (reed canary grass) is found on
 the upland edge and *Lemna minor* (common duckweed) occurs
 throughout. Several previous studies have been conducted in
 EW5; for example, Hey et al. (1994) found high removal rates
 for nutrients and suspended solids, and Fennessy et al. (1994)
 documented a shift from dominance by *P. arundinacea* to *Typha*
 spp. when water levels were raised (see Ecological Engineering
 Special Issue Volume 3(4)).

3. Methods

3.1. Physical conditions

DPRWDP staff recorded daily water levels from May to Octo-
 ber from 2001–2004 at each weir of the eight-wetland cells,
 and in 2003 and 2004 at the outlet weir of EW5. We recorded
 hourly water temperatures during the growing season of 2001
 in cells 1–4 with HOBO® Temp (H01-001-01) loggers from Onset
 Computer Corporation. The loggers were encased in clear plas-
 tic waterproof cases, which were attached to stakes at the
 water/sediment interface approximately 1 m north of the out-
 let weirs for cells 1–4.

3.2. Existing vegetation

In 2000, we randomly located three transects along the length
 of the cell in each of the eight-wetland cells (Fig. 2). In each
 transect we permanently marked 4 square 1-m² plots, for a

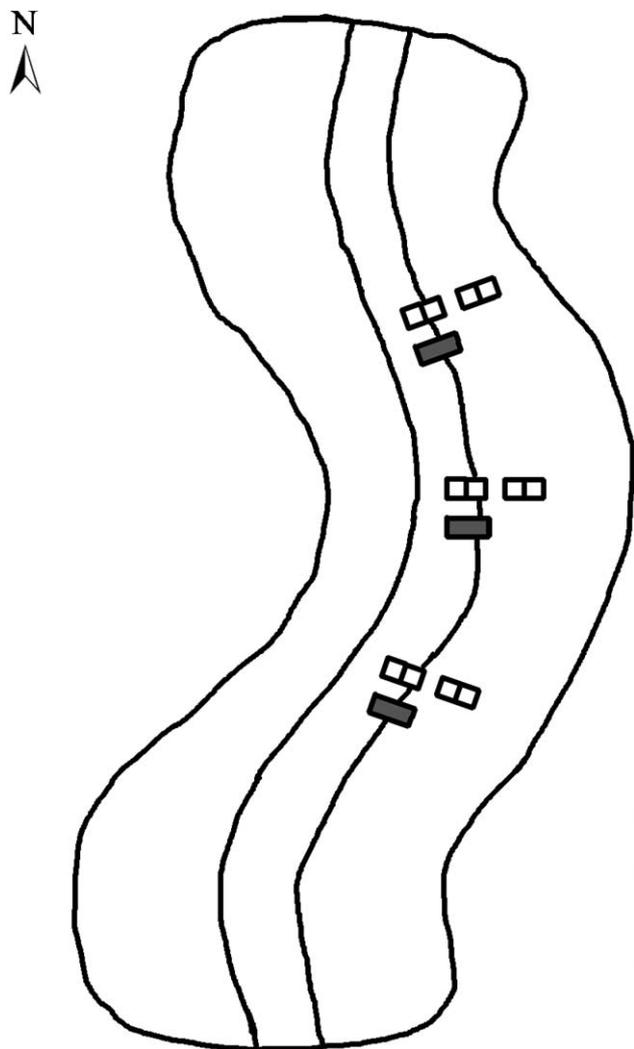


Fig. 2 – Conceptual drawing of a wetland cell (not to scale). A narrow channel runs down the center, with water flowing from north to south. We sampled community composition in the 12 white squares (3 transects, each with 2 pairs of plots). Our planting experiment took place in the three solid rectangles.

182 total of 96 plots. The transects extended from the *T. × glauca*-
 183 dominated channel up the elevation gradient into the wet
 184 meadow area on the sloping portion of the cell. Each transect
 185 included two contiguous plots in the channel and two con-
 186 tiguous plots in the wet meadow, with a 1-m space between
 187 the channel and wet meadow plots. The upland edges of the
 188 cells were not included in the transects. In order to focus our
 189 study on herbaceous plant communities, we rejected transect
 190 locations that were dominated by woody plants, such as *Salix*
 191 spp.

192 We determined the elevation of all plots and weirs using a
 193 Leica 530 global positioning system, which provides 3-cm ver-
 194 tical precision. To determine the plot elevation, we recorded
 195 the elevation at each corner of the plot and used the aver-
 196 age of the four measurements. This method was appropriate
 197 because there is little vertical relief within each plot. Using
 198 plot elevation and wetland water level data, we calculated the

199 average number of days each plot was flooded per growing
 200 season from 2001 to 2004 to characterize the hydroperiod of
 201 the plots. A plot was considered to be flooded if the water level
 202 at the outlet of the wetland cell was higher than the average
 203 elevation of the plot.

204 In 2000 and 2001, we measured standing aboveground
 205 biomass and characterized the relationship between
 206 *T. × glauca* biomass and biomass of all other species under a
 207 range of hydroperiods. We collected biomass from 0.25-m²
 208 plots adjacent to the permanent plots in each cell. In each
 209 0.25-m² harvested plot we cut live plant material at substrate
 210 level, separated it into *T. × glauca* and other species, and
 211 dried it in a 60 °C oven to constant weight. We did not collect
 212 non-rooted species, such as *Lemna minor*, because they flowed
 213 in and out of the plots with changing water levels.

214 In order to characterize the plant species diversity of the
 215 96 1-m² permanent plots, we measured stem density of each
 216 species in 2000 and 2001, and percent cover of each species
 217 from 2001 to 2004. In each permanent plot, we visually esti-
 218 mated percent cover of each species using an 8-point log base
 219 2 scale (i.e. 1, 2, 4, 8, 16, 32, 64, >64). We identified species using
 220 Voss (1985) and Chadde (1998); taxonomic nomenclature fol-
 221 lows the University of Wisconsin-Madison Herbarium.

222 We used Swink and Wilhelm's (1994) coefficient of conser-
 223 vatism (CC) for each species to calculate two indices for each
 224 plot: mean (CC) and the Floristic Quality Assessment Index



Fig. 3 – EW5 in July 2002 (photos by Boers). (a) *T. × glauca* monotype prior to cutting and seeding; (b) a large plot with *T. × glauca* removed by cutting.

225 (Eq. (1)):

$$226 \text{ FQAI} = \frac{\sum \text{CC of all species in the area}}{\sqrt{\text{number of species in the area}}} \quad (1)$$

227 A CC is a number given to each plant species by a group of
228 experts in the regional flora to describe its likelihood of being
229 found in pristine habitats. A CC of 10 indicates a species only
230 found in pristine habitats, a CC of 0 indicates a species that
231 can be found in any habitat, even the most degraded.

232 3.3. Seed introductions

233 We divided EW5 into five blocks along the perimeter, and
234 established four plots within each block. In each block, we
235 located two of the plots in shallow water and two in deeper
236 water, with an elevation difference of 15 cm between the sets.
237 We selected the plots by traveling a random distance along the
238 perimeter of the wetland, then walking into the wetland per-
239 pendicular to the upland edge until the desired elevation was
240 reached. Each elevation of each block has 1 large treatment
241 plot with a 4 m radius and 1 small treatment plot with a 2 m
242 radius, randomly assigned within blocks, for a total of 20 plots
243 (Fig. 1).

244 We lowered the water level of wetland EW5 to the soil sur-
245 face of the lower elevation plots in July of 2002. While the
246 water level was low, we severed all vegetation in all plots at the

247 base using a brush cutter (Fig. 3). We immediately raised the
248 water level by approximately 30 cm to drown the rhizomes of
249 the cut *T. × glauca*. Two months of elevated water levels effec-
250 tively killed *T. × glauca* within the plots and had no apparent
251 effect on plants outside plots. In September 2002, we low-
252 ered water levels again, at which time the cleared plots were
253 seeded with a mix of 24 native wetland species obtained from
254 Prairie Moon Nursery, Winona, MN (Table 2). We seeded the
255 plots using a split-plot design. Each plot was divided into quar-
256 ters, two quarters received 8 graminoid and 2 forb seeds per
257 square foot (~0.093 m²), and the other two quarters received
258 10 times as many seeds (Fig. 4). We added more graminoid
259 seeds than forbs in an attempt to establish a cover crop of
260 graminoids (Bonilla-Warford and Zedler, 2002). Within the
261 forb and graminoid groups, the number of seeds per species
262 was equal. To allow seeding establishment, we maintained
263 low water levels (no standing water) throughout the winter
264 and early spring. After spring seedling establishment, we
265 increased water levels to create water depth treatments where
266 the shallower plots had water levels that remained saturated
267 throughout the growing season, and the deeper plots had
268 standing water. Staff at the DPRWDP monitored water levels
269 throughout the 2003 and 2004 growing season at the outflow
270 weir.

271 In order to determine seedling establishment and survival
272 and *T. × glauca* re-invasion rates, we measured seedling stem
273 density and *T. × glauca* ramet density. In September of 2003

Table 2 – Species seeded in EW5, number of subplots each species was found in, and total stem count for all subplots in 2003 and 2004

	2003		2004	
	Number of subplots	Total stems	Number of subplots	Total stems
Graminoid species				
<i>Bromus ciliatus</i>	0	0	0	0
<i>Calamagrostis canadensis</i>	10	74	14	194
<i>Carex hystrix</i>	0	0	0	0
<i>Carex lacustris</i>	25	154	9	23
<i>Carex stricta</i>	6	70	5	18
<i>Glyceria grandis</i>	0	0	0	0
<i>Leersia oryzoides</i>	12	133	16	110
<i>Schoenoplectus acutus</i>	0	0	0	0
<i>Schoenoplectus tabernaemontani</i>	0	0	0	0
<i>Bolboschoenus fluviatilis</i>	0	0	0	0
<i>Sparganium eurycarpum</i>	3	4	6	27
<i>Spartina pectinata</i>	12	56	7	42
Average	5.7	40.9	4.8	34.5
Forb species				
<i>Alisma subcordatum</i>	6	7	11	17
<i>Angelica atropurpurea</i>	0	0	0	0
<i>Asclepias incarnata</i>	0	0	0	0
<i>Aster novae-angliae</i>	0	0	0	0
<i>Bidens cernuus</i>	24	560	65	342
<i>Eupatorium maculatum</i>	0	0	0	0
<i>Eupatorium perfoliatum</i>	1	1	0	0
<i>Impatiens capensis</i>	1	1	0	0
<i>Lycopus americanus</i>	0	0	0	0
<i>Mentha arvensis</i>	0	0	0	0
<i>Sagittaria latifolia</i>	0	0	2	5
<i>Verbena hastata</i>	1	1	0	0
Average	2.8	47.5	6.5	30.3

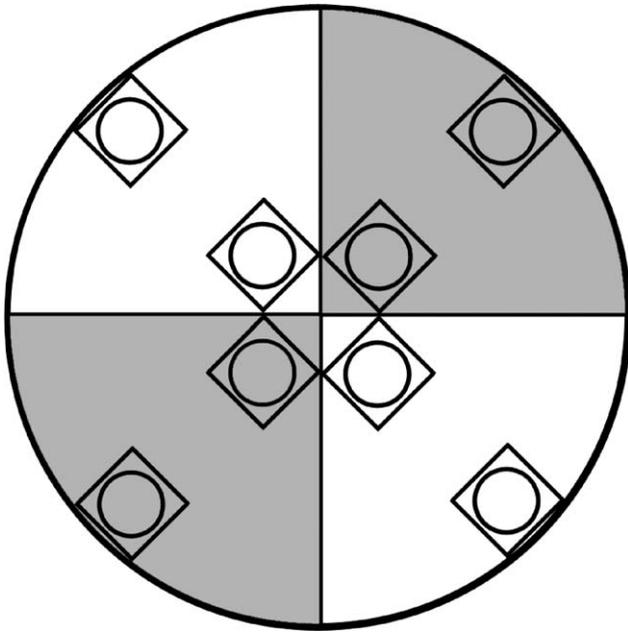


Fig. 4 – A seeded plot in EW5. We used 10× greater seed density in 2 of the 4 quarters of the plot (shaded in gray). In each quarter of the plot we measured *T. × glauca* ramet density in two square subplots, and stem density of all other species in two circular subplots.

and 2004, we sampled two subplots in each quarter of each plot (as defined by the split plot seeding density); one located near the center of the plot and another on the outside edge. In large plots, we measured *T. × glauca* density within square 1-m² subplots and stem density of other species (seeded and volunteer species) within a 0.5-m² circular frame placed in the center of the subplot; in small plots, we used a square 0.25-m² subplot and a 0.125-m² circular frame (Fig. 4). We used smaller subplots in the smaller plots to maintain equal sampling effort, in this way we sampled the same percentage (4%) of the area of each plot. We used circular frames to sample stem density of seeded and volunteer species to minimize the amount of edge of the sampling frame per unit area. By decreasing the edge:area ratio, we could more accurately count stems of species with high stem density that are located across the edge of the frame.

3.4. Whole-plant introductions

We removed *T. × glauca* from three 3 m × 1 m plots in each of the eight-wetland cells by scraping and removing 20 cm of topsoil and existing plant roots with a large backhoe with a smooth-edged bucket (Fig. 2). We measured the elevation of each plot using methods described in Section 3.2. There was little vertical relief within a plot. In August 2000 we planted each plot with 10 species (8 plants of each species, 80 plants total per plot) in a repeated random pattern with each plant spaced 20 cm apart. The plants were 2-year-old, 5 cm × 5 cm plugs from Taylor Creek Nurseries, Brodhead, WI. We chose to plant *Calamagrostis canadensis*, *Helianthus grosseserratus*, *Acorus calamus*, *Pycnanthemum virginianum*, a mix of *Aster lanceolatus*

and *A. puniceus*, *Asclepias incarnata*, *Lycopus americanus*, *Carex stricta*, *Carex comosa*, and *Spartina pectinata* because they represent a variety of plant types (grasses, sedges and forbs) and they are known to occur in a variety of wetland conditions (Curtis, 1971).

In 2001, we monitored the scraped plots for survival and growth of planted and volunteer species. In July and September 2001, we measured total stem length of the planted species. For forbs, we measured the stem length to the nearest cm at the natural height of the top leaf buds. For graminoids, we measured each stem to the nearest cm from the base to the tip of the top leaf, fully extended. To estimate canopy cover of planted species and volunteers we randomly placed three 0.25-m² subplots in the plot, visually estimated cover in the subplots, and averaged the values. In September 2001, we determined standing aboveground biomass of the planted and volunteer species in the planted plots. We cut the plants at substrate level, sorted them by species, and dried them in a 60 °C oven to constant weight. In order to assess survivorship of planted species and colonization ability of volunteer species, we recorded presence/absence of all species per plot (not survivorship of each planted individual as in 2001) each September from 2002 to 2004.

4. Results

4.1. Physical conditions

In 2001, mean daily water temperatures for wetland cells 1–4 ranged from 29 °C in cell 3 on August 8 to 10.9 °C in cell 1 on September 25, with an average of 20 °C. The hydroperiods of the eight-wetland cells varied by wetland cell and by year, and the 96 plots were chosen to represent an array of elevations. We therefore characterize each plot's unique hydroperiod using the number of days it was flooded during the growing season (May–October). Over the 4-year study the average number of days flooded per plot per year was 76, ranging from 7 to 150.

In 2001, Cari Ishida and Dr. Kimberly Gray of Northwestern University investigated water chemistry of the inlet and outlet water of cells 1–4 of the eight-wetland cells (Table 1). Ishida and Gray calculated nutrient removal and turbidity decrease percentages by comparing the values found at the inflow to values at the outflows of cells 1–4. These data indicate that the Des Plaines River had a low concentration of nitrogen and a normal to low concentration of phosphorus.

In August 2003, Jessica Seck and Dr. Kimberly Gray of Northwestern University investigated nutrient levels in the sediment of EW5 at a 5–7 cm depth and provided the following data: In comparison to examples of wetland sediment conditions presented by Mitsch and Gosselink (2000), organic matter content was low (7.2–10.5%) and total and extractable phosphorus (P) content was high (388–559 mg P/kg sediment total P; 72–133 mg P/kg sediment extractable P). These values indicate a mineral soil, which is expected in a recently constructed wetland. Nitrogen (N) content of the sediment was measured as Total Kjeldahl N (1.34–2.39%), nitrate-N (0.27–1.02 mgNO₃-N/kg sediment), and extractable ammonium-N (8.3–35.7 mg NH₄-N/kg sediment).

4.2. Extant wetland vegetation

4.2.1. Species diversity and composition

Species richness at the scale of the 4 ha wetland complex (eight-wetland cells) was surprisingly high. We found a total of 94 species (and 11 unidentifiable seedlings) over 4 years of monitoring 96 1-m² permanent plots. Of the 94 species, 52 were classified as obligate wetland species, and 21 as facultative wetland species; totaling 73 species that occur in wetlands >67% of the time (US Fish and Wildlife Service, 1988). We found six non-native species: *P. arundinacea*, *Aster subulatus*, *L. salicaria*, *Sonchus oleraceus*, *Xanthium strumarium* and *Phragmites australis*. In 2001, the overall FQAI for the site was 35.9 and the overall mean CC was 4.5.

Typha x glauca dominated the eight-wetland cells; its average cover in the permanent plots sampled from 2001 to 2004 was 40% (mean based on cover class midpoints). All other species combined had an average cover of only 28% over the 4-year period. *T. x glauca* had greater than 64% cover of the 1-m² plots in 37% of the plots throughout the 4-year study. *T. x glauca* also contributed the most to total biomass (median value of 86%).

There was an average of 21 species per wetland cell (~0.5 ha) over the 4 years of study, ranging from an average of 9 ± 2.7 species in cell 1, to 26 ± 2.1 in cell 7. We found an average of 5.9 ± 0.17 species per 1-m² plot over the 4-year study. The maximum richness per 1-m² plot (18 species) occurred in cell 6 in 2001 and the minimum (only *T. x glauca*) occurred twice in 2002 and 2003, and 17 times in 2004.

4.2.2. *Typha x glauca* dominance, species richness, and hydroperiod

Average species richness of the 1-m² permanent plots over 4 years of sampling was negatively correlated with average *T. x glauca* cover ($R^2 = 0.72$, $p < 0.001$, $F_{1,88} = 226.2$) (Fig 5) and average number of days flooded ($R^2 = 0.11$, $p < 0.002$, $F_{1,88} = 11.6$); and average *T. x glauca* cover was positively correlated with average number of days flooded ($R^2 = 0.16$, $p < 0.001$, $F_{1,88} = 17.1$). FQAI also declined as *T. x glauca* abundance

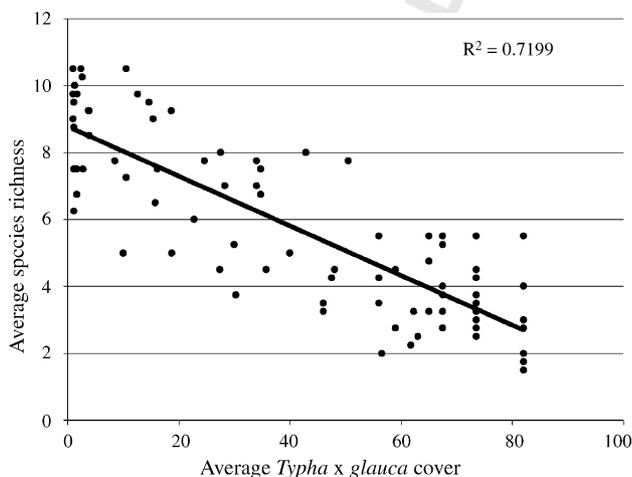


Fig. 5 – Relationship between average species richness of each plot and average *T. x glauca* cover. Data points are average values of 4 years of sampling.

increased (negative correlations with ramet count, $R^2 = -0.59$, $p < 0.005$; and biomass, $R^2 = -0.38$, $p < 0.005$). Biomass and ramet counts of *T. x glauca* were positively correlated ($R^2 = 0.60$, $p < 0.005$). Over the 4 years of sampling, plots that averaged less than 35 days flooded all had less than 40% cover of *T. x glauca*, with an average of 14%. Plots that averaged greater than 35 days flooded had a broader range of values of *T. x glauca* cover, with an average of 49%. The species that occurred in plots with high *T. x glauca* density typically had low CC and occurred in plots across a wide range of *T. x glauca* densities and plot elevations. For example, *Bolboschoenus fluviatilis* occurred in one plot with 80 *T. x glauca* ramets and in another plot with only 10. *Polygonum punctatum*, *P. arundinacea*, *Leersia oryzoides*, *Eleocharis erythropoda*, and *Schoenoplectus tabernaemontani* were similarly found in plots with both low and high *T. x glauca* densities.

4.3. Experimental seeding

4.3.1. Seedling establishment

Eleven of the 24 species seeded in wetland EW5 in fall 2002 were recorded in the subplots sampled in September 2003 (Table 2). An additional seeded species was found in 2004. Six of the 12 graminoid species were recorded in the subplots sampled, as well as 6 of the 12 forb species. *Bidens cernuus*, an annual forb, had the greatest number of stems m⁻² after both one and two growing seasons (5.6 and 3.42, respectively). Excluding *B. cernuus*, stem densities after both the first and second years were much lower for the other 11-seeded forb species (averaging 0.009 stems m⁻² in 2003 and 0.02 stems m⁻² in 2004) than the 12 seeded graminoid species (averaging 0.41 stems m⁻² in 2003 and 0.35 stems m⁻² in 2004). The 4× difference in initial seeding rate (4:1 graminoid:forb seeds) does not account for the >20× difference in establishment. Of the 160 sampled subplots, *B. cernuus* was found in 24 subplots in 2003 and 65 subplots in 2004, while all other seeded forb species were found in only 9 subplots in 2003 and 13 subplots in 2004. Seeded graminoid species were found in 68 subplots in 2003 and 57 subplots in 2004.

Each of the six-seeded graminoids found in EW5 in 2003 was also recorded in 2004; with *C. canadensis* and *Sparganium eurycarpum* increasing in both number of subplots found and total stem count, and *Leersia oryzoides* increasing in number of subplots found, but not stem count. Only 2 of the 5 forb species that were found in the first year were found in the second year. Both *Alisma subcordatum* and *B. cernuus* were found in more subplots in 2004 than 2003, but only the former had a greater stem count in 2004. Each of the 3 forb species that were recorded in 2003 but not 2004 (*Eupatorium perfoliatum*, *Impatiens capensis*, and *Verbena hastata*) was present in only one subplot in 2003. A forb, *S. latifolia*, was the only seeded species to appear in 2004 that was not found in 2003.

In 2003, subplots that received 10× as many seeds had about 4× as many stems m⁻² of seeded species (8.42 in high seeding density, 2.19 in low) and had an average of nearly 3 times as many seeded species per subplot (0.47 in high seeding density, 0.16 in low). In 2004, the differences between the seeding density treatments decreased. After 2 growing seasons, the subplots with 10× greater seeding density had about 1.6× as many stems m⁻² of seeded species (4.78 in high

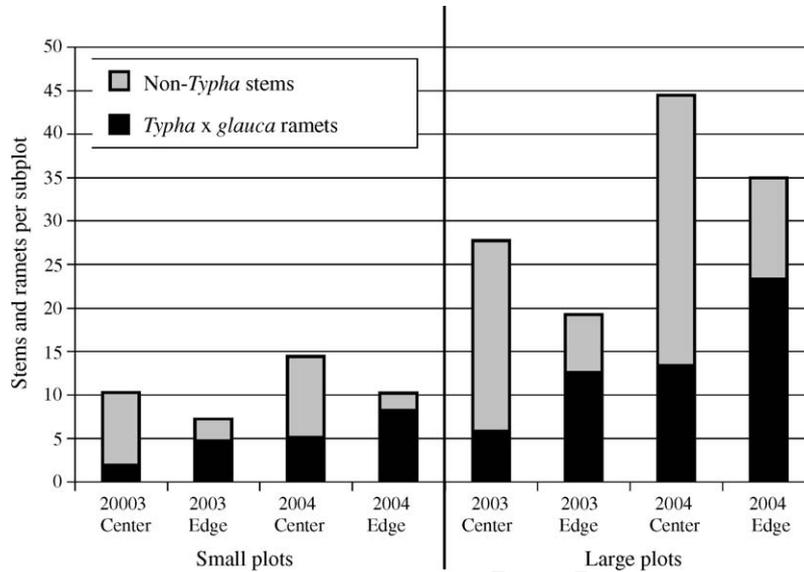


Fig. 6 – Comparison of *T. x glauca* ramet and non-*Typha* stem densities in subplots near the center and edges of plots. See Section 3 for subplot sizes.

452 seeding density, 3.00 in low) and almost the same number of
 453 seeded species per subplot (0.43 in high seeding density, 0.42 in
 454 low).

455 The stem density of non-*T. x glauca* plants was greater in
 456 the center of plots than near the edge in both large and small
 457 plots in 2003 and 2004 (Fig. 6). There was a positive correlation
 458 between elevation of the plot and stem density of non-
 459 *T. x glauca* plants in small plots in 2003 ($R^2 = 0.12$; $p < 0.002$).
 460 Stem densities cannot be directly compared between large and
 461 small plots because larger subplots were measured in larger
 462 plots. However, if the number of stems in small plots is multiplied
 463 by four to equalize subplot sizes a comparison can be
 464 made, and stem density is not significantly different in large
 465 and small plots.

466 4.3.2. *T. x glauca* reinvasion

467 After *T. x glauca* was removed from the plots in wetland EW5
 468 in July 2002, it reinvaded by vegetative spread. No *T. x glauca*
 469 seedlings were observed within the plots. In 2003, large plots
 470 averaged 9.2 *T. x glauca* ramets m^{-2} , and small plots averaged
 471 3.2 ramets $0.25 m^{-2}$. *T. x glauca* densities doubled from
 472 2003 to 2004, increasing to 18.3 ramets m^{-2} in large plots and
 473 6.7 ramets $0.25 m^{-2}$ in small plots (Fig. 6). Reinvasion was most
 474 rapid near the edges of plots. Density of *T. x glauca* ramets was
 475 greater in subplots on the edges of plots than in the center in
 476 2003 and 2004 for both small and large plots (Fig. 7).

477 In 2003 there were significantly more *T. x glauca* ramets
 478 m^{-2} in the center of saturated (9.05 ± 1.65) than flooded
 479 (2.55 ± 0.73) water level plots ($p = 0.0009$); in 2004 these densities
 480 increased to $19.65 (\pm 2.39)$ and $7.05 (\pm 1.26)$, respectively
 481 ($p < 0.001$). No significant relationships between *T. x glauca*
 482 ramet density and water depth were found in small plots or
 483 subplots near the edge of large plots. As above, in order to compare
 484 the different sampling areas of large and small plots the
 485 ramet density in small plots was multiplied by four. *T. x glauca*
 486 ramet density m^{-2} is greater in small plots than large plots in



Fig. 7 – Large plots with *T. x glauca* removed and seeds added (photo by Boers). (a) One year after seeding showing low density of *T. x glauca* and an abundance of seeded species, including *Bidens cernuus*, *Calamagrostis canadensis*, and *Carex stricta*. (b) Two years after seeding, showing high density of *T. x glauca* and fewer seeded species.

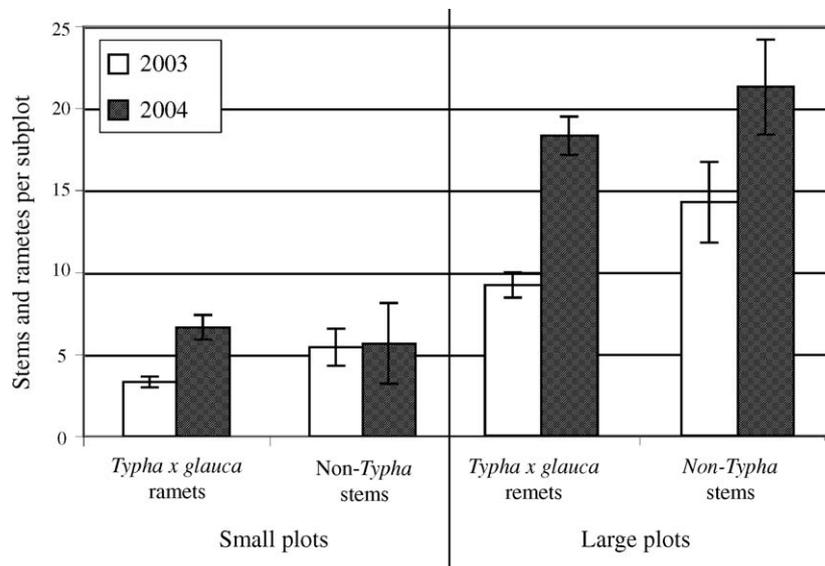


Fig. 8 – Changes in *T. x glauca* ramet and non-Typha stem density in large and small plots from 2003 to 2004. See Section 3 for subplot sizes.

2003 (13.3 ± 1.3 and 9.2 ± 0.8 , respectively; $p < 0.007$) and 2004 (26.6 ± 1.7 and 18.3 ± 1.2 , respectively; $p < 0.001$).

There is a negative correlation between *T. x glauca* ramet density and the stem density of all other species (including both seeded and volunteers) in large plots in 2004 ($p < 0.006$). This indicates that in subplots far away from the remnant *T. x glauca* stand other species became established and may be competing with the re-invading *T. x glauca*. There were negative correlations between *T. x glauca* ramet density and stem density of seeded species in small plots in 2003 ($p < 0.05$) and in large plots in 2004 ($p < 0.04$). In small plots density of *T. x glauca* ramets doubled from 2003 to 2004, but stem density of other species did not change (Fig. 8). In contrast, in large plots *T. x glauca* ramet density doubled, but stem density of other species showed a significant increase ($p < 0.005$). This indicates that the large plots, where center subplots are further away from the unmanaged *T. x glauca*, have more time to develop a native plant community before *T. x glauca* re-invades.

4.4. Experimental plantings

4.4.1. First year survivorship

The stress of being transplanted caused 49% mortality within 8 months of planting into the scraped plots of the eight-wetland cells. In spring 2001, following fall 2000 planting, 3 of the 6 forb species (*Aster lanceolatus/puniceus*, *H. grosseserratus*, and *Pycnanthemum virginianum*) had extremely low survival rates and too few survived to be included in the following statistical analysis. The graminoids (*C. canadensis*, *Spartina pectinata*, *Carex stricta*, and *Carex comosa*) had higher survival rates (93, 92, 92, and 85%, respectively). Two species, *A. calamus*, a dicot considered a graminoid for this analysis, and *Asclepias incarnata*, a forb, had intermediate survival rates of 67 and 39%, respectively. The most productive species were *Spartina pectinata* (mean aboveground biomass = 11.3 g per plant), *Carex stricta* (9.9 g), *Carex comosa* (5.2 g), and *C. canadensis* (4.4 g).

Certain species were positively correlated with the elevation at which they were planted, although the relationships were not very strong. Plots at lower elevations had greater inundation. The means of aboveground biomass per plant of *Carex stricta* ($R^2 = 0.376$, $p = 0.108$, $F_{1,6} = 3.563$), *Carex comosa* ($R^2 = 0.3715$, $p = 0.109$, $F_{1,6} = 3.546$), and *C. canadensis* ($R^2 = 0.4448$, $p = 0.071$, $F_{1,6} = 4.808$) were positively related to elevation. Elevation was also positively correlated to six other response variables: mean aboveground biomass of planted and volunteer species per plot (simple linear regression relating responses in each plot to elevation, $R^2 = 0.1916$, $p = 0.032$, $F_{1,22} = 5.214$), mean aboveground biomass per plant per plot ($R^2 = 0.1418$, $p = 0.06$, $F_{1,22} = 3.825$), mean number of plants alive post-treatment per plot ($R^2 = 0.3873$, $p = 0.001$, $F_{1,22} = 13.91$), mean total stem length per plot ($R^2 = 0.2873$, $p = 0.007$, $F_{1,22} = 8.869$), mean number of stems per plot ($R^2 = 0.3899$, $p = 0.001$, $F_{1,22} = 14.06$), and mean number of volunteer species per plot ($R^2 = 0.2591$, $p = 0.01$, $F_{1,22} = 7.694$). Under baseline conditions, the plots ranged from 17 cm above to 23 cm below the water line.

4.4.2. Four-year survivorship

In September 2004, 4 years after being planted into the scraped plots of the eight-wetland cells, the graminoid species had much higher survivorship than forbs. The graminoid species were found in 97.5% of the plots in 2001, and they declined to 71% in 2004, during which time the forb species decreased from being present in 27.5–6% of the plots (Fig. 9).

Species recruited into the planted plots from the surrounding plant community and seedbank. Seventy-one volunteer species were found in the plots over 4 years of monitoring. Of these, *T. x glauca* was the most common invader (found in 74% of the plots over 4 years), followed by *Salix exigua* (63%), *E. erythropoda* (54%) and *P. arundinacea* (47%). By 2004 *T. x glauca* was found in 20 of the 24 plots; more than any of the species

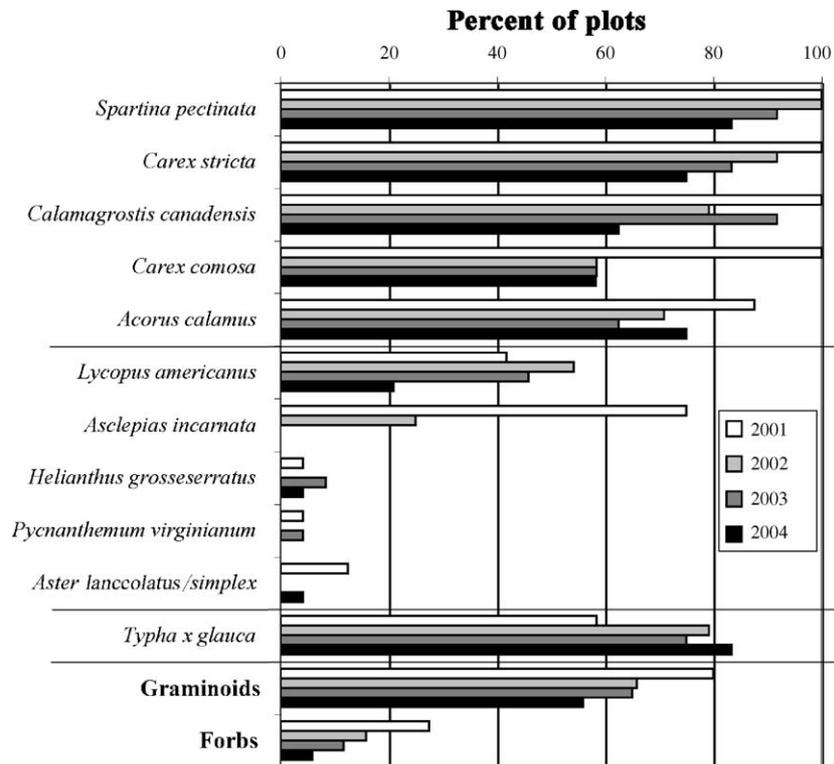


Fig. 9 – Percent of plots containing planted species and *T. x glauca* from 2001 to 2004. Species are arranged by life form: graminoids (*Spartina* to *Acorus*), forbs (*Lycopus* to *Aster*), then *T. x glauca*. The species list is followed by the average frequency of the planted graminoids and forbs.

556 planted in the plots, except *Spartina pectinata* which persisted
557 in 20 of the plots.

5. Discussion

5.1. *T. x glauca* suppressed species richness

558 *T. x glauca* was able to suppress other species and dominate
559 wetland EW5 and the eight-wetland cells, despite low nutri-
560 ent concentration of inflowing water relative to many urban
561 wetlands (Mitsch and Gosselink, 2000). Total species richness
562 of the eight-wetland cells was high, but species richness and
563 floristic quality were low where *T. x glauca* abundance was
564 high. Most of the diversity of the wetlands was found in plots
565 away from the channel where they were less flooded and
566 had low cover of *T. x glauca*. The negative correlation between
567 *T. x glauca* cover and species richness can be explained by
568 *T. x glauca*'s rapid growth and its ability to tie up resources
569 (light, nutrients, root space) (Galatowitsch et al., 1999). The
570 *T. x glauca* was able to produce a canopy over 3 m tall at a den-
571 sity of 80 ramets m⁻². Dry *T. x glauca* litter shaded the ground
572 with up to 100% cover by accumulating horizontally and diago-
573 nally up to 1.5 m above the ground. Thus, *T. x glauca* continued
574 to intercept nearly all of the light long after its leaves died.
575 These characteristics prevented most other species from coex-
576 isting with *T. x glauca*.

577 In the permanent plots of the eight-wetland cells,
578 *T. x glauca* density was positively correlated with the number
579

of days a plot was flooded. Plots that were flooded for only
580 a short time during the growing season (less than 35 days)
581 each had low cover of *T. x glauca*, and plots flooded longer
582 than 35 days frequently had higher *T. x glauca* cover values
583 and had a much higher average cover, suggesting a threshold.
584 Plots that were flooded beyond the threshold were likely to
585 be dominated by *T. x glauca*, and those flooded less were not.
586 Plots that had high cover of *T. x glauca* were strongly corre-
587 lated with low species richness. On average, plots with 80%
588 *T. x glauca* cover had one third as many species as plots with
589 10% *T. x glauca* cover. Eutrophication is associated with fre-
590 quent flooding, and it favors *Typha* over native plants (Newman
591 et al., 1996; Woo and Zedler, 2002). Not only do floodwaters
592 bring in nutrients, but they also cause wetland soils to release
593 P, via a process called internal eutrophication (Koerselman et
594 al., 1993; Venterink et al., 2002; Aldous et al., 2005). Only a few
595 species were present where *T. x glauca* had dense cover, and
596 all were generalist perennials. They were *P. arundinacea*, an
597 aggressive invasive species, and four species that tolerate deep
598 water: *Schoenoplectus tabernaemontani*, *Leersia oryzoides*, *Poly-*
599 *gonum punctatum*, and *Bolboschoenus fluviatilis* (Chadde, 1998).
600

5.2. Seedling establishment

601 *T. x glauca* can be effectively removed by cutting plants at the
602 soil surface and flooding the site to smother roots and rhi-
603 zomes. This technique is likely to be most effective in mid-
604 summer when plants are transporting resources above ground
605 to support flowering and seed production (Beule, 1979; Sale
606

and Wetzel, 1983; Ball, 1990). After removing *T. × glauca* from plots in EW5, we were able to establish several native species in the former *T. × glauca* monotype. Graminoid species tended to have higher rates of establishment and persistence than forbs; however, the most common seeded species was a forb, *B. cernuus*. Increased seeding density did increase the number of stems of seeded species for both the first and second growing season after seeding. Sowing 10× as many seeds resulted in only 4× as many stems of seeded species in the first year and 1.6× as many in the second year. Therefore, it should not be expected that increased seeding density will correspondingly increase plant density. In our experiment, the less-than-perfect correspondence might result from seeds moving from the higher seeding density subplots to lower density subplots before germination, and expansion of plants into neighboring subplots in the second year, through both vegetative spread and seed dispersal. Seeded and volunteer species grew to a greater stem density at higher elevation, which means less flooded conditions, indicating that prolonged flooding might act directly to suppress diversity (Kercher and Zedler, 2004).

5.3. *T. × glauca* rapidly re-invaded seeded plots

If *T. × glauca* is not completely removed from a site it will re-invade seeded areas vegetatively, and it is likely to outcompete native species. Re-invasion was rapid in plots in EW5, *T. × glauca* ramet density doubled from the first year to the second year after removal, and in some subplots approached the density recorded prior to removal. Seeded species were less able to establish on the edges of the plots, near the remnant *T. × glauca* stand. The plots near the edges were quickly re-invaded and supported fewer species. Seeded plants were better able to establish in subplots that were located in the center of the plots, further from the *T. × glauca* stand, especially in large plots where the distance is greater. Density of *T. × glauca* was nearly the same in the center of plots in the second year following removal as it was on the edges of plots in the first year. This period of time before re-invasion of *T. × glauca* allowed other species to become better established in the center of large plots. However, *T. × glauca* was able to spread vegetatively across the 4 m distance into the center of large plots in 2 years. *T. × glauca* ramet density increased much more quickly than stem density of other species, and *T. × glauca* dominance is to be expected. Rapid re-invasion indicates that for other species to become established, *T. × glauca* must be removed from an entire wetland, or at least from areas much larger than our 50-m² plots. Any *T. × glauca* remaining on site will re-invade rapidly (at a rate of several meters per year). Continued site maintenance would be needed to prevent re-invasion by *T. × glauca* and restore a native plant community.

5.4. Planted graminoids persisted better than forbs

Graminoid species survived transplantation into scraped plots in the eight-wetland cells much better than forbs. The high winter mortality of forbs might be attributed to soil characteristics, planting time, inundation during spring, or transplant shock. The soil at the site is a silt loam (Vepraskas et al., 1995), which differed from the fairly porous medium in which the plant plugs were grown. Planting was done during a water

drawdown in late August and early September. The plant roots were too poorly developed to anchor plants and many were partially or completely frost-heaved out of the ground. During spring inundation, some plugs began to sprout while floating in 10 cm of water. The plugs were replaced in their planting holes once they were identifiable, but some had already rooted horizontally on the soil surface.

Graminoid species outperformed forbs over 4 years in survivorship and growth. In an analysis of plant survival in restored grasslands Pywell et al. (2003) similarly found that grasses outperformed forbs. Grasses and sedges were robust in the face of flood pulses, frost heave, spring inundation, and bare substrate, all conditions that are found in newly constructed wetlands. Part of the differences in 4-year survival may be due to a greater ability of graminoids to re-sprout after being harvested for biomass analysis after the first growing season. However, differences in survival between graminoids and forbs were apparent prior to biomass collection, and all planted species are perennials.

The degree of inundation (i.e., based on elevation relative to baseline water depth) was an important factor for the survival of certain species. *Carex* spp. and *C. canadensis* were stressed by standing water in the early growth phase. These species did not stand erect in standing water, even when the leaves were long enough to protrude from the water. Sediment deposition appeared to weigh down their leaves and prolong their submergence. Standing water was also a problem for *Lycopus americanus*, a species of short stature; only two plants survived and grew in plots below baseline elevation. These responses to elevation were more obvious in the experimental plantings than in the extant vegetation, perhaps because young plants have fewer reserves belowground and are more vulnerable to inundation. Three native plants (all graminoids) were tolerant of unnatural hydrologic regimes found in urban wetlands and survived well for 4 years after planting. *Spartina pectinata*, *Carex stricta* and *Carex comosa* could be added to urban wetlands along with other, more commonly used native species, such as *Schoenoplectus* spp. *Spartina pectinata* was the most promising native species for urban wetland restoration, since it grew equally well across the range of elevations. Our findings support those of Bonilla-Warford and Zedler (2002), who tested this species' tolerance to multiple hydroperiods and found its growth to be similar in response to weekly short duration flooding early in the season, late in the season, and no flooding. Mortality of plantings would likely be reduced by allowing a month or more for establishment prior to the first frost and by minimizing the duration of high water levels in the first year.

Although we were able to establish graminoid species by planting, their survivorship gradually declined over time. Over 4 years, *T. × glauca* re-invaded the planted plots and became the most common species. Like the seeded plots, the planted plots are at risk of reverting to a *T. × glauca*-dominated state, especially those that are more frequently flooded.

6. Conclusions and implications

We found that wetlands in an urbanizing landscape can support high plant species diversity. However, at the 1-m²

plot scale, species richness was often low, especially in plots that were frequently flooded. *T. × glauca* dominated these frequently flooded plots, and caused low species richness and low floristic quality over large areas of the experimental wetlands. We were unable to restore a species-rich native plant community to *T. × glauca*-dominated areas, as our seeded plots and planted plots were quickly re-invaded by *T. × glauca*.

Replacement of a species-poor *T. × glauca*-dominated area with a diverse native plant community requires long-term invasive species control and establishment of an appropriate hydrologic regime. In the absence of continual control measures, *T. × glauca* will rapidly invade and replace the native plant community. Extended hydroperiods favor *T. × glauca* over native species, and should be avoided. Establishment of water levels that are similar to natural conditions in reference wetlands would promote diversity in urban wetlands. In addition, eutrophication should be minimized because it has been found to increase *T. × glauca* growth. Because grasses and sedges established well from seed or planting in openings in a *T. × glauca*-dominated wetland, we suggest using a cover crop of these species to stimulate the development of a native plant community. In an urban setting, converting a *T. × glauca*-dominated wetland to a more species rich system requires more than *T. × glauca* removal and introduction of other species. With the appropriate management of the hydrologic regime and invasive species, urban wetlands could become more valuable by supporting biodiversity.

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Causes and Consequences of Invasive Plants in Wetlands: Opportunities, Opportunists, and Outcomes

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Wetlands seem to be especially vulnerable to invasions. Even though $\leq 6\%$ of the earth's land mass is wetland, 24% (8 of 33) of the world's most invasive plants are wetland species. Furthermore, many wetland invaders form monotypes, which alter habitat structure, lower biodiversity (both number and "quality" of species), change nutrient cycling and productivity (often increasing it), and modify food webs. Wetlands are landscape sinks, which accumulate debris, sediments, water, and nutrients, all of which facilitate invasions by creating canopy gaps or accelerating the growth of opportunistic plant species. These and other disturbances to wetlands, such as propagule influx, salt influx, and hydroperiod alteration, create opportunities that are well matched by wetland opportunists. No single hypothesis or plant attribute explains all wetland invasions, but the propensity for wetlands to become dominated by invasive monotypes is arguably an effect of the cumulative impacts associated with landscape sinks, including import of hydrophytes that exhibit efficient growth (high plant volume per unit biomass).

Keywords dominance, exotic species, landscape sink, monotype, *Phalaris*, *Typha x glauca*

I. INTRODUCTION

Many wetland plants fit the definition of "invasive plants" as species or strains that rapidly increase their spatial distribution by expanding into native plant communities (Richardson *et al.*, 2000). For example, southern Brazil's *Alternanthera philoxeroides* [Mart.] Griseb.; (alligator weed) arrived in Australia via ballast water in the 1940s. Within 60 years, it was considered a noxious weed throughout the continent because it roots in ponds, stream edges, floodplains, and wet croplands, and it expands vegetatively *via* hollow stems that facilitate flotation (Sainty *et al.*, 1998). Also, its dense mats clog waterways, increase sedimentation, degrade pastures and crops, and enhance mosquito breed-

ing (Sainty *et al.*, 1998). Such invasive plants not only affect biodiversity and ecosystem functioning but also human use and enjoyment of wetlands.

The susceptibility of communities to invasion needs more attention (Prieur-Richard and Laval, 2000). Why are so many of the worst weeds invaders of wetlands? In Australia, little of the continent is wet, yet four of the most invasive weeds occur in wetlands (<http://www.dlwc.nsw.gov.au/care/wetlands/facts/paa/weeds/>), and a dozen other wetland species are serious problems (G. Vivian-Smith, Weed Ecologist, Alan Fletcher Research Station, Department of Natural Resources, Mines & Energy and CRC for Australian Weed Management, personal communication, 2004). Also, why do so many wetland plant invaders form monotypes rather than simply adding to native plant richness? We argue that wetlands are vulnerable to invasion in part because wetlands are landscape "sinks" that accumulate materials resulting from both terrestrial and wetland disturbances (excess water, nutrients, sediments, salts, heavy metals, other contaminants, and debris). Nearly every disturbance to an upland watershed causes some change downstream. For example, sediments that flow into wetlands transform topographically heterogeneous sites, such as tussocky meadows, into flat plains that support few plant species (Figure 1; Werner and Zedler, 2002; Larkin *et al.*, In press). In addition, debris that floats downstream tends to accumulate in wetlands, where it can smother vegetation and create canopy gaps. We propose that the accumulation of materials in wetlands makes them particularly vulnerable to invasion, while at the same time supplying invaders with the resources they need to form monotypes.

Below we discuss a selection of invasive wetland plants and the wetlands they invade. Wetland invaders differ from many upland invaders in that (1) seeds are often dispersed *via* water—61% of the 441 wetland plant species listed in Middleton's (1999) Appendix 1 are known to be water dispersed; (2) whole plants and plant fragments can be dispersed *via* flotation;

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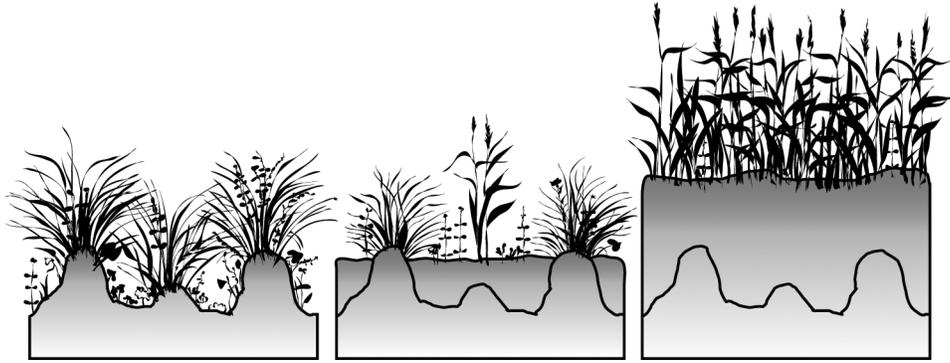


FIG. 1. Sedimentation flattens Wisconsin's topographically heterogeneous tussock sedge meadows; *P. arundinacea* becomes dominant (from Werner and Zedler, 2002; redrawn by K. Elliot).

(3) abundant aerenchyma (air tissue) protects belowground plant tissues from flooding and anoxic soils (Soukup *et al.*, 2000), as well as allowing efficient use of carbon in above- and below-ground growth; and (4) rapid nutrient uptake, allowing rapid growth.

Many invaded wetlands differ from invaded uplands in having, among other consequences of being landscape sinks, (1) through-flowing water, (2) frequent canopy gaps due to inflowing materials, (3) anoxic soils, and (4) ample nutrient influxes. While several hypotheses have been proposed to explain causes and consequences of invasions, we focus on five for which experimental data are available; these concern enemy release, broader tolerance, efficient use, hybrid vigor, and allelopathy. We then describe several "opportunity–opportunist matches" that help explain the tendency for lowlying wetlands to support invasions.

We confine our review to flowering plants. We exclude submersed and floating plants of aquatic (deepwater) habitats—not because deeper water wetlands are less threatened by invasives, but to limit the scope of our review. Thus, we consider emergent species that occupy permanent standing water, plants that occur in wet soils and soils with intermittent drying, and vegetation in transitions from wetland to upland. The following sections concern the following: invasion opportunities (factors that make wetlands vulnerable), opportunists (wetland invasive species and their attributes), current hypotheses of plant invasiveness (experimental evidence), opportunity–opportunist matches, outcomes (both negative and positive impacts) of invasives on wetland functions, the vulnerability of wetlands to invasions, and conclusions.

II. OPPORTUNITIES: WHAT MAKES A WETLAND VULNERABLE TO INVASION?

Various authors note that lowlying lands support high proportions of exotic species (*e.g.*, Sobrino *et al.*, 2002). But alien species abundance overall correlates with road density, suggesting that landscape position interacts with dispersal routes and disturbances to facilitate plant establishment. If dispersal routes

are a strong factor, then it is understandable that riparian habitats are especially prone to invasion, as claimed by Stohlgren *et al.* (1998) and Tickner *et al.* (2001). Also, riparian wetlands are subject to flood pulses and mechanical disturbance, as well as inflows of materials from surface-water flows. Most wetlands occur in the low positions of the landscape, and many occur along river networks. Most are wetted by surface runoff in addition to rainfall and, in many cases, groundwater (Brinson, 1993). Hence, it is not surprising that Detenbeck *et al.* (1999) found a high number of exotics species in wetlands of the Great Lakes region in the U.S.

Wetlands fed by surface water from agricultural and urbanized watersheds tend to have many invasive species (Galatowitsch *et al.*, 1999). Species richness is low and plants are of low "quality" (Kercher and Zedler, 2004). By quality we refer to coefficients of conservatism (CC) that have been assigned by expert botanists who distinguish high-quality species as those occurring in the least-disturbed remnants of native vegetation (Lopez and Fennessy, 2002; Mushet *et al.*, 2002; Bernthal, 2003; Matthews, 2003). Such species score up to $CC = 10$, while the weediest species are scored as $CC = 0-1$. Invasive species in Great Lakes wetlands tend to be accompanied by species with $CC < 5$ (C. Frieswyk, University of Wisconsin, personal communication).

Wetlands that are not fed primarily by surface water (*e.g.*, slope wetlands, vernal pools, and high-altitude fens, bogs, and pools) have small watersheds and depend more on rainfall or groundwater than on surface-water runoff for their water supplies (*e.g.*, Bedford and Godwin, 2003). These wetlands tend to be species rich and relatively free of invasive plants. Fens in the U.S. are noted for both their high species richness and high number of rare, threatened, and endangered species (Amon *et al.*, 2002)—for animals as well as plants (Bedford and Godwin, 2003). Their high species richness is generally attributed to low nutrient concentrations in groundwater. The exceptions would be wetlands that receive large influxes of nitrogen from the atmosphere (Koerselman and Verhoeven, 1995).

Studies in Wisconsin show that wetlands with a history of hydrological disturbance (as evidenced by the presence of culverts

and drainage ditches) show more widespread invasions than “reference sites” (high-diversity vegetation where indicators of hydrological disturbance are lacking; Kercher *et al.*, In press). In comparing 12 sites (3 reference and 9 disturbed), we found an interaction between hydrological disturbance indicators and dominance by an invader that shows two patterns: (1) fewer species of native plants occur where the invader is present in plots in hydrologically disturbed wetlands, and (2) species of lower quality are mostly what is found in that situation (Figure 2). Hydrological disturbance affects nutrient availability, not just water levels, as nitrates are readily leached from oxidized soil during drainage and phosphorus is liberated upon rewetting (Olde Venterink *et al.*, 2002). We concluded that disturbance facilitates wetland invasion and that the result is a decline in both the quantity and quality of native plant species.

The effect of nutrient inflows on wetland plant diversity was further investigated by Drexler and Bedford (2002) in New York fens. Eutrophication of one fen occurred by multiple pathways—the phosphorus and potassium loadings were traced to surface water from a nearby farm, while nitrogen loadings were enhanced by groundwater inflow from the same field. In both cases, diversity was reduced and a few plant species (*e.g.*, *Calamagrostis Canadensis* [Michx.] Beauv. [bluejoint], *Typha latifolia* L. [broadleaf cattail]) produced monotypic stands.

Despite our emphasis on increased influxes as an invasion-causing disturbance, dewatering of landscapes also affects wetlands through drought-induced impacts on obligate wetlands

plants. Some invasives are particularly abundant where dams have reduced flood flows (*e.g.*, *Tamarix* L. [tamarisk] spp.; Cox, 1999). Both increased and decreased runoff will alter wetland water regimes; the general point is that landscape sinks can be expected to respond to changes in the influx of materials.

III. OPPORTUNISTS: WHICH SPECIES INVADE WETLANDS?

Invasive wetland plants are often exotic (*e.g.*, *Lythrum salicaria* L. [purple loosestrife]), but not always. Some are native (*Typha domingensis* Pers. [southern cattail] in the Florida Everglades), some are hybrids (*e.g.*, *Typha x glauca* Godr., which is a cross between the native *T. latifolia* and the exotic *T. angustifolia* L. [narrowleaf cattail]; Galatowitsch *et al.*, 1999), and some are exotic strains of a species that is native (*e.g.*, *Phragmites australis* [Cav.] Trin. Ex Steud. [common reed] in the U.S.; Saltonstall, 2002). Still others are native strains that display invasiveness in response to environmental change. One population of *Phragmites australis* that invaded a wetland along Lake Superior was hypothesized to be exotic, but genetic analysis proved it to belong to the native strain (Lynch and Saltonstall, 2002). Finally, some wetland invasive species have uncertain origins. *Phalaris arundinacea* L. (reed canary grass) in the U.S. might be native, an exotic strain from Europe, or a hybrid strain (Galatowitsch *et al.*, 1999).

We describe about two dozen species for which invasions into wetlands are treated in recent scientific publications (Table 1; naming as in USDA, 2004). Of these, *Arundo donax* L. (giant reed), *Polygonum cuspidatum* Sieb. & Zucc. (Japanese knotweed = *Fallopia japonica* = *Reynoutria japonica*), *Lythrum salicaria*, *Melaleuca quinquenervia* (Cav.) Blake (punktree), *Mimosa pigra* L. (black mimosa), *Schinus terebinthifolius* Raddi (Brazilian peppertree), *Spartina anglica* C. E. Hubbard (common cordgrass), and *Tamarix ramosissima* Ledeb. (saltcedar) are among the 100 “Worst Invasive Alien Species” listed by the Global Invasive Species Database (LFT, 2004). The following descriptions focus on plant attributes and characteristics of the wetlands they invade. Of all the cases considered, the invasion ecology of *Spartina alterniflora* Loisel. (smooth cordgrass) in European coastal wetlands is probably the most researched and best understood.

A. Grasses

Spartina alterniflora (Poaceae) was accidentally introduced to England; by 1872, it had hybridized with the native *S. maritima* (M. A. Curtis) Fern. (small cordgrass) to form *S. x townsendii* H. & J. Groves, and it became fertile after chromosome doubling (forming *S. anglica*). Rapid spread is attributed to its fertile seeds and its ability to spread vegetatively (30 cm/year in Dovey Estuary) and the fact that it grows well on tidal mudflats that are too frequently inundated for native plants to colonize (Thompson, 1991). Other attributes noted are its ability to establish tussocks that accrete sediment, its C₄ photosynthetic

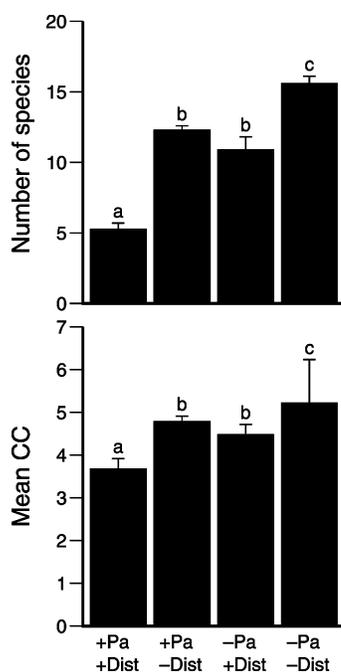


FIG. 2. Lower species richness (top graph shows mean number of species per m² plot) and lower vegetation quality (bottom graph shows mean coefficient of conservatism per m² plot; see text) are associated with sites that have indicators of hydrological disturbances. Plots came from 12 stands that had indicators of hydrological disturbance (+dist) or not (–dist) and either had *P. arundinacea* present (+Pa) or did not (–Pa) (From Kercher *et al.*, In press).

TABLE 1
Selected invasive wetland plants and seven of their attributes in invaded regions

	Forms monotype?	Clonal?	Viable seed?	Perennial or annual?	Hollow stems?	Tall?	Salt tolerant?
Grasses							
<i>Spartina anglica</i>	Yes	Yes	Yes	P	Yes	<2 m	Seawater
<i>Spartina densiflora</i>	Yes	Yes	?	P	Yes	<2 m	Seawater
<i>Phragmites australis</i>	Yes	Yes	No	P	Yes	>2 m	Seawater
<i>Phalaris arundinacea</i>	Yes	Yes	Copious	P	Yes	~2 m	
<i>Arundo donax</i>	Yes	Yes	No	P	Yes	>2 m	
<i>Polypogon monspeliensis</i>		No	Copious	A	Yes	<1 m	Somewhat
<i>Parapholis incurva</i>		No	Copious	A	Yes	<1 m	
<i>Agrostis avenacea</i>			Copious	A	Yes	<1 m	
Graminoids							
<i>Typha x glauca</i>	Yes	Yes	No	P	Yes	>2 m	Somewhat
<i>Typha domingensis</i>	Yes	Yes	Copious	P	Yes	>2 m	Somewhat
<i>Typha orientalis</i>	Yes	Yes	Copious		Yes	>2 m	Somewhat
<i>Juncus articulatus</i>		Yes	Yes	P	Yes		
Forbs							
<i>Polygonum cuspidatum</i>	Yes	Yes	No	P	Yes	>2 m	
<i>Lythrum salicaria</i>			Copious	P	Yes?	~2 m	
<i>Alternanthera philoxeroides</i>	Yes	Yes	?	P	Yes	<1 m	
<i>Impatiens glandulifera</i>	Yes	No	Yes	A	Yes?	2.5 m	
Shrubs and trees							
<i>Mimosa pigra</i>				P	No	4–5 m	
<i>Melaleuca quinquinervia</i>	Yes		Copious	P	No	>2 m	
<i>Schinus terebinthifolius</i>	Yes		Copious	P	No	>2 m	
<i>Tamarix ramosissima</i>	Yes		Copious	P	No	>2 m	Up to 1/2 seawater
<i>Triadica sebifera</i>	Yes		Copious	P		>2 m	Somewhat

pathway, salt tolerance, allopolyploid vigor, and morphological variation (both phenotypic and genetic; Thompson, 1991).

S. alterniflora was also introduced to the U.S. Pacific Northwest Coast, in this case deliberately to stabilize dredge spoils. It has recently become highly invasive in three states, Washington, Oregon, and California's San Francisco Bay (Ayres *et al.*, 1999; CSCC, 2004). It is now problematic in over 8,093 ha along the coast of Washington (Hedge *et al.*, 2003). As in Europe, it occupies habitats lower than native vegetation, but it also occupies higher elevations, with a vertical intertidal range of ~1 m. Oyster growers and bird watchers both complain that it has eliminated valuable mudflat habitat. In San Francisco Bay, it grows upslope into native stands of *S. foliosa* (Callaway and Josselyn, 1992), with which it hybridizes (Ayres *et al.*, 1999; Hedge *et al.*, 2003). Vigorous hybrids of *S. alterniflora* and *S. foliosa* threaten to displace the native *S. foliosa* throughout San Francisco Bay (Daehler and Strong, 1997; Ayres *et al.*, 1999).

In Humboldt Bay, California, *Spartina densiflora* (dense-flower cordgrass; Poaceae) occurs in all 393 ha of salt marsh, where it was long considered to be a tussock-forming variant of *S. foliosa*. Chromosome and morphological comparison showed it to be an exotic from South America (Spicher and Josselyn,

1985) that was likely introduced with ballast water from ships involved in the timber trade. The species is also expanding in San Francisco Bay (Callaway and Josselyn, 1992; CSCC, 2004), where it was planted and where it occupies an elevation that is broader than the native *S. foliosa*. While it is a prolific seed producer (~2000 viable seeds/plant), germination is limited to episodes of lowered salinity; hence, most spread is vegetative (Kittelson and Boyd, 1997).

Phragmites australis (Poaceae) has a nearly global distribution, but recent genetic work shows the USA invasive strain to differ from more natural and noninvasive populations (Saltonstall, 2002). Along the USA Atlantic Coast, this species has greatly increased its distribution into the upper reaches of salt marshes (invading *Spartina alterniflora*), where it was considered a less desirable species for wildlife and fish. Recent research, summarized in a special issue of *Estuaries* (Vol. 26, No. 2B) somewhat rebuts the claim that *P. australis* fails to support native fish and wildlife. Nevertheless, many salt marsh restoration projects have as a principal goal the replacement of *P. australis* with *S. alterniflora*. Although plants are sterile, the fragments of rhizome and stems can disperse and expand vegetatively (Bart and Hartman, 2003). The invasive strain is

highly productive (Farnsworth and Meyerson, 2003). It is drawing notice throughout its temperate-region distribution in the U.S. because its salt tolerance allows it to expand along highways where salt is used to melt snow and ice (Galatowitsch *et al.*, 1999).

Phalaris arundinacea (Poaceae) is invasive across its temperate-region range in North America (Galatowitsch *et al.*, 1999; Paveglio and Kilbride, 2000). In Wisconsin alone, it dominates (>80% cover) more than 40,000 ha of wetlands (Bernthal and Willis, 2004). In addition to seed and rhizome reproduction, it forms roots in the axils of its branches, and branches and node-bearing plant fragments can both establish new plants. European strains were introduced to North America (and are still used) for forage and streambank erosion control. Few species remain where this plant dominates (Kercher *et al.*, In press). Wetlands with enhanced runoff, sediments, and nutrients are particularly vulnerable to invasion by this species (Kercher and Zedler, 2004).

Arundo donax (Poaceae) was introduced from the Mediterranean and elsewhere in the Old World to many regions, including Mexico, the Caribbean, and California for use in thatching adobe buildings of the Spanish missions. It occurs widely throughout the southern U.S. (USDA, 2004) and has recently expanded its distribution along coastal California, especially in riparian wetlands (J. Zedler, personal observation). Plants resemble *Phragmites australis* but grow much taller (up to 10 m). It does not produce viable seed, but it reproduces vegetatively by both rhizomes and node-bearing plant fragments (Dudley, 2000).

Polypogon monspeliensis (L.) Desf. (annual rabbitsfoot grass; Poaceae) is an annual grass that expands episodically in high salt marshes of southern California. When rainfall is sufficient to lower soil salinities, the numerous seeds of this species germinate and establish seedlings (Callaway and Zedler, 1998; Kuhn and Zedler, 1997). Since annual grasses are not a natural component of this community, its presence is obvious during the dry summer, when its pale dead stems contrast with evergreen halophytes. In experiments, *P. monspeliensis* produced higher biomass than a native associate, *Salicornia virginica* (Callaway and Zedler, 1998).

Parapholis incurva (L.) C. E. Hubbard (curved sicklegrass; Poaceae) is another annual species that occurs in coastal states and, in southern California, invades the high salt marsh of coastal wetlands. At Tijuana Estuary, the plants co-occur with an endangered species, *Cordylanthus maritimus* Nutt. ex Benth. ssp. *maritimus* (saltmarsh bird's-beak), which is a hemiparasite. Because the hemiparasite is an annual, and because it must tap into roots of a perennial-plant host in order to obtain sufficient water and nutrients to live long enough to produce seeds, *P. incurva* can interfere with the endangered species' survival. Fellows (1999) showed that *C. maritimus* can attach to the roots of *P. incurva* but that this host dies before the endangered plant can reproduce. The endangered species is "tricked" by the invasive host, like a habitat sink. At Tijuana Estuary, where the endangered plant persists, up to 92% of seedlings were exotics, with *P. incurva* the most abundant (Noe and Zedler, 2001).

Agrostis avenacea J. F. Gmel (Pacific bentgrass; Poaceae) is an Australian annual and facultative perennial grass that is becoming a strong threat to biodiversity by rapidly invading vernal pools in southern California (Zedler and Black, In review). These pools support several rare and endangered plants and animals; hence, dominance by an invasive threatens an entire rare ecosystem. Over 90% of historical vernal pools of southern California have been urbanized, as the depressions occur within flat mesas near the coast, which are prime sites for housing developments.

B. Graminoids

Typha x glauca (Typhaceae), a hybrid between the native *T. latifolia* and the exotic *T. angustifolia*, is an aggressive invader of disturbed wetlands across much of the eastern U.S. (Galatowitsch *et al.*, 1999). F1 plants are sterile, but the parents are abundant and widely sympatric, and offspring expand aggressively *via* rhizomes. Hybrids are common wherever both parents occur (Galen Smith, University of Wisconsin, personal communication, 2004). This invader responds more rapidly to nutrient addition than sedge meadow vegetation (Woo and Zedler, 2002), and it crowds out many native species, leaving only those of low quality (thus having a monotype form of dominance, cf. C. Frieswyk, University of Wisconsin, personal communication). Great Lakes wetlands have an abundance of this invader, especially where watersheds are urbanized, such as along Lake Erie and within Lake Michigan's Green Bay (Frieswyk *et al.*, In review).

Typha domingensis (Typhaceae) has greatly expanded its distribution in the Florida Everglades in response to increased phosphorus runoff from sugar cane fields (Miao and Sklar, 1998). Its distribution into native *Cladium jamaicense* Crantz (Jamaica swamp sawgrass) vegetation follows canals that drain agricultural lands; from there it expands vegetatively into the native vegetation. *T. domingensis* also tends to be invasive in southern California, where its expansion into saline wetlands is catalyzed by freshwater inflows (Beare and Zedler, 1987). Once established (during low-salinity windows), it persists vegetatively.

Typha orientalis C. Presl (cumbungi; Typhaceae) is native to eastern but not western Australia. Near Perth, this species moves into *Juncus kraussii* marshes where soil salinity is reduced by urban runoff (Zedler *et al.*, 1990). Gaps in the canopy along drainage ditches would thus allow seedlings to establish, and rhizome growth would allow penetration into native vegetation (Zedler *et al.*, 1990).

Juncus articulatus L. (jointleaf rush; Juncaceae) is native to the U.S. and Europe and invasive in Australian temporary wetlands, creeks, and drainage channels, where it germinates from long-lived seed banks and expands *via* rhizomes (Smith and Brock, 1998). *J. articulatus* produced many more tillers and much higher biomass than a native associate, *Glyceria australis*, in experiments by Smith and Brock (1996).

Another graminoid to watch is *Juncus acutus* L. (spiny rush; Juncaceae), which is common in coastal wetlands of the Mediterranean Sea and is native (but rare) in southern California coastal

wetlands. This species appears to be increasingly weedy in western Australia (J. Zedler, personal observation), especially in wet places where agricultural activities cause secondary salinization of soil (Williams, 2001).

C. Forbs

Polygonum cuspidatum (Polygonaceae) is native to eastern Asia but it is now widespread in central and northern Europe and it occurs in most of the U.S. It is most invasive in riparian wetlands (Brock *et al.*, 1995; Sukopp and Starfinger, 1995). Plants are tall, rhizomatous, herbaceous to shrubby, persistent, and difficult to control (Seiger and Merchant, 1997). Sometimes called a “giant herb,” it can grow to 4.5 m tall and accumulate biomass of 200 t/ha (Sukopp and Starfinger, 1995). Because seeds of this species produced outside Japan are not viable, reproduction is largely by rhizomes or rhizome fragments (Bailey *et al.*, 1995) and stem fragments (Brock *et al.*, 1995). Dispersal occurs via flowing water (Sukopp and Starfinger, 1995). In the U.S. Pacific Northwest, Toney *et al.* (1998) identified this plant as the most rapidly spreading invader, and in Switzerland Weber (2000) listed it as a species of “high concern.” In the British Isles, *P. cuspidatum* crosses with native species to form invasive hybrids that produce hybrid seeds (Bailey *et al.*, 1995), suggesting increasing invasiveness.

Lythrum salicaria (Lythraceae) is a shrub from Europe that was introduced to North America for its purple flowers; however, it probably also arrived accidentally by dispersal of its copious small seeds (Galatowitsch *et al.*, 1999). It is now highly invasive along riverbanks and in wetlands across temperate North America (Galatowitsch *et al.*, 1999; Lindgren, 2003), where it is a competitive dominant (Hagert, 2004) that forms monotypes (Thompson *et al.*, 1987). In Manitoba, infestations increased 13-fold between 1991 and 2001, with over 4000 ha infested in the central part of the province. Blossey *et al.* (2001) cite multiple impacts of this species on ecosystem functioning (cf. section VI) and on the native *L. elatum*, which can have reduced pollination and lower seed production in the presence of *L. salicaria*.

Alternanthera philoxeroides (Amaranthaceae) is a clonal forb that is native to South America but highly invasive in California and Florida waterways and in Australia (Sainty *et al.*, 1998). It was deliberately introduced to Australia as a vegetable and medicinal herb. Stems are long, branched and hollow; dispersal occurs as fragments, as reproduction is entirely vegetative. It establishes readily from stem nodes and rhizomes, especially along riverbanks; plants can break away from the parent clone and persist as free-floating mats (Sainty *et al.*, 1998).

Impatiens glandulifera Royle (ornamental jewelweed; Balsaminaceae) is a tall (~2.5 m) annual forb from Himalaya that forms monospecific stands along river banks and other moist habitats in UK and Europe (Beerling and Perrins, 1993; Tickner *et al.*, 2001). Beerling and Perrins (1993) describe its distribution in UK as widespread and among the top 20 alien problems. While each plant produces only 4 to 16 seeds per flower, a square

meter with 20 plants produces 700 to 800 seeds, which are dispersed via explosive dehiscence (up to 4 m from the plant); in the following year, seeds germinate synchronously to produce a monotype (Beerling and Perrins, 1993). Adventitious roots help it remain upright. Extrapolating from data on water content of stems (91%) and tall growth form (Beerling and Perrins, 1993), which are shared by our Wisconsin congener, *I. capensis* Meerb. (jewelweed), we speculate that this species has “efficient growth” (section IV) via hollow stems. *I. capensis* behaves as an invasive in Wisconsin, although its ability to dominate appears to be moisture and competition limited (personal observation).

Other notable forbs that invade wetlands are *Heracleum mantegazzianum* Sommier & Levier (giant hogweed, Apiaceae)—a 5-m tall perennial (rhizomatous) plant from the Caucasus that is invasive in a few northern states in the U.S. of great concern in riparian areas of UK (Tickner *et al.*, 2001), and expanding along streambanks in Ireland (Caffrey, 2001)—and *Lepidium latifolium* L. (broadleaved pepperweed, Brassicaceae), which is expanding rapidly in northern California (Howald, 2000). Like *Pastinaca sativa* L. (wild parsnip) in the U.S., *H. mantegazzianum* produces phototoxic chemicals that sensitize the skin where people touch the plants.

D. Shrubs and Trees

Mimosa pigra (Mimosaceae), from Central and South America, is a highly invasive shrub in Australia, Southeast Asia, and Florida, where it grows to 6 m in shrubby, prickly thickets (Langeland and Craddock Burks, 2000). Introduced as a curiosity plant, its seeds are dispersed in annual floodwaters, and its establishment is facilitated by grazing disturbances on floodplains (Zedler and Rea, 1998). Infestations covering 800 km² are described for Australia (Langeland and Craddock Burks, 2000). In Northern Territory, it germinates en masse on floodplains and grows rapidly to reproductive maturity (Rea, 1998).

Melaleuca quinquenervia (Myrtaceae) was planted as an ornamental in Florida and now infests over 200,000 ha of south Florida wetlands, of which 10,000 to 20,000 ha are virtual monocultures (Turner *et al.*, 1998). The Everglades “river of grass” is being transformed into wooded swamps dominated by this fire-adapted tree. Fire not only leads to resprouting, it also releases copious seeds (~20 million per tree) that readily establish seedlings on the fertile ash bed. The species invades along canal banks and roads, as well as in cypress swamps, pine flatwoods, bottomland forests, and mangrove swamps (Turner *et al.*, 1998). It is Florida’s greatest invasive threat in wetlands, causing up to 80% loss in biodiversity (Turner *et al.*, 1998). The species matures rapidly and can produce up to 5 seed crops per year (Turner *et al.*, 1998). In Puerto Rico, it forms monotypes in abandoned agricultural fields where both flooding and fire occur; this combination of disturbances is not tolerated by any native tree (Lugo, 2004).

Schinus terebinthifolius (Anacardiaceae) is a small tree (10 m tall) that forms densely intertwined branches (thickets). It is native to South America but was introduced as an ornamental to the

southern U.S. It is highly invasive in Texas and Florida wetlands. In the Florida Everglades areas that were rock plowed (porous limestone substrate crushed to allow cultivation), nutrients (especially phosphorus) were released and a monoculture of this tree developed (Simberloff *et al.*, 1997; Li and Norland, 2001). Concentrations of phosphorus in leaves were 5 times those of the native sawgrass (Simberloff *et al.*, 1997; Li and Norland, 2001). While trees could be bulldozed and burned, the complete removal of nutrient-rich soil was necessary to prevent their recolonization (Dalrymple *et al.*, 2003).

Tamarix ramosissima (Tamaricaceae) and its congeners are native trees in Europe and Asia and highly invasive in Texas and the western U.S. (Stevens, 1989; Cox, 1999; Lesica and Miles, 2001; Ellis *et al.*, 2002) and Australia. This tree colonizes open riparian wetlands and floodplains, especially where dams have reduced flood frequency (Ellis *et al.*, 2002; Sher *et al.*, 2002). It grows rapidly to 4 m in the first year of growth. Its abundant, wind-dispersed seeds germinate upon wetting, including in soils that are saline at the surface, and seedlings rapidly grow roots that reach the water table (Lesica and Miles, 2001). Branches that are buried by flood-borne sediments grow into new shoots, forming clones (Lesica and Miles, 2001); it also forms adventitious roots. Its ability to accrete sediments is seen as a cause of increased flooding, and its high water use and evapotranspiration rates have high economic impacts throughout its arid-region distribution (Zavaleta, 2000). Cox (1999) reports that 90% of New Mexico's bosque (woodland) is heavily modified, and remnants are dominated by three species of *Tamarix*, along with many other invasive species.

Triadica sebifera (L.) Small (= *Sapium sebiferum*; tallowtree; Euphorbiaceae) from eastern Asia is expanding its already widespread distribution in the southeastern U.S., where it occurs in wetlands and moist uplands (USDA, 2004). This tree grows rapidly and forms monotypes, crowding out native plants. In Louisiana and Texas, it replaces imperiled coastal prairie (Barrilleaux and Grace, 2000; Rogers and Siemann, 2003). It also replaces forested wetlands following hurricanes (Conner *et al.*, 2002). The species is considered naturalized along the coastal plain from Texas to North Carolina (Conner *et al.*, 2002).

Another tree of concern is *Acer negundo* L. (boxelder, Aceraceae) from North America, as it is increasingly abundant in Wisconsin's riparian woodlands (J. Zedler, personal observation) and invading riparian habitats in southwestern France (Tabacchi and Planty-Tabacchi, 2003).

IV. WHY ARE SOME WETLAND PLANTS HIGHLY INVASIVE?

Several hypotheses have been proposed to explain invasiveness in plants in general (Rejmanek, 2000), and the ability to predict species that might become pests has improved (Daehler *et al.*, 2004). For *P. arundinacea*, any one of the following traits might confer invasiveness: some strains were bred for productivity; it is wind pollinated; it is highly productive of seeds; its seeds germinate within six days of wetting; germination rates are high

upon wetting, but some seeds remain dormant and can germinate after storage for 3 years; new populations can be established from dispersed seeds, whole plants, and branch fragments; it produces rhizomes with numerous buds; new ramets benefit from a clonal subsidy; plants can grow into tussocks as well as swards; it grows over a longer season than most native plants in Wisconsin; it can make use of nutrient pulses; it has a broad ecological niche; it displays morphological plasticity (*e.g.*, branching upright when stems fall); its leaves and stems show little evidence of herbivory in Wisconsin; and its hollow stems allow great height growth per biomass investment. Indeed, all of the species we discuss (section III) possess multiple characteristics that might be what makes them formidable invaders. It is the systematic testing of alternatives that advances understanding.

In a review of 150 studies, Levine *et al.* (2003) found that fewer than 5% tested the processes responsible for plant invasions. We focus on five that have been tested experimentally, or are testable, using wetland species: release from natural enemies, broad tolerance limits or tolerance of harsh conditions, more efficient or complete use of resources, hybrid vigor, and allelopathy. This list is not exhaustive, nor are the hypotheses of invasiveness exclusive of one another.

A. The Enemy Release Hypothesis

This hypothesis predicts that exotic species are released from pathogens when introduced into new areas and that a relatively greater release from pathogens correlates with increased invasiveness. Support for this hypothesis comes from Klironomos (2002) and Mitchell and Power (2003). Using *Lythrum salicaria* as the test species, however, Willis and Thomas (1999) found no evidence that a plant with fewer enemies allocated fewer resources to defense and increased its competitive ability. In contrast, Siemann and Rogers (2001) found that invasive genotypes of *Triadica sebifera* from recently colonized areas in North America had the strongest growth but poorly defended leaves, while native Asian genotypes had the weakest growth and well-defended leaves, and genotypes from its original introduction site in North America were intermediate in both growth and leaf defense. Rogers and Siemann (2003) also found *T. sebifera* to be herbivore tolerant. While most experimental tests of the predator/pathogen release hypothesis have focused on agricultural and upland species, wetland species may have different susceptibilities to pathogenic viruses, fungi, and herbivores. The screening of potential biocontrol agents is inherently an experimental test of the enemy release hypothesis, and several studies report reductions in the productivity and vigor of invasive wetland plants upon exposure to host-specific biocontrol agents (*e.g.*, for *Lythrum salicaria* in North America, Blossey *et al.*, 1994a, 1994b; Voegtlin, 1995; Nyvall and Hu, 1997; for *Spartina alterniflora* in Washington, U.S. Grevstad *et al.*, 2003).

B. The Broader Tolerance Hypothesis

This hypothesis predicts that invasive species have broader tolerance limits, tolerate extreme environmental conditions

better than noninvasive species, or both. Goodwin *et al.* (1999) identified 165 congeneric pairs of European plant species; each pair consisted of one species that has invaded North America and one species that has not. Upon comparing life form, stem height, flowering period, and European range as predictors in a logistic regression model, only the latter was reliable, predicting invasiveness correctly 70% of the time. Greater tolerance would favor wetland plant invasions where hydrological shifts occur (Newman *et al.*, 1996; Kercher and Zedler, In review).

Several studies have tested growth responses under different hydroperiods. Experiments with invasive cattail *Typha domingensis* and the native Everglades species *Cladium jamaicense* and *Eleocharis interstincta* (Vahl) Roemer & J. A. Schultes (knotted spikerush) showed that only *T. domingensis* responded positively to increased water depth (15, 30, and 60 cm) by increasing biomass as much as 60% (Newman *et al.*, 1996). Greater flood tolerance in *T. domingensis* over the native species may be due to higher levels of aerenchyma in the former (Chabbi *et al.*, 2000). Likewise, *P. arundinacea* had higher biomass and higher aerenchyma than 16 other taxa tested across four hydroperiods (Kercher and Zedler, In review). Similarly, *Spartina anglica* exhibited enhanced exchange of O₂ and H₂S between the rhizosphere and atmosphere compared to that of its native North American congener *Spartina alterniflora* (Lee, 2003). Evidence against the hypothesis of greater tolerance to harsh conditions comes from a study of six species in the family Lythraceae, including *Lythrum salicaria*. All six species had very similar responses to flooding (Lempe *et al.*, 2001).

Hydrological shifts also include changes in salinity, sedimentation, and pollutant inflows. Lowered salinity increased invasion by *Polygonum monspeliensis* into salt marshes (Callaway and Zedler, 1998), sedimentation increased *P. arundinacea* invasions into sedge meadows (Werner and Zedler, 2002), and *Lythrum salicaria* was able to grow even with lead levels as high as 2000 mg per liter (Uveges *et al.*, 2002). Further tests of the greater-tolerance hypothesis are warranted, since shifts in hydrology involve multiple environmental factors and potential interactions.

C. The Efficient Use Hypothesis

This hypothesis states that invasive species make more efficient or complete use of light and nutrient resources than noninvasive species. Several experimental studies have demonstrated relatively greater growth responses in invasive species to increases in light, nutrients, or both. To facilitate light capture, invasive species may have one or more of the following: an extended growing season, morphological plasticity or a fixed but advantageous architecture, and higher photosynthetic rates. These traits have been reported to occur in invasive species in uplands (*e.g.*, Grotkopp *et al.*, 2002; Morris *et al.*, 2002; Stratton and Goldstein, 2001) as well as wetlands (*e.g.*, for phenology and growth form of *P. cuspidatum* along alpine rivers Marigo and Patou, 1998; for phenology of *Rhamnus cathartica* Harrington *et al.*, 1989).

As with light, some invasive plants have a greater capacity to utilize nutrients to promote their expansion at the expense of noninvasive species. For example, Newman *et al.* (1996) found that nutrient enrichment increased growth of *T. domingensis* but not Everglades marsh natives. Similarly, Woo and Zedler (2002) found increased *Typha x glauca* biomass but no change in native *Carex* L. spp. biomass due to nutrient addition. Green and Galatowitsch (2002) showed increases in *P. arundinacea* biomass and suppression of native wet meadow species with high levels of nitrate-N addition, and Kercher and Zedler (2004) found that nutrient enrichment caused a greater relative increase in *P. arundinacea* than in native wet prairie species.

Kercher and Zedler (2004) tested a related hypothesis concerning fluctuating resources (Davis *et al.*, 2000), which states that invasion occurs when the system has an excess of resources, either through reduced uptake by resident species or increased supply. *P. arundinacea* became more invasive in a wet prairie assemblage as nutrients, sediment, and flooding increased (3 levels of each factor, full-factorial design). In one growing season, factors synergized to produce a monotype of *P. arundinacea* in 3 of 28 treatments (Kercher and Zedler, 2004).

D. The Hybrid Vigor Hypothesis

This hypothesis focuses on invaders with different species as parents. Ellstrand and Schierenbeck (2000) present evidence that hybridization is a major and underappreciated cause of invasiveness. They documented 28 examples supported by strong evidence that hybridization events preceded invasiveness, including the wetland taxa *Spartina anglica*, *Lythrum salicaria x L. alatum* Pursh (winged lythrum), and *Spartina alterniflora x S. foliosa* Trin. (California cordgrass) in North America (see also Ainouche *et al.*, 2004 re. *Spartina* hybrids). *Typha x glauca* is another example of a hybrid invasive wetland plant (Galatowitsch *et al.*, 1999). Highly invasive *Tamarix* spp have also been shown to be novel hybrids of European genotypes that were geographically isolated in Eurasia (Gaskin and Schaal, 2003; Schaal, *et al.*, 2003). Experimental work on *Polygonum cuspidatum* in the Czech Republic has shown that hybrids that are genetically intermediate between the parents have greater regeneration rates (Pysek *et al.*, 2003).

E. The Allelopathy Hypothesis

This hypothesis predicts that some plants become invasive monotypes through the release of biochemical toxins that inhibit the growth and germination of species in the area of introduction, as those species have not had a chance to evolve resistance to the phytotoxins. To date, the most convincing example is a new study on *Centaurea maculosa*, an invasive plant of grasslands (Bais *et al.*, 2003). Although the case for allelopathy in wetland invasive species is weaker, phytotoxic compounds have been isolated in several *Typha* species (reviewed in Gallardo *et al.*, 1998a, 1999, 2002), and experiments with root tissue extracts of invasive *T. domingensis* have revealed detrimental effects on the germination and growth of some species (*e.g.*, Gallardo *et al.*,

1998b). Clearly, allelopathy is worthy of more rigorous biochemical and ecological research regarding invasiveness.

F. Overview

The above tests of five hypotheses involve only a few wetland species, notably *Typha* spp. The results for *Typha* provide evidence in support of four hypotheses, indicating that multiple traits can confer invasiveness. At the same time, a trait that enhances invasiveness in one species might not in another. For example, the production of copious seeds should increase invasiveness (and probably does for *Impatiens grandulifera* and *Melaleuca quinquenervia*), but one species that does not produce viable seed outside its native range is one of the worst invaders of wetlands in Europe and parts of North America (*Polypogon cuspidatum*), and the non-seed-producing *Typha x glauca* is also a widespread invader. Likewise, tall plants should shade out competitors, but annual grasses of short stature are among the most troublesome invaders in California wetlands (*Parapholis incurva*, *Polypogon monspeliensis*). Although no single trait explains all invasions, some traits provide multiple benefits to wetland invaders. A high proportion of aerenchyma (air tissue) simultaneously improves flood tolerance by increasing oxygen flow to roots, allows detached plants to float (disperse), and allows a plant to achieve high volume and height per biomass invested (efficient growth). Wetland plant traits and invasiveness do not follow a single or simple pattern.

V. OPPORTUNITY–OPPORTUNIST MATCHES

From the perspective of the potentially invaded community, no single species is invasive in all types of wetlands, although some species can invade multiple wetland types. So, with a variety of wetland species that have multiple “invader” attributes and a variety of potentially invaded wetland types that are sinks for a variety of materials and other disturbances, what generalities emerge? We agree with Sobrino *et al.* (2002) that invasions can be explained by considering the ecological requirements of the alien species and environmental factors. We argue that wetland opportunists are particularly invasive by virtue of having multiple attributes that match one or more of the opportunities afforded by disturbances that are common to landscape sinks.

Opportunities arise whenever natural or human-caused disturbances either introduce or free up resources (Davis *et al.*, 2000). Increased flooding, sedimentation, and debris deposition are especially common in wetlands, and they combine multiple impacts that favor invaders. First, flooding can disadvantage resident vegetation, creating canopy gaps that allow high-light-requiring invaders to establish (*P. arundinacea*; Lindig-Cisneros and Zedler, 2001, 2002a). Simultaneously inflowing water and sediments add or liberate nutrients from sediments, thereby enhancing growth of opportunistic plants (*P. arundinacea*; Kercher and Zedler, 2004). We propose several opportunity–opportunist matches (Table 2):

A. Examples

- Runoff is augmented when native habitats are replaced by agricultural fields or urban hardscapes. Species that readily disperse by water, and whose seeds, plant fragments, or whole plants establish well on bare ground, are well equipped to invade bare spaces along stream banks and floodplains (Tickner *et al.*, 2001). When flooding occurs, sediments are both scoured and deposited, and flowing debris can create canopy gaps by ripping out some plants during transport while smothering others upon deposition. However formed, a canopy gap that is created by flooding can be quickly colonized by species with propagules that are carried to the site by the same floodwaters. Plants with floating propagules should be at an advantage, especially plant fragments that benefit from soaking in water (*e.g.*, *P. cuspidatum*; Bimova *et al.*, 2003) and mats that can continue growth while floating and establish rapidly upon settling (*e.g.*, *Alternanthera philoxeroides*; Sainty *et al.*, 1998). Flowing water and dispersal are integrally linked. In fact, a model by Campbell *et al.* (2002) suggests that river network characteristics can accurately predict plant dispersal rates.
- A flush of nutrients typically accompanies runoff from agricultural and urban land into wetlands. Species that can take up nutrients rapidly (*e.g.*, *T. domingensis* in the Florida Everglades; Miao and Sklar, 1998) can benefit from such nutrient pulses. *T. domingensis* is able to take up and use nutrients by funneling them into growing tissues, while the native species it replaces (*Cladium jamaicense*), if it responds at all, retains a limited quantity of nutrients in stem bases or belowground plant parts (Miao and Sklar, 1998). *T. x glauca* behaves similarly in Wisconsin (Woo and Zedler, 2002). Nutrient pulses are matched by nutrient slurpers. Flushes of phosphorus accompany peat fires, and species with high phosphorus uptake capability (*e.g.*, *T. domingensis*) can respond rapidly to this disturbance (Smith and Newman, 2001).
- Sediments are exposed by floodwater scouring and sediment deposition. Species that establish readily and stabilize loose sediments can take advantage of this opportunity. *Tamarix* spp. are notable for this ability (Ellis *et al.*, 2002), as is *P. arundinacea*, and both have been deliberately planted for the purpose of streambank erosion control. The former not only germinates well in open moist soil but also produces adventitious branches from buried roots and branches.
- Floodwaters accumulate in wetlands, and anoxia challenges all but the most flood-tolerant species, *e.g.*, plants with aerenchyma or pressure ventilation. Plants with aerenchyma can also achieve high plant volume per biomass investment (*i.e.*, “efficient growth”), potentially growing tall very rapidly (*e.g.*, *P. cuspidatum*;

TABLE 2
Opportunities in wetlands and the opportunists that appear to take advantage of them, based on the literature and personal observation

Opportunity	Opportunist with	Examples of species
Canopy gap	Propagules that require high light levels	<i>Melaleuca quinquenervia</i> , <i>Phalaris arundinacea</i> , <i>Impatiens glandulifera</i>
Canopy gap	Rapid height growth, e.g., via hollow stems	<i>Arundo donax</i> , <i>Phalaris arundinacea</i> , <i>Phragmites australis</i> , <i>Polygonum cuspidatum</i>
Flattened vegetation after flooding	Rapid upright branching to recapture light	<i>Phalaris arundinacea</i>
Nutrient pulse	Rapid nutrient uptake	<i>Schinus terebinthifolius</i> , <i>Typha domingensis</i>
Fresh sediment from scouring or sediment deposition	Rapid anchoring of shoreline	<i>Tamarix</i> spp., <i>Phalaris arundinacea</i>
Fresh sediment (flood scouring or sediment deposition)	Hydrochory or viable floating propagules	<i>Polygonum cuspidatum</i>
Unvegetated mudflat	Inundation tolerance	<i>Spartina anglica</i> , <i>Spartina alterniflora</i>
Increased water depth	Aerenchyma	<i>Alternanthera philoxeroides</i> , <i>Typha x glauca</i>
Increased water depth	Adventitious roots and tussock formation	<i>Phalaris arundinacea</i>
Warm water inflows in spring and fall	Prolonged growing season	<i>Phalaris arundinacea</i>
Flooding, rapidly flowing water	Dense rhizome mats that float	<i>Alternanthera philoxeroides</i> , <i>Phalaris arundinacea</i> , <i>Typha x glauca</i>
Altered hydroperiod	Broad ecological tolerance	<i>Agrostis avenacea</i>
Increased salinity	Salt tolerance	<i>Tamarix ramosissima</i>
Sea level rise	Salt and inundation tolerance	<i>Spartina</i> spp.
Decreased salinity (low-salinity window)	Rapid germination of seeds plus salt-tolerant adults	<i>Parapholis incurva</i> , <i>Polypogon monspeliensis</i> , <i>Typha domingensis</i> , <i>Typha orientalis</i>

L. Seiger, personal communication). Roots that are rich in aerenchyma can extend further per unit biomass and take up nutrients over larger areas than roots without. While the value of belowground aerenchyma in moving oxygen to active tissues is well known (Jackson and Armstrong, 1999), efficient growth is not typically considered. Plants with aerenchymatous roots can make use of saturated soils, thereby solving the water-availability constraints of hollow stems. Plants with aerenchyma match several opportunities afforded by wetlands that experience excess water inflows.

- Species that initiate growth earlier in spring and continue growth late in fall effectively extend the grow-

ing season. This trait has been shown to be effective for an upland invader (*Rhamnus cathartica*) that outcompetes native shrubs without having a higher photosynthetic rate (Harrington *et al.*, 1989). That is, the species can outgrow natives by photosynthesizing at a similar rate but for a longer time. *P. arundinacea* begins to sprout earlier than wet prairie and earlier than many sedge meadow plants in Wisconsin, and it is more capable of invading wet prairie than sedge meadow, presumably because more light is available (Maurer and Zedler, 2002; Lindig-Cisneros and Zedler, 2002b). The prolonged seasonal growth of *P. arundinacea* is well known; in fact, its persistent green color after

native species have senesced allows it to be mapped from satellite imagery (Bernthal and Willis, 2004). Wetlands are made vulnerable to early-growing plants when snow on urban and agricultural lands begins to thaw. Dark-colored fields, asphalt streets, and rooftops produce early spring meltwater that flows downstream, where it warms the wetland soil next to drainage channels, accelerates thawing, and prompts early-spring growth of *P. arundinacea* (J. Zedler, personal observation). Late in fall, runoff likely continues longer from fields and towns, allowing such species a late-season advantage over species that senesce with the first cold weather. Thus, species with extended growing seasons are well matched to wetlands that receive agricultural and urban runoff.

- Open and standing water develops when runoff accumulates in wetlands or impoundments (dams) obstruct outflows. Species that produce tightly intertwined roots and rhizomes, especially if they are aerenchymatous, can allow plants to expand their distributions into water that would otherwise be too deep for emergent plants. *Alternanthera philoxeroides* extends outward from stream banks as floating mats (Sainty *et al.*, 1998), while *P. arundinacea* forms tussocks that emerge above standing water. The propensity for the latter species to produce adventitious roots (Kercher and Zedler, In press) contributes to its ability to grow tussocks (J. Zedler, personal observation). Rising water is inhabitable if an invader can elevate itself by 20 to 30 cm, which *P. arundinacea* readily accomplishes (Werner and Zedler, 2002). Increased flooding and stabilized water levels are well matched by opportunists that form floating mats or tussocks.
- Many structures (dams, levees, berms, culverts) placed in the landscape alter hydroperiods (frequency, depth, timing, and duration of high water). Species that are broadly tolerant of different hydroperiods (*e.g.*, *P. arundinacea*; Miller and Zedler, 2003) should be well matched to sites that experience unusual hydroperiods due to such structures. A new invader, *Agrostis avenacea*, was first collected in San Diego County in 1987 in a vernal pool that had become larger and deeper when highway construction formed a berm that impounded water longer than natural vernal pools (Zedler and Black, In review). By 1998 *A. avenacea* had spread widely by “tumbleweed dispersal” into adjacent natural vernal pools that lacked significant human disturbance. This species grows taller and more robust than the region’s native vernal pool grasses, most of which are diminutive. Since many opportunists are transported by vehicles, species that can take advantage of roadway-modified wetlands should have both a dispersal and invasion advantage.
- Salinity regimes are altered when the boundary between fresh and saline waters shifts position. Where

wetland soils become more saline, as where roads are salted to melt ice, or where secondary salinization occurs in arid regions due to the intensification of agriculture, diversion of water, and mining activities (Williams, 2001), an opportunity is provided for invasion by species with euryhaline propagules (*i.e.*, seeds or fragments that are tolerant of a wide range of salinities). *Typha angustifolia* and *Phragmites australis* are frequent invaders of Midwestern road ditches, no doubt benefitting from vehicle dispersal and road construction disturbances, along with reduced cover by salt-intolerant native vegetation (Galatowitsch *et al.*, 1999). Where sea levels rise due to subsidence or global warming, invasive salt marsh species, *e.g.*, *Spartina* spp., can be expected to move inland.

Where wetland soils become less saline, due to an unusually pulse of freshwater, species with stenohaline propagules can invade, and if the adult plants can tolerate salt they can persist. For example, *T. domingensis* invaded the San Diego River in 1980 during a prolonged period of freshwater inflows; the initial flood pulse was a natural event, but inflows were extended for months by reservoir releases that were intended to increase floodwater storage capacity upstream (Beare and Zedler, 1987). Subsequent experiments showed that seed germination and seedling stages were sensitive to salt, while rhizome-bearing plants could tolerate hypersaline conditions (Beare and Zedler, 1987). The same pattern held for *Polypogon monspeliensis* in high salt marsh (Callaway and Zedler, 1998) following heavy rainfall events and *T. orientalis* invasions to the Canning Estuary in Western Australia following excavation of drainage ditches to accommodate urban runoff (Zedler *et al.*, 1990).

B. Overview

The kinds of disturbances that occur in wetlands and the attributes of wetland invaders seem to be well matched and sufficiently different from those in uplands to warrant separate attention. The interaction of opportunity and opportunist often involves more than one aspect of either the site or the species. Some opportunities attract multiple opportunists, and some opportunists respond to multiple opportunities. Hence, predictions of which species will invade a wetland can only be general, based on the likelihood of bare space being made available, the simultaneous presence of an invader’s propagules, and knowledge of any constraints on establishment, such as unusual salinity or hydroperiod (including drought) as well as any catalysts (*e.g.*, nutrient pulses). Rarely would we know all of these factors for specific sites. But we do know that bare space does not remain bare for long in shallow-water wetlands, and that given time and chance dispersal of invasive plant propagules, invasive species are likely to establish. We also recognize that habitats subject to frequent mechanical disturbance, such as flood scouring, are readily colonized by “weedy” species, such as *A. negundo* and many species of *Salix* L., so it is not surprising that colonizers

native to one region become invasive in other regions and continents.

Because some of the disturbances that create space also catalyze plant growth, wetlands are vulnerable to invasions. As demonstrated in tests of excess water, nutrients, and sediments on invasion by *P. arundinacea*, synergisms among flooding, nutrient influxes, and sediment influxes doubled the invasion rate over what was predictable by adding the individual treatment effects (Kercher and Zedler, 2004). Because stormwater runoff includes all three factors (flooding, nutrients, and sediments), it is understandable that wetlands downstream of agricultural lands or overfertilized lawns are susceptible to invasion and conversion to monotypic *P. arundinacea*. More multifactor experimental tests along these lines would lead to a more comprehensive understanding of wetland-invasive plants.

VI. OUTCOMES: HOW ARE WETLANDS ALTERED BY THEIR INVADERS?

Invasive plants impact ecosystem functions both directly and indirectly. Direct impacts involve canopy height and other attributes of architecture, shifts from herbaceous to woody plants (or vice versa), increased productivity and litter, different litter-breakdown rates, altered nutrient regimes, and either increased or decreased flammability. Indirect impacts concern associations with microorganisms such as bacteria and mycorrhizae and larger invertebrate and vertebrate animals. The ecosystem functions mediated by plants that have received the most attention in the ecological literature involve biodiversity support, productivity, and nutrient cycling. Recent work on food web effects in marshes invaded by *Phragmites australis* is notable, however.

A. Impacts on Habitat Structure

Many invasives are unwanted because of the effects they have on habitat structure. In the U.S. Pacific Northwest, *Spartina alterniflora* changes tidal mudflats into salt marsh, thereby eliminating oyster habitat and bird-foraging habitat. In the Everglades, *Melaleuca quinquenervia* shifts the sawgrass-dominated "river of grass" to a swamp, and in Puerto Rico, it shifts diverse forests to monotypes (Lugo, 2004). Unlike *Tamarix* spp., *M. quinquenervia* does not increase transpiration (Allen *et al.*, 1997). In the arid southwestern U.S., *Tamarix* spp. replace desert and riparian species (willows and cottonwood; Stohlgren *et al.*, 1998) along intermittent streams and washes, shifting vegetation from deciduous to evergreen and notably dewatering sites in the process by increasing transpiration rates. In addition, *Tamarix* spp. stabilize river banks and contribute to downcutting of river flow channels, resulting in narrow, deep channels that reduce the ability of rivers to meander and flood (Figure 3). The ultimate effect is to inhibit the natural regime of flood pulsing (Ellis *et al.*, 2002). At the same time, the increased density of these flammable woody plants and litter increases

fire frequency and intensity (Cox, 1999), and the invader lowers water tables to the disadvantage of native species. The magnitude of water loss due to invasive species is hard to estimate, although Le Maitre *et al.* (2000) calculated that South African catchments lose billions of cubic meters of water per year due to exotic invasive shrubs and trees.

P. australis has multiple impacts on marsh geomorphology by building up the marsh plain elevation (via increased sedimentation and organic matter production). Accretion of materials, including litter, can be twice as high as in marshes that this species replaces (Rooth *et al.*, 2003) with rates that are 3 to 4 mm higher than uninvaded sites. In addition, *P. australis* is known for its ability to fill in small creeks (Lathrop *et al.*, 2003). At Hog Island, New Jersey, a *P. australis* invasion of 20+ years appears to have eliminated 8% of the length of first-order tidal creeks. When marsh elevation increases more rapidly than sea level rises, the marsh becomes drier; when creeks are filled in, access to the marsh by nekton is reduced. Together, the effect is to eliminate aquatic microhabitats that are important to juvenile mummichugs (Figure 4).

Species that greatly alter the physical structure of a site have high potential for shifting hydrological conditions and animal use. It is doubtful, however, if structural shifts and their secondary impacts are more dramatic in wetlands than in uplands.

B. Impacts on Biodiversity

Invasive wetland plants are generally assumed to reduce both plant and animal diversity, and our recent studies confirm this assumption (Werner and Zedler, 2002; Kercher *et al.*, In press; Kercher and Zedler, 2004). As low species richness sometimes confers greater invasibility, the potential for positive feedbacks exists. An invader that causes a site to lose native species could become even more invisable.

Wetlands near Madison have the fewest species and lower quality species where *P. arundinacea* is present in sites with indicators of hydrological disturbance (*e.g.*, drainage ditches that lower water tables or culverts that direct agricultural or urban runoff into the site) and where invasive species are present (Kercher *et al.*, In press). Canopy architecture is also altered when native species are lost and invasives become dominant (A. Herr-Turoff, University of Wisconsin, unpublished data). Richburg *et al.* (2001) found that high salt concentrations and *P. australis* act independently to decrease species richness, evenness, and cover of native species in a fen community. Thus, invasive species degrade plant community integrity in multiple ways.

Evidence of plant invasion impacts on animal diversity is accumulating. Mensing *et al.* (1998) identified correlations between bird diversity and near-stream landscape condition and between fish composition and broader land use patterns. Blossey *et al.* (2001) reported reduced habitat in *Lythrum salicaria* stands for numerous insect and bird species that are habitat specialists (*e.g.*, marsh wrens); likewise, Benoit and Askins (1999) found significantly fewer species of birds and

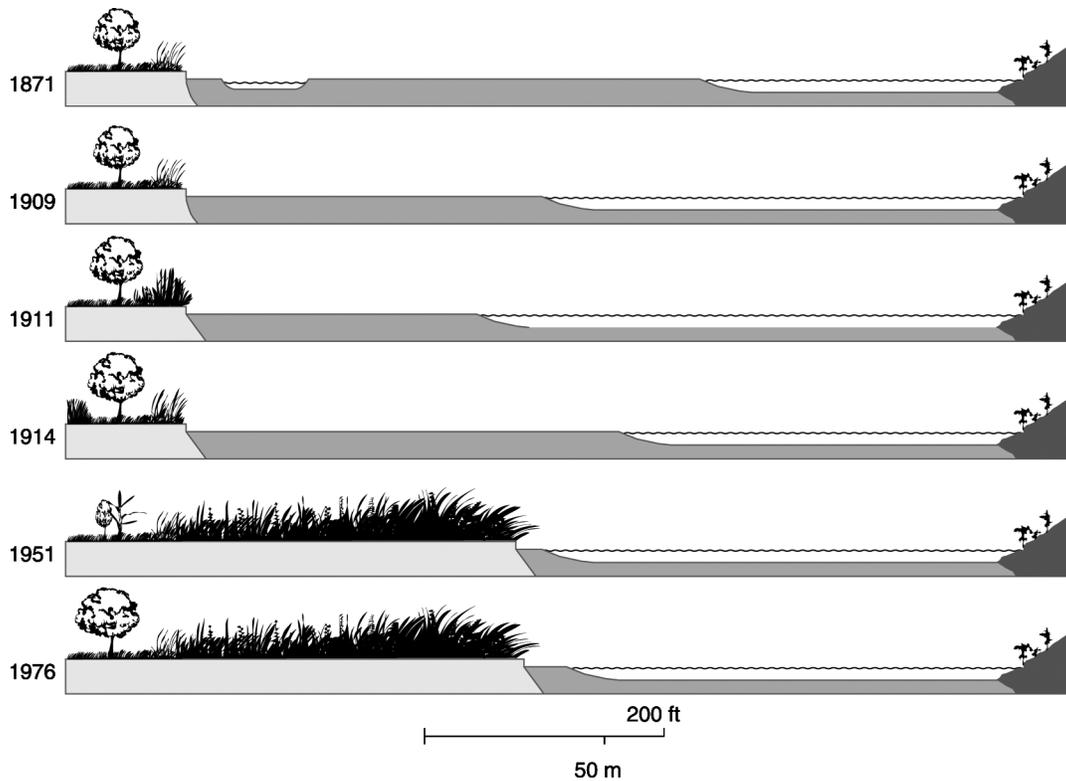


FIG. 3. Geomorphological impacts of tamarix on the Green River, Utah, as recorded from 1871 to 1976. Note that the invader is credited with destabilizing the floodplain and river banks, such that the channel became narrower and deeper and no longer able to meander. Redrawn by K. Elliot from Graf (1978), with the author's permission.

state-listed species in phragmites-dominated wetlands than in native cordgrass marshes. However, E. Kirsch and M. Meier (USGS LaCrosse, WI, personal communication) did not find major differences in bird use of wet meadows dominated by natives *versus* those invaded by *P. arundinacea*, although some differences in invertebrate foods were evident.

Cox (1999) lists many impacts of *Tamarix* invasions on animal species, including reducing bird diversity and numbers, and reduced use by mule deer (*Oidocoileus hemionus*), beaver (*Castor canadensis*), and white-throated woodrats (*Neotoma leucopus*). Several studies have compared animal diversity in marshes invaded by *P. australis* with uninvaded *Spartina alterniflora* marshes. Fell *et al.* (1998) reported similar macroinvertebrates (snails, amphipods, and isopods) and use by the fish, *Fundulus heteroclitus*; Meyer *et al.* (2001) likewise found no differences in nekton abundance, biomass, and use in *P. australis* and native *S. alterniflora* marshes. Impacts on food webs, however, are detectable (see below). According to Able and Hagan (2000), the effects on *F. heteroclitus* are size specific; they found negative effects on larval and small juvenile fish but less or no effect on larger fish and on decapod crustaceans. Talley and Levin (2001) reported lower abundances of epifaunal gastropods (*Succinea wilsoni* and *Stagnicola catascopium*) and fewer arachnids, midges, tubificid, and enchytraeid oligochaetes in phragmites marshes than in uninvaded marshes; however, phragmites stands

supported more podurid insects, sabellid polychaetes, and peracarid crustaceans, and had greater habitat-wide taxon richness, as measured by rarefaction, than the uninvaded stands. Nevertheless, variations in salinity, age of stand, and seasonal effects may have influenced the patterns observed.

It is rarely clear how an invader eliminates individual native species. Two exceptions concern rare plant species. *L. alatum* had lower seed set in experiments with pure *versus* mixed pollen (Brown and Mitchell, 2001). In this case, pollen from *L. salicaria* interferes with the congener's reproduction. In the study of *Parapholis incurva* and *Cordylanthus maritimus* ssp. *maritimus*, root-attachment points on the invasive annual grass were too short-lived to support the endangered hemiparasite's haustoria (Fellows, 1999).

C. Impacts on Productivity, Nutrient Cycling, and Microorganisms

Invasive plants that differ from native species in biomass and productivity, tissue chemistry, plant morphology, or phenology can alter soil nutrient dynamics (Ehrenfeld, 2003). Ehrenfeld's recent review of upland and wetland plants provides tables comparing invasives *versus* natives for variables related to biomass, soil carbon, soil nitrogen, and other soil properties and fluxes (Ehrenfeld, 2003). Most of the species for which data are

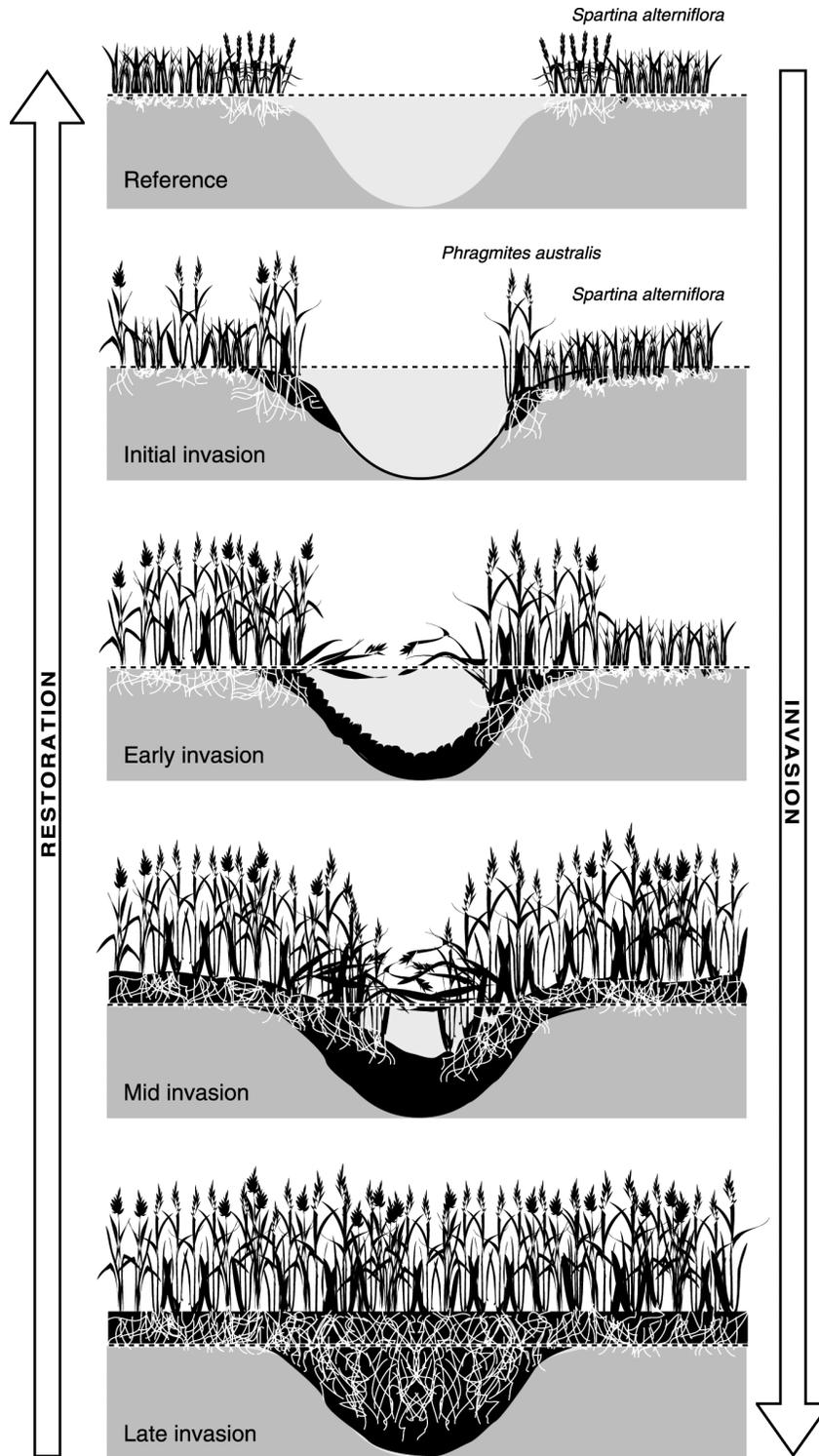


FIG. 4. *P. australis* changes marsh microtopography by filling in tidal creeks. Redrawn by K. Elliot from Able *et al.* (2003), with permission of the Estuarine Research Federation and approval from Ken Able.

available are terrestrial plants, but *L. salicaria*, *P. australis*, and *Tamarix* sp. appear repeatedly in the survey. While there are many studies that document effects of invasives, there are inconsistencies in pattern for different species and for the same

species in different places (Ehrenfeld, 2003). Impacts on ecosystem function can be site and species specific.

Much of the work on the effects of wetland invasive species on productivity, biomass, and nutrient cycling has been done in

the northeastern U.S. In Windham and Meyerson's (2003) review, *P. australis* was described as increasing N standing crop, slowing whole-plant decomposition rates, and allocating more N to leaves, with less to stems, in comparison with the species it replaced. Effects on marsh N pools were highly variable and attributed to specific site effects. Ravit *et al.* (2003) found reduced diversity of phospholipid fatty acids, which in turn indicate lower activity of microbial populations in soils dominated by *P. australis* than *S. alterniflora*. Otto *et al.* (1999) evaluated microbial biomass and nutrient pools in stands of *P. australis* and *L. salicaria* that were invading *Typha angustifolia* in the Hudson River freshwater tidal marshes. *P. australis* had higher biomass than that of typha, and both *P. australis* and *L. salicaria* had higher N concentration in plant tissues, suggesting greater sequestration than typha. Soil nitrogen was reduced in *L. salicaria* and available inorganic N was higher in *P. australis*, changes that indicate important differences in N processing and retention, because the site has low N concentrations. Likewise, Templer *et al.* (1998) reported higher biomass for *P. australis* (~2×) and *L. salicaria* than for *T. angustifolia*, and *P. australis* had higher N content (~3×) than *T. angustifolia*. These authors conclude that the recent invaders have "subtle but ecologically significant effects on nutrient cycling," while Otto *et al.* (1999) concluded that they had no evidence that *P. australis* and *L. salicaria* changed nitrogen-removal capacity of this Hudson River wetland. Since *T. angustifolia* is also an invasive species, albeit an earlier arrival, the lack of major differences in nutrient-processing among these three species is understandable.

D. Impacts on Food Webs

Invasive species can affect food webs in multiple ways, by altering the quantity or quality of food, by changing food accessibility, or by changing vulnerability to predators. Perhaps the best-studied case concerns *P. australis* in the Northeastern U.S. There, Abel *et al.* (2003), Raichel *et al.* (2003), Osgood *et al.* (2003), and Fell *et al.* (2003) all found fewer juvenile fish on the marsh surface where *P. australis* was dominant compared to *S. alterniflora*, and Currin *et al.* (2003) suggested that fish consume *P. australis* somewhat in relation to its abundance in marshes, although benthic microalgae are more important sources of assimilated food. Both Raichel *et al.* (2003) and Osgood *et al.* (2003) found fewer invertebrates in *P. phragmites* versus *S. alterniflora* stands at some, but not all, times of the year. Jivoff and Abel (2003) found that *Callinectes sapidus* Rathbun (blue crab) preferentially fed on *S. alterniflora* compared to *P. australis* marsh surfaces. Fell *et al.* (2003) related higher numbers of *Palaemonetes pugio* Holthius (ghost shrimp) and lower numbers of *Uca minax* (LeConte; redjointed fiddler crab) to differences in marsh elevation where *P. australis* was dominant. The effect of *P. australis* on nesting by long-legged wading birds gave mixed results in a Delaware Bay study that compared the invaded marsh with upland habitats: four species nested equally in *P. australis* and upland, one species avoided *P. australis*, and one species confined itself to *P. australis*. One species had a higher reproductive rate in nests formed within *P. australis*. To

summarize, the effects of *P. australis* on animals are not all negative. Impacts on invertebrates and food webs appear to be tightly linked with the effects that this invader has on marsh elevation and microtopography: by reducing hydroperiod and the area of tidal pools, habitat for aquatic animals is diminished (Figure 4).

Synthesizing the above, a reasonable scenario is that *Phragmites* invasion reduces topographic heterogeneity and raises the marsh plain elevation. Both of these "structural effects" would reduce the number and area of pools that would otherwise support benthic microalgae and invertebrates. The structural effect also involves a reduction in the length of small creeks, which would reduce the number and extent of access routes used by mummichog larvae to gain access to food reservoirs on the marsh surface. With fewer fish on the marsh surface, birds might have less food available. At the same time, primary productivity might increase, but if the biomass is less palatable to key consumers, it would not sustain the natural food web. One might expect a shift from a grazer-based toward a detritivore-based food web.

VII. ARE WETLANDS MORE VULNERABLE TO INVASIONS THAN UPLANDS?

We have not considered all wetland invaders nor compared the proportions of upland and wetland plants that are invasive. We offer one calculation: The Global Invasive Species Database lists 33 plants among the 100 worst alien species; the fact that 8 of the 33 plants are wetland species seems disproportionate to the area of wetlands globally (4 to 6% of the global land mass; Mitsch *et al.*, 1994). That is, 24% of the worst plant invaders plague systems that cover ≤6% of the earth. We encourage a more thorough comparison of upland and wetland invasions.

We also encourage broader comparisons of the dominance forms of invasive and native plants in uplands versus wetlands. The dominance index of C. Frieswyk (University of Wisconsin, personal communication) provides a straightforward means of comparing species behavior across wetlands and larger spatial scales. For the Great Lakes region, species known to be invasive (*Typha x glauca*, *P. arundinacea*, and *P. australis*) all exhibited the monotype form of dominance, while native dominants tended to serve as matrix species that coexisted with several other native species (Frieswyk *et al.*, In review). Even if wetlands do not host a disproportionate share of the world's invaders, they seem to be particularly vulnerable to invasions that become monotypes (Figure 5 and Table 1).

The formation of monotypic stands occurs among clonal species, nonclonal perennials, and some annuals (*e.g.*, *I. glandulifera*; Beerling and Perrins, 1993). The fact that wetlands are landscape sinks for water and nutrients helps to explain the widespread development of monotypes (Figure 6). As shown by Kercher and Zedler (2004), the strong synergism between flooding, nutrients, and sediments promoted the formation of monotypes of *P. arundinacea*, with the highest biomass of the invader and greatest loss of resident species occurring where flooding was continuous, nutrients were added at the highest level, and sediment addition was nutrient-rich topsoil.



FIG. 5. *Tamarix ramossissima* monotype on the Rio Grande River, Texas. Photo taken in 1992 by Michael Collier, U.S. Geological Survey, courtesy of Environmental Defense (Mary Kelley).

Sedimentation is both a cause and an effect of wetland invasions. Where topographically complex wetlands are smothered in inflowing sediments, invasive plants find canopy gaps and bare soils to colonize (Werner and Zedler, 2002, Figure 1). Where sturdy invasive plants colonize streambanks, sediments accrete and change riparian geomorphology (Figures 4 and 5). The outcomes are similar—a simplification of topographic heterogeneity that is detrimental to the native community's ability to support species-rich vegetation. At the same time, sediments carry nutrients (especially phosphorus) that cause eutrophication and more rapid growth of many invasive plants.

Many invasive plants respond to the influx of water, nutrients, and sediments by increasing their growth rates. We argue that rapid height growth is achieved by many wetland plants *via* efficient growth; stems that are hollow and tissues that have high aerenchyma use little biomass. There are some constraints, however. Continuous water uptake is needed to compensate for high transpiration rates (caused by a low investment in biomass and lack of sclerophylly), and wetlands have ample water to replace evaporative losses. Also, hollow-stemmed plants cannot necessarily remain upright, as plants that invest little in structural material are vulnerable to windthrow, water damage, or trampling. Hollow stems should be able to remain upright,

however, if they have a leaf or branch structure allows them to (1) intertwine (as in *Alternanthera philoxeroides*), (2) rest on their own standing dead biomass (as in *Typha* spp.), or (3) produce upright branches once the main stem has been flattened (as in *P. arundinacea*). Thus, we propose that plants with efficient growth *via* hollow stems and low investment in structural biomass have an advantage in wetlands.

A belowground attribute that likely contributes to monotype formation is the ability to produce dense root and rhizome mats. Those who attempt to excavate belowground biomass in *Typha x glauca* stands (*e.g.*, I. Woo, personal communication) find little space for other species. Very likely the ability to form dense mats is related to the existence of aerenchyma, which both allows a high volume of belowground material and ensures that dense roots can remain functional by supplying oxygen.

Because wetlands function as sinks for water, nutrients, sediments, and other materials, and because many wetland invasive plants can take advantage of conditions, growing tall *via* efficient growth, wetlands appear to be more vulnerable than uplands to the formation of invasive monotypes (Figure 6). Elsewhere, we suggest that when a single disturbance, such as a stormwater pulse, simultaneously makes the wetland more invasible and the invader more invasive, the resident plant community will go

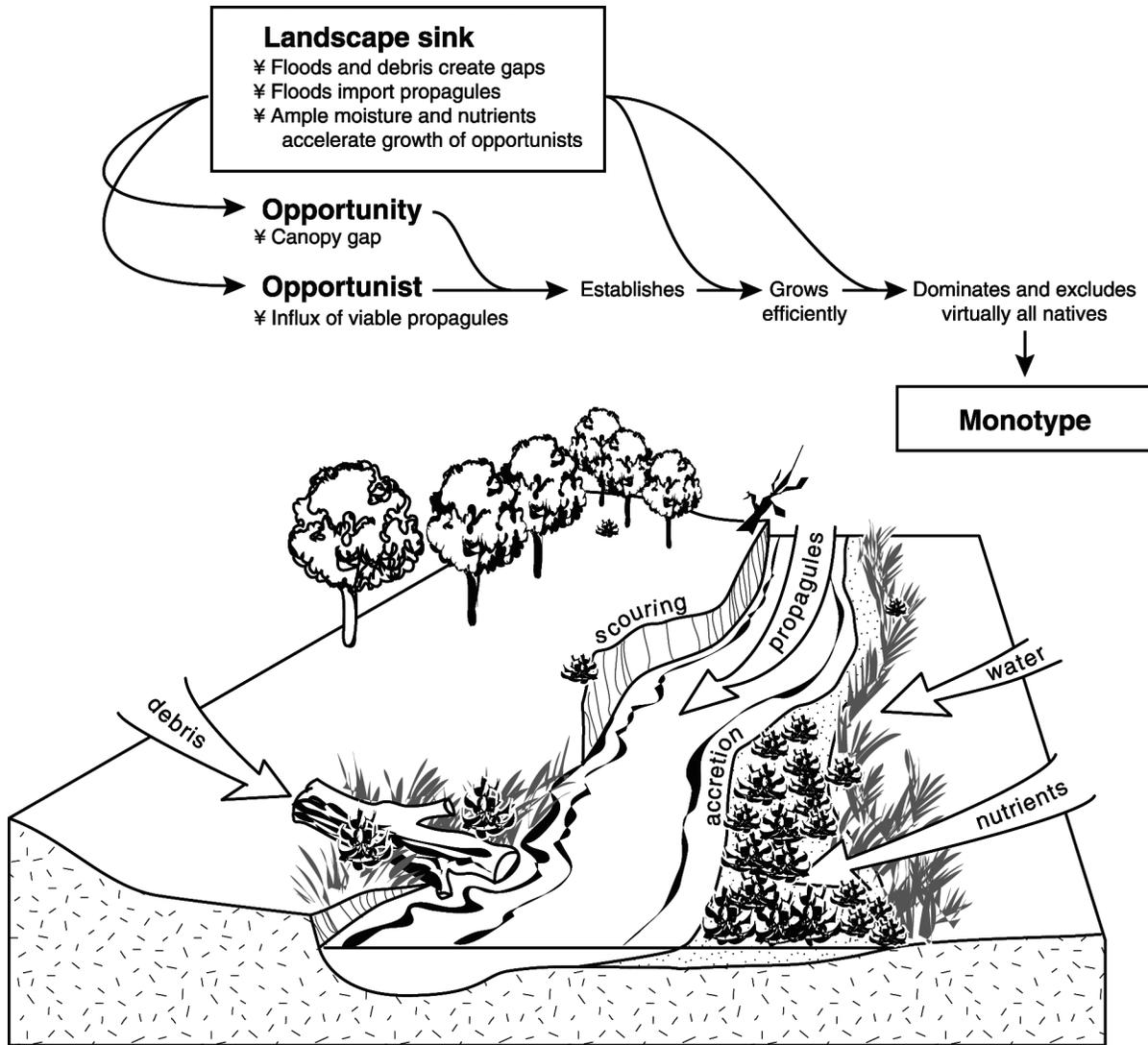


FIG. 6. Conceptual model showing how wetland position (as a landscape sink) has multiple influences on the formation of monotypes by wetland invasive plants: (1) Landscape sinks are subject to inflowing debris and flooding, which create canopy gaps that create opportunity for invasion, (2) floods bring in propagules (seeds, viable plant fragments, floating mats) of opportunistic species, and (3) flooding supplies water and nutrients that accelerate invasion and formation of monotypes. The opportunist is often one that initiates growth early in spring and grows tall quickly (e.g., *P. arundinacea*, which grows efficiently, producing high plant volume per unit biomass via hollow stems and aerenchyma). Illustrated by K. Elliot.

beyond accommodating the new species; it will likely shift toward a monotype (Maurer *et al.*, 2003; Kercher *et al.*, In press).

VIII. CONCLUSIONS

- Invasive plants in wetlands include grasses, graminoids, forbs, shrubs, and trees.
- Comparison of ~20 invasive wetland plants, including 8 that are among the 100 most invasive species on earth, failed to reveal any one attribute that explains their invasiveness.
- Wetland invaders share features with upland species (e.g., high productivity with nutrient influxes and abil-

ity to extend the growing season), as well as features that are not common to most upland plants (highly efficient growth, *i.e.*, high plant volume per unit biomass; tolerance to waterlogging; and water dispersal of propagules, including seeds, floatable plant parts, and vegetatively reproducing mats).

- Five hypotheses (enemy release, broader tolerance, efficient use, hybrid vigor, and allelopathy) have been tested, and each helps explain some wetland invasions. While no theory predicts the species that will invade a site or a region, several hypotheses have explanatory value *a posteriori*.
- Invasions in wetlands can be explained by simultaneously considering the nature of the opportunity and

the availability of opportunists. Invasive plants establish where soils are bare (mudflats, riverbanks) and where disturbances create bare soil (erosion, sedimentation, debris deposition), all of which are associated with landscape sinks (wetlands). The species that take advantage of each opportunity depend on access (dispersal mode) and constraints (e.g., salt, native competitors). *A posteriori*, the opportunities seem well matched by the opportunists. Some opportunities attract multiple opportunists; some opportunists respond to multiple opportunities.

- Disturbances that involve multiple factors (e.g., stormwater inflows that involve flooding, nutrients, and sediments) likely increase invasion rates substantially, accelerating the rate of conversion from species-rich native vegetation to a monotype of an invasive species.
- Wetland invasive plants have substantial and persistent effects on habitat structure (including vegetating bare mudflats, stabilizing riverbanks, and reducing microtopographic heterogeneity), biodiversity (generally reducing numbers of species of plants and animals), and food web functioning (sometimes increasing food supplies, sometimes changing food quality). For the most part, outcomes are considered detrimental. Wetland that becomes dominated by invasive plants tend to support fewer native animal species, and ultimately more invasive animals will likely be attracted.
- We propose that wetlands are especially susceptible to invasions that become monotypes due to their landscape sink position, where disturbances, moisture, and nutrients all accumulate.

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Wetland effects on lake water quality in the Minneapolis/St. Paul metropolitan area

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Abstract

A method developed to evaluate the cumulative effect of wetland mosaics on water quality was applied to 33 lake watersheds in the seven-county region surrounding Minneapolis-St. Paul, Minnesota. A geographic information system (GIS) was used to record and measure landscape variables derived from aerial photos. Twenty-seven watershed land-use and land-cover variables were reduced to eight principal components which described 85% of the variance among watersheds. Relationships between lake water quality variables and the first six principal components plus an index of lake mixis were analyzed through stepwise multiple regression analysis. A combination of three landscape components (wetland/watershed area, agriculture/wetlands, and forest/soils components) explained 49% of the variance in a trophic state index, even though most of the lakes examined were already highly eutrophic, and thus were influenced by internal loading. The regression equations explained a range of 14 to 76% of the variation in individual water quality variables. Forested land-use was associated with lower lake trophic state, chloride, and lead. High lake trophic state was associated with agricultural land-use and with wetland distance from the lake of interest. The extent of wetlands was associated with low total lead and high color in lakes downstream. Wet meadows or herbaceous, seasonally-flooded wetlands contributed more to lake water color than did cattail marshes.

1. Introduction

The rapid loss of wetland area in the United States by draining and filling (Tiner 1984) has made it imperative to assess not only the effect of individual wetland loss on lake water quality, but also the cumulative effect of changes in the wetland mosaic on lake water quality. In the past, permit regulation for wetland drainage and filling has been based strictly on the nondegradation clause in Section 404 of the Clean Water Act, and permits have been con-

sidered on a case-by-case basis. However, environmental impact statements prepared under mandate of the National Environmental Policy Act of 1969 must also address the issue of cumulative impacts (Council of Environmental Quality; 38 CFR 1500.6). Cumulative impacts have been defined as 'the impact on the environment which results from the incremental impact of the action when added to other past, present, and reasonably foreseeable future actions. . . .' (40 CFR 1508.7).

Management of lake water-quality within a de-

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veloping landscape such as the Minneapolis-St. Paul metropolitan area requires consideration of both lake morphometry and external watershed variables, including wetland distribution. For lakes which have experienced high historical loading rates, the morphometry of individual lake basins is a controlling factor in maintaining lake trophic state. Lakes that are shallow relative to their surface area are more likely to be frequently mixed by wind and wave action (Osgood 1988) and internal nutrient loading from the sediments may have an equal or greater contribution than external loading from the watershed.

Conversely, in lakes without a long history of high external nutrient loads, conditions within the watershed will have a greater effect on lake productivity. In a relatively homogeneous, undeveloped landscape, lake trophic status (total phosphorus, total nitrogen, chlorophyll *a*) can be predicted simply as a function of the watershed area/lake volume ratio, an index of external loading (Schindler 1971). As land-use changes with the advent of agriculture and/or urban development, landscapes become more heterogeneous, and landscape-level predictors of lake-water quality become more complex (e.g. Oberts 1981). The extent, distribution, and juxtaposition of different land-cover, land-use, and soil types within each watershed all contribute to variation in surface water quality among watersheds (Johnston *et al.* 1990).

Landscape components within a watershed can act as sources, sinks, or transformers for nutrient, sediment, and pollutant loads to a given lake. Nutrient yields from landscape sources can be predicted from empirical relationships developed through comparison of watersheds with one predominant land-use type in a given ecoregion (Omernik 1976). For example, measured total phosphorus exports are 50–100% greater from predominantly urban watersheds as compared to predominantly agricultural watersheds for regions in the Great Lakes states outside of the Minneapolis/St. Paul metropolitan area (Chesters *et al.* 1978). Percent urban land-use has been found to be positively correlated with total phosphorus export from predominantly urban watersheds in the Minneapolis/St. Paul metropolitan area (Walker 1987)

and with average total phosphorus levels in lakes within urban/residential watersheds for one Minneapolis suburb (Ayers *et al.* 1980). Both total nitrogen and total phosphorus exports are lower for forested watersheds than for either agricultural or urbanized watersheds (Omernik 1976).

Although average nutrient yields can be predicted on the basis of predominant land-use, the relative magnitude of nutrient export from agricultural watersheds as compared to urban watersheds can vary by one to two orders of magnitude depending on land-use practices employed (Omernik 1976). Within agricultural landscapes, sediment and nutrient yields have been modelled as a function of agricultural practices, soil properties, and topography (Young *et al.* 1989). Surface waters within watersheds containing steep slopes and highly erodible soils are expected to receive greater inputs of nutrients and sediments from nonpoint source runoff.

Stream or lake water-quality depend not only on the extent of sediment or nutrient sources within a landscape, but also on the extent of landscape sinks or transformers of nutrients and pollutants. Beyond exporting lower levels of nutrients, forested riparian zones can physically trap particulate-associated phosphorus derived from adjacent agricultural fields and reduce groundwater nitrate levels through denitrification (Peterjohn and Correll 1984; Cooper *et al.* 1986; Whigham and Chitterling 1988). A review of nutrient budgets for freshwater tidal, riverine, palustrine, and lacustrine wetlands revealed that all of these wetland types can act as net sinks for nitrogen and phosphorus either seasonally or annually (van der Valk *et al.* 1978). However, Prentki *et al.* (1978) and Lie (1977) suggested that lakeshore wetland plants and macrophytes act as nutrient pumps from the sediment, while Sager *et al.* (1985) suggested that lake-shore marshes act as nutrient transformers rather than as nutrient sinks. The efficiency of different wetland types in removing or transforming nutrients, sediments, and heavy metals depends on many factors, including the magnitude and frequency of flow (Bayley *et al.* 1985; Novitzki 1979), water retention time (Walker 1987), the degree of water-sediment contact (Bowden 1987), the magnitude and nature

of inputs (dissolved, fine particulates, or coarse particulates; Oberts 1981; Richardson and Nichols 1985), and the composition of wetland sediments (Richardson 1985).

Not only the extent, but also the distribution of landscape sources and sinks relative to surface waters is important. In a previous study of stream watersheds in the seven county Twin Cities metropolitan area, Johnston *et al.* (1990) found that streams with wetlands in close proximity to the outlet had lower annual concentrations of inorganic suspended solids, fecal coliform counts, nitrate, flow-weighted ammonium, flow-weighted total phosphorus, and a lower proportion of phosphorus in dissolved form than those streams associated with wetlands farther upstream. Other researchers have demonstrated that land-use within the buffer zone surrounding surface waters can have a greater influence on water-quality than does land-use for the watershed as a whole (Osborne and Wiley 1988).

Multivariate analyses have been used in the past to explain differences in biological communities or water chemistry among lakes as a function of multiple lake morphometry and watershed variables (Zimmerman *et al.* 1983; Paloheimo and Zimmerman 1983). In this study, we apply an empirical multivariate approach developed to evaluate the cumulative effect of wetland mosaics on surface water quality to 33 lake watersheds in the seven-county region surrounding Minneapolis-St. Paul, Minnesota (Johnston *et al.* 1990). Twenty-seven variables were derived to describe the extent and distribution of wetland and land-use types, soil characteristics, topography, and lake morphometry. Principal components analysis was used to derive a smaller set of composite landscape variables that a) explained the variation among watersheds and b) were independent of one another. These principal components were then used as independent variables in a multiple regression analysis of lake water-quality variables.

Partial correlation analysis has also been used to partition variability in lake water quality among related watershed variables (*e.g.* Gorham *et al.* 1986). In the current study, partial correlation analysis was used to explore relationships between

water quality and selected watershed variables while holding constant other watershed variables that were highly correlated with principal components used in the original multiple regressions. In this way, the importance of individual watershed variables, which may have been obscured by the dominating explanatory variables, could be examined. In general, the statistical analyses were used in an exploratory manner to identify possible casual relationships between landscape and water quality variables.

1.1. Study region

The low relief (180 m) and interrupted drainage of the Minneapolis/St. Paul metropolitan area have made it an area of numerous lakes and wetlands. There are 942 lakes ranging in area from 4 to 5,791 ha which constitute 6.7% of the total land area in the 7,330 km² metro region (McBride 1976). The majority of these lakes are small (< 40 ha), shallow (< 5 m), and eutrophic (Metropolitan Council 1981). Although only about half of the pre-settlement wetland area remains (Anderson and Craig 1984), wetlands still constitute about 7.6% of the region (Owens and Meyer 1978).

2. Methods

2.1. Study site selection

Thirty three lake watersheds covering 589 km² were selected as study sites (Table 1, Fig. 1). Lakes were defined as areas of open water greater than 8 ha in size and ≥ 2 meters deep (Cowardin *et al.* 1979). We restricted our study sites to those lakes with total watersheds greater than 300 ha in size.

The primary objective was to relate lake water quality to wetlands and other watershed characteristics, therefore study sites were selected based on the availability of: (1) epilimnetic water quality data, and (2) aerial photographs of the monitored watershed taken concurrent with water quality data collection. We selected dimictic lakes as much as possible, using mixing ratio (mean depth/square

Table 1. Watershed size and lake morphometry for 33 lakes in the Twin Cities metropolitan area, MN (from McBride 1976).

lake	lake no.	map code	year of aerial photo	lake surface area (km ²)	contributing watershed area ^a (km ²)	dilution ratio lake vol/ contributing area (m)	mean depth (m)	mixing ratio mean depth/√surface area
Bald Eagle	1	BA	1987	4.5	29	0.36	2.4	1.2
Bass	2	BS	1980	0.7	12	0.17	2.7	3.3
Bryant	3, 4	BR	1966, 1984	0.8	11	0.36	5.2	5.8
Chub	5	CH	1980	1.0	5	0.27	1.2	1.2
Coon	6	CO	1980	6.3	19	0.97	3.0	1.2
Crystal	7, 8	CR	1966, 1980	0.4	5	0.63	2.7	2.5
Cynthia	9	CY	1980	0.9	41	0.04	2.1	2.4
Diamond	10	DI	1980	1.7	2	1.43	1.5	1.2
Dutch	11	DU	1980	0.7	6	0.48	4.4	5.3
Eagle	12	EA	1980	1.4	7	0.93	3.6	2.6
Fish	13	FI	1980	0.8	7	0.69	5.4	5.7
Forest	14, 15	FO	1957, 1980	0.3	3	3.53	2.7	1.3
George	16	GE	1980	2.0	6	1.08	2.7	1.8
Golden	17	GO	1980	0.2	28	0.02	2.4	5.4
Independence	18	IN	1980	3.3	31	0.66	6.1	3.3
Johanna	19	JO	1980	0.8	8	0.62	6.1	6.6
Lotus	20	LO	1980	0.9	5	1.45	6.4	6.3
Marion	21	MA	1980	2.2	19	0.48	4.6	3.3
Medicine	22	ME	1980	4.4	42	0.46	5.2	2.7
Minnewashta	23	MI	1980	2.9	9	1.65	4.6	2.6
Orchard	24	OR	1980	1.0	5	0.45	2.4	2.5
Otter	25	OT	1980	1.3	3	0.83	1.8	1.6
Owasso	26	OW	1980	1.8	12	0.33	2.7	2.3
Parley	27	PA	1984	1.2	48	0.07	1.8	1.3
Pierson	28, 29	PI	1957, 1980	1.2	4	2.38	6.1	5.2
Riley	30, 31	RI	1980, 1984	1.2	19	0.48	7.6	7.0
Sarah	32	SA	1980	2.3	15	0.94	6.1	4.0
Schutz	33	SC	1984	0.4	4	0.80	5.0	6.6
Spring	34	SP	1980	3.1	47	0.33	5.6	3.4
Waconia	35	WA	1980	13.7	29	2.17	4.8	1.3
White Bear	36	WH	1980, 1987	9.9	26	2.26	6.1	2.0
Wolsfeld	37	WO	1980	0.2	6	0.07	3.0	8.0
Zumbra	38	ZU	1984	0.9	1	3.15	4.3	4.5

^aincludes lake area

root of surface area) as a predictor of mixis (Os-good 1988). The water column of a dimictic lake is thoroughly mixed during spring and fall overturn periods, but remains vertically stratified during the growing season. Contributions from internal nutrient generation, which could obscure relationships between lake water quality and watershed characteristics, should be less in these lakes than in polymictic lakes, which are continually mixed. Lakes were excluded from study if there were (1) known point sources of pollution in the watershed

(e.g. sewage treatment plants), (2) artificial water additions or withdrawals from the lake (McBride 1976), or (3) lake water-quality management programs (e.g. hypolimnetic aeration) in effect. Of the 33 lakes selected, six had both water quality data and aerial photographs available for two separate periods, so that a total of 39 site-years were identified.

LAKE WATERSHEDS TWIN CITIES METROPOLITAN AREA

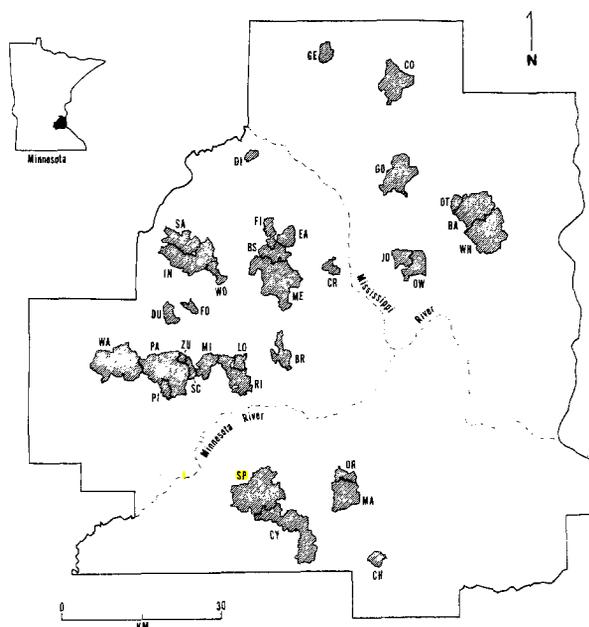


Fig. 1. Location of 33 selected lake watersheds in the Minneapolis-St. Paul metropolitan area. Lakes corresponding to two-letter codes are listed in Table 1.

2.2. Landscape analyses

Landscape analyses used to characterize individual watersheds were described in detail by Detenbeck *et al.* (1991) and Johnston *et al.* (1988; 1990). Several variables were used to characterize lake and drainage basin morphometry (Tables 1 and 2). Drainage basins were delineated and measured for each of the lakes using 7½ minute U.S.G.S. topographic maps. A dilution ratio was calculated for each lake by dividing lake volume by contributing watershed area (Schindler 1971). Lake volume, depth, and surface area were obtained from a U.S.G.S. database maintained for metropolitan area lakes (McBride 1976).

Existing aerial photographs were used to map the lake drainage basins for each site-year (Table 2). Because water quality and runoff is potentially affected by all land within a watershed, both upland and wetland cover types were mapped for each date of photography. Photo enlargements were used whenever possible. Stereoscopic magnifica-

tion (3×) was required to interpret the 1957 air photos because they were only available as 9" × 9" contact prints.

Mapping of the five drainage basins larger than 4,000 ha (Cynthia, Medicine, Parley, Spring, and Waconia) was done by U.S. Public Land Survey quarter-quarter sections (~40 acres each). The quarter-quarter section boundaries correspond with land use boundaries (*e.g.*, roads, fields, fence lines, woodlot boundaries), so they are easily delineated on aerial photos. A clear mylar overlay gridded into 40 acre (16 ha) cells prepared for each air photo scale was used as a guide for locating the actual quarter-quarter boundaries on the photos. In this way, the ground location of each area mapped was exactly the same from year to year, despite air photo scale differences. The forty acre resolution was too coarse for small watersheds, so a 10 acre (4 ha) grid size was used to map the remaining 28 watersheds smaller than 4,000 ha (34 site-years).

Each cell was classified by the land use which constituted the majority of its area: agriculture, forest, urban/residential, lake, or wetland. If the major cover type was wetland, it was further classified into one of seven wetland categories based on U.S. Fish and Wildlife Service criteria (Cowardin *et al.* 1979): open water permanent, open water semi-permanent, herbaceous semi-permanent, herbaceous seasonally-flooded or saturated, herbaceous temporarily-flooded, woody semi-permanent, and woody seasonally-flooded/saturated. Within the Twin Cities metropolitan area, seasonally-flooded wetlands generally correspond to weedy or cultivated depressions flooded only briefly following periods of heavy run-off, or to weedy or scrub/shrub wetlands within the floodplain of a stream. Saturated wetlands correspond to wet meadows dominated by grasses or sedges. Semi-permanent open water wetlands correspond to shallow-deep marshes typically dominated by cattails (*Typha* spp.) and bulrush (*Scirpus* spp.). National Wetlands Inventory maps were used for 1980, and additional wetland mapping was done under the supervision of air photo interpreters having 5 or more years experience with the National Wetlands Inventory. The land-use code for each grid cell was recorded on 1:24,000 maps and then digitized.

Table 2. Average, standard error (s.e.), and range of landscape and lake morphometry variables for 33 lake watersheds in the Twin Cities metropolitan area, MN (% W = % watershed, % LF = % 200 m lake fringe area, n = 38 watershed-years).

variable	code	units	average	s.e.	min	max
Watershed area	WAREA	km ²	17	2.4	2	50
Contributing watershed area	CAREA	km ²	15	2.1	1	48
Dilution ratio = Lake volume/Contr'g area	DILRATIO	m	1.03	0.15	0.02	3.53
Lake mixing ratio = Avg depth/ $\sqrt{\text{Surface area}}$	MIXRATIO	—	3.6	0.32	1.2	8.0
Wetland acreage	WTLND	% W	14	1.5	0	41
Agricultural acreage	AGR	% W	38	2.9	3	71
Forested acreage	FOR	% W	12	1.2	2	36
Urban/residential acreage	URB	% W	19	3.6	0	83
Other lakes acreage	OLAKES	% W	1.2	0.35	0.0	9.4
Herbaceous semi-permanent wetlands	HERBSP	% W	3.2	0.41	0.0	7.6
Average watershed-lake elevation	ELEVDIFF	m	15.9	1.03	2.1	28.0
Average K-factor (erodibility)	KFCTR	—	0.29	0.010	0.18	0.38
Urban lake fringe	URBLKFR	% LF	42	4.9	0	97
Wetland lake fringe	WTLDLKFR	% LF	18	2.0	0	50
Herbaceous semi-permanent wetland lake fr.	HRBSPLFR	% LF	8	1.5	0	32
Average wetland distance upstream	WTLDDIST	km	2.2	0.31	0.0	6.7
Average soil phosphorus	SOILP	Index (1–3)	2.69	0.066	1.50	3.00
Lake rank downstream (headwater = 0)	NDWNSTRM	No. of lakes	1.3	0.20	0.0	5.0
Average watershed slope	AVGSLP	%	0.76	0.060	0.17	2.38
Average soil pH	SOILPH	Estimated pH	5.98	0.048	5.80	6.73
Stream fringe area	STRFRG	% W	11.0	2.30	0.0	24.1
Herbaceous seasonally-flooded/saturated wetlands	HRBSSWD	% W	6.0	0.79	0.0	18.8
Woody seasonally-flooded/saturated wetlands	WDYSSWD	% W	3.3	0.73	0.0	20.6
Agricultural lake fringe	AGRLKFR	% LF	26	3.3	0	86
Forested lake fringe	FORLKFR	% LF	16	2.4	0	71
Herbaceous seasonally-flooded or saturated lake fringe wetlands	HRBSSLF	% LF	6.5	0.98	0.0	24.1
Woody seasonally-flooded or saturated lake fringe wetlands	WDYSSLF	% LF	2.3	0.64	0.0	16.1
Average wetland size	AVWTLDSZ	km ²	0.218	0.0037	0.000	1.03
Average size of stream wetlands	STWTLDSZ	km ²	0.37	0.0083	0.00	2.13

Digital data of soil K-factor (erodibility), surface soil phosphorus, surface soil pH, average slope, and mean elevation at a 40 acre (16 ha) resolution were obtained for the region from the Minnesota State Planning Agency. Values for soil K-factor and available surface soil phosphorus in these data coverages do not represent measurements made within each pixel, but have been derived by state-agency soil scientists through interpretation of soil type and geomorphic units (see Minnesota Soil Atlas 1973; 1980). Available soil phosphorus is expressed as an index value from 1 (low) to 3 (high). The maximum elevation difference (ELEVDIFF) was calculated as the difference between minimum and maximum elevation values associated with pixels within each watershed.

Three different PC-based geographic informa-

tion systems were used to enter, measure, and analyze the wetland and land-use data. ARC/INFO was used for digitizing, EPPL7 (Minnesota State Planning Agency 1987) was used to read the digital soil and topographic files, and an ERDAS GIS was used for digitizing and data analysis. Files were exchanged between ARC and ERDAS using the ARC/INFO grid conversion programs, and between EPPL7 and ERDAS using a program written by Anderson and Scheer (1987).

Land use, watershed boundaries, and streams were digitized from U.S.G.S. 1:24,000 topographic maps. Land use and wetland types were measured using the ERDAS GIS, and expressed as both a percentage of the lake fringe area (a 200 m band or 4 ha pixel width surrounding each lake) and total watershed area (Table 2). The GIS also was used to

extract individual watersheds from the regional data files, and to compute average soil (pH, available soil P) and topographic variables (maximum elevation difference: Table 2) for each watershed. Streams flowing into each lake were divided into 1 km increments from the inlet to the headwaters using a map wheel. The position of wetlands in the drainage network was then determined by intersecting the stream segment file with the wetland file, and computing an average distance upstream (weighted by wetland area) for all wetlands within a watershed. The average size of individual wetlands was computed for each watershed as a whole and for stream-associated wetlands.

2.3. Water quality data

Recent water-quality data for metropolitan area lakes were retrieved from the computerized STORET database (U.S. Environmental Protection Agency). As part of the routine surveys of lakes managed for fish and wildlife, limited data had been collected prior to 1970; these data were obtained from a database recently automated by the Minnesota Dept. of Natural Resources (Dave Pederson, personal communication). Most of the water quality data used in this study were collected as part of an ongoing study conducted by the Minneapolis-St. Paul Metropolitan Council (Metropolitan Council 1981; 1982; 1984).

Water quality data included nutrients (total and dissolved phosphorus, total Kjeldahl nitrogen, ammonium, nitrate + nitrite), dissolved oxygen, chloride, hardness, total alkalinity, turbidity, pH, specific conductivity, color, total and volatile suspended solids, Secchi depth, total and phaeophytin-corrected chlorophyll *a*, fecal coliform, metals (total lead, zinc, cadmium) and arsenic. Water quality variables reported by the Metropolitan Council, Barr Engineering, MN Pollution Control Agency (MPCA) and the MN DNR were analyzed according to Standard Methods (APHA 1936 through 1980) or according to EPA-approved procedures (U.S. EPA 1979). Most samples were analyzed by the MN Dept. of Transportation (metals), MN Dept. of Health (MPCA samples), or by the

Metropolitan Waste Control Commission (Metropolitan Council samples). Methods used by these laboratories are listed in Table 3 for comparison. Detection limits for samples analyzed by the MWCC were $0.01 \text{ mg P} \cdot \text{L}^{-1}$ for total or dissolved P, $0.02 \text{ mg N} \cdot \text{L}^{-1}$ for Kjeldahl nitrogen, $0.05 \text{ mg N} \cdot \text{L}^{-1}$ for nitrate, and $0.02 \text{ mg N} \cdot \text{L}^{-1}$ for NH_2 (Metropolitan Council 1981).

In calculating water quality values for a given sample date, data were averaged among samples taken at different depths within the epilimnion, or for the entire water column during periods of complete mixis. Epilimnetic or water column averages for each sampling date were then combined to calculate growing season averages for the period of stratification (mid-May to early September) for each year of record. For Diamond Lake, which exhibited constant mixing over the summer months, averages were calculated over the typical stratification period for dimictic lakes. When available, averages for three consecutive years were combined to minimize the influence of year-to-year climatic variability. To reduce the potential problem of autocorrelation in subsequent regression analyses, data points representing the same lake were each weighted by 0.5. A Wilks-Shapiro test was used to test the normality of distributions for water chemistry variables (STATISTIX 1987). Log₁₀ (log) or arc sine (arcsin) transformations were performed on water quality variables where necessary to stabilize the variance (Snedecor and Cochran 1980). Principal components were approximately normally distributed according to Wilks-Shapiro statistic and thus were not transformed before inclusion in stepwise linear regressions.

2.4 Statistical analyses

To reduce the large number of watershed characteristics to a smaller number of variables, we performed a principal components analysis (PCA) without rotation on selected watershed variables (Norusis 1988). The original watershed variables were not expressed in common units and thus had a wide range of variances (Table 2). Therefore, PCA was performed on standardized variables, *i.e.*

Table 3. Comparison of analytical methods used.

storet code	variable	agency	methods	years methods used	ref ^a
00410	Alkalinity, total	MPCA	Potentiometric endpoint, pH 4.5	1953–74	1
			Automated Colorimetric Modified	1974–1976	1
			Titration Brom Cresol Green End Point	1976–1988	1
00680	Carbon, total organic	MDNR	Colorimetric endpoint (methyl orange)		1
		MPCA	Dohrman DC-80 TOC Analyzer	1987–88	2
33211	Chlorophyll <i>a</i>	MC	Dohrman DC-50A/52A Analyzer	1980–87	2
		MPCA	Spectrophotometric	1976–88	3
31505	Coliform, fecal	MC	Spectrophotometric	1980–87	1
		MPCA	Multiple tube technique	1953–1984	1
31625	Coliform, fecal	MC	Membrane filter technique	1980–87	3
00080	Color	MPCA	Visual comparison with standards	1953–88	1
00095	Conductance, specific	MPCA	Conductivity meter	1967–88	1
00300	Dissolved oxygen	MPCA, MDNR	Winkler, mod'd Azide method	1953–88	1,
					2
00900	Hardness, total	MPCA	EDTA method	1953–72	1
		MPCA	Selective ion electrode	1972–75	4
		MPCA	Summation (Ca + Mg)	1975–88	2
00610	Nitrogen, ammonia	MPCA	Distillation, colorimetric Nesslerization	1960–79	1
		MPCA	Alkaline oxidation, diazotization (aut'd)	1979–88	5
		MC	Automated colorimetric phenate method	1980–87	2
00630	Nitrate + nitrite	MPCA	Cadmium reduction, colorimetric	1974–88	1
		MC	Hydrazine reduction, colorimetric	1980–87	2
00605	Organic N	MPCA	Acid digestion, Colorimetric Nesslerization	1960–79	1
		MPCA	TKN minus NH ₃ -N	1979–88	1
00625	Total Kjeldahl N	MPCA	(Ammonia-N + Organic-N)	1953–79	1
		MPCA	Block digest, AAII Salicylate	1979–88	1
		MC	Manual digestion, aut'd colorimetric phenate	1980–87	2
00403	pH	MPCA	Electrode	1953–88	1
70507	Orthophosphorus	MPCA	Colorimetric, Ascorbic acid	1977–88	1
00665	Total phosphorus	MPCA	Persulfate digestion, manual colorimetric	1974–79	1
			Block digester, aut'd colorimetric	1979–88	1
			Persulfate digestion, automated colorimetric	1980–87	2
00530	Total suspended solids	MPCA, MC,			
		MDNR	Gravimetric, dried at 105 C	1953–88	1
00535	Volatile susp'd solids	MPCA, MDNR	Gravimetric, ignition at 600 C	1953–77	1
		MPCA, MC,			
00076	Turbidity	MDNR	Gravimetric, ignition at 550 C	1977–88	1
		MPCA	Helige turbidimeter	1953–69	1
	Metals	MPCA, MDNR	Hach turbidimeter	1970–88	1
		MC	Low level: flameless AA spectrophotometric	1980–87	2

^aReferences: 1 = APHA (1980 and earlier editions); 2 = US EPA (1979); 3 = USEPA (1973); 4 = Orion Research (1973); 5 = Richards and Kletsch (1964).

with the correlation matrix used in place of the covariance matrix (Johnson and Wichern 1982). Because mixing ratio is an important predictor of internal nutrient regeneration and was not strongly correlated with any of the landscape principal components we used, we excluded it from subsequent

PCAs and included it as a separate independent variable in regression analyses.

Many of the variables were linearly related because they were expressed as percentages of a fixed total:

$$\% \text{ agricultural} + \% \text{ urban/residential} + \\ \% \text{ forested} + \% \text{ lakes} + \% \text{ wetlands} = 100$$

or because they represented the sum of a subset of variables:

$$\% \text{ wetlands} = \% \text{ herbaceous wetlands} + \% \text{ woody wetlands.}$$

The presence of linearly related variables will produce a singular matrix (and computer overflow errors) or an ill-conditioned matrix with associated round-off errors (Draper and Smith 1981). To resolve this problem, we chose a subset of 27 watershed variables to eliminate redundant combinations and gave preference to variables of known importance to water quality (Table 2). For example, when summary variables (*e.g.*, % wetlands) were included, we eliminated one or more components of that summary variable (*e.g.*, % herbaceous temporarily-flooded wetlands).

If the water quality data matrix had been complete with no missing values, it would have been appropriate to apply canonical correlation analysis to the whole data set to identify relationships between multivariate landscape components and multivariate water quality components. Instead, because selected water quality data were missing for some site-years, a second PCA was performed on a smaller complete matrix that included eight water quality variables (dissolved oxygen, Secchi depth, log total phosphorus, log total nitrogen, log organic nitrogen, log chlorophyll *a*, log (nitrate + nitrite), log ammonium) and 28 site-years. The water-quality principal components were used as dependent variables in subsequent regressions. However, regressions also were performed using the original water quality variables because a greater number of cases were available for analysis.

To relate watershed variables with water quality variables, we performed stepwise multiple regression analyses with principal components 1 to 6 and lake mixing ratio (MIXRATIO) as the independent variables and a water quality parameter or water quality principal component as the dependent variable (Norusis 1988). Principal components are appropriate variables to use in multiple regression because they are uncorrelated so that problems of

multicollinearity of independent variables are reduced (Tatsuoka 1971). Thus, estimates of regression coefficients do not depend on the order in which independent variables are included in regression analyses.

Independent variables were selected for inclusion in regression equations based on the magnitude of partial correlations with the dependent variable. Selected variables were then included ($p < .05$) or rejected ($p > .10$) on the basis of F-tests (Norusis 1988). To reduce the probability that regression results are spurious, we restricted the final number of variables included in equations at the *end* of stepwise variable selection so as to produce a case:parameter ratio of 5:1 or greater. Regression results were checked for the presence of influential outliers using Cook's distance (Norusis 1988). Finally, the influence of each original watershed variable that was highly correlated ($p < .01$) with principal components included in regression equations was tested through an analysis of partial correlations (Norusis 1988). Landscape variables were transformed to approximate normal distributions before performing partial correlation analyses.

3. Results

3.1. Watershed, lake and wetland characteristics

Our study watersheds contained slightly more wetlands and less developed land (average: 39% agricultural, 19% urban, 14% wetland, 12% forest) than the Twin Cities metropolitan area as a whole, *i.e.*, 27% urban land, 8% wetlands (Oberts and Jouseau 1979). Spring Lake watershed had the most agricultural area (71% agriculture) and Crystal Lake watershed was most highly developed (*e.g.* 83% urban/residential), while Chub Lake (36% forest) and Golden Lake watersheds (41% wetlands) were the least developed watersheds. Total watershed area ranged from 2 to 50 km², with an average of 17 km² (Table 2). Because lakes had been selected in a stratified fashion to cover the range of lake sizes found in the Twin Cities metropolitan area, lakes in our subsample were larger on average (0.2–15.0 km²) than Twin Cities metropolitan area

Table 4. Variance explained by first eight principal components of landscape or lake morphometry variables for 33 lake watersheds in Minneapolis-St. Paul metropolitan area (n = 38 site-year observations).

principal component	eigen-value	percent variance explained	cumulative percent variance
1 Wetlands/watershed area	7.0	26	26
2 Agriculture/wetlands	4.0	15	41
3 Agriculture/urban-residential	3.7	14	54
4 Herbaceous wetland type	2.4	9	63
5 Forest/soils	2.0	7	70
6 Dilution ratio	1.6	6	76
7 Other lakes	1.3	5	81
8 Watershed relief	1.1	4	85

lakes as a whole (Metropolitan Council 1981). Thus, 6% of our 33 lakes are less than 0.25 km² in size, as compared to 71% of Twin Cities metropolitan area lakes.

Half of the lakes we selected (16 of 33 lakes) had a mixing ratio between 3 and 9, and, hence they are lakes transitional between summer polymictic and dimictic lakes (Osgood 1988). Mixing ratios for the remaining lakes were less than 3, which according to Osgood's criteria were polymictic. However, when temperature profiles were checked for each lake, only one lake (Diamond Lake) exhibited frequent mixing.

Wetlands constituted between 0 and 41% of the 33 watersheds studied. The majority of wetlands (63%) were herbaceous, with woody wetlands and open water wetlands constituting 25% and 12% of total wetland area, respectively. The predominant wetland water regime was seasonally-flooded/saturated (66% of total wetland area), followed by semi-permanently and permanently flooded. Temporarily-flooded wetlands constituted a negligible proportion of the total (<1%).

3.2. Principal components analysis of watershed variables

To reduce the number of variables considered, we extracted only the first eight principal components which had eigenvalues greater than 1.0. These eight principal components (PCs) explained 85% of the

variance of the 27 original landscape variables (Table 4). The first six of these PCs, explaining 76.3% of the variance, were used in subsequent regression analyses. PC7 and PC8, which explained only a small fraction (9%) of the variance, were omitted to maximize the case:variable ratio.

Three of the first eight PCs (PC1, PC2, and PC4) were strongly related to wetland variables (Table 5). The first principal component (PC1) was correlated with 18 of the 27 landscape variables ($p < .05$), but was most strongly correlated with variables associated with wetland size and extent, and to a lesser extent with total and contributing watershed area. The second PC represented the contrast between wetland extent and agricultural land-use. The graph of watershed locations in principal component space defined by PC1 and PC2 (Fig. 2) demonstrates the tendency of the larger watersheds with high PC1 values (*e.g.* Parley, Cynthia, Spring, and Coon) to have a wider variation in agricultural land-use relative to wetland extent (AGR = 19–71%, WTLD = 6–38%), as compared to the smaller watersheds at the left end of the PC1 axis (*e.g.* Zumbra, Crystal, and Lotus Lakes) which show little variation (AGR = 3–35%, WTLD = 0–2.3%).

PC4 represented the dominance of herbaceous semi-permanently-flooded versus herbaceous seasonally-flooded/saturated wetlands (*e.g.* wet meadows) in different watersheds. Watersheds with a high positive value for PC4 had predominantly herbaceous semi-permanently flooded wetlands

Table 5. Significant correlations ($p < .05$, $p < .01$) between 27 landscape or lake morphometry variables and 8 principal components (pc) for 33 lake watersheds in Minneapolis-St. Paul metropolitan area. Fringe areas defined as 200 m width band surrounding lake or stream. (n = 38 site-year observations).

	pc1 ^a	pc2 ^b	pc3 ^c	pc4 ^d	pc5 ^e	pc6 ^f	pc7 ^g	pc8 ^h
Watershed area	0.72	0.34	-0.36					
Contributing watershed area	0.75	0.39	-0.32					
Dilution ratio	-0.37					-0.71		
Average wetland size	0.86							
Stream wetland size	0.83							
Wetland distance upstream	0.83	0.37		-0.32				
% Wetland	0.75	-0.54						
% Wetland lake fringe	0.32	-0.39	0.55	0.53				
% Herbaceous semi-permanent wetlands	0.61			0.60				
% Herb. semi-perm. wtd lake fringe	0.33		0.44	0.70				
% Herb. seasonally-flooded/saturated wtds	0.47	-0.56		-0.51				
% Herb. seas-fl/sat'd wetland lake fringe		-0.46	0.53				0.36	0.40
% Woody seas-fl/sat'd wetlands	0.58	-0.54						
% Woody seas-fl/sat'd wetland lake fringe	0.34	-0.50				0.37		
% Agricultural	0.42	0.53	0.57					
% Agricultural lake fringe		0.62					-0.43	
% Forested	-0.33		0.50		0.68			
% Forested lake fringe			0.52		0.52	0.32		-0.36
% Urban/residential	-0.43		-0.72					
Average slope	-0.53		0.40		0.37			
Average elevation difference		0.73				0.32		0.47
K-factor		0.39	0.59		-0.33			
Soil phosphorus	-0.42		0.32		-0.46			
Soil pH				0.51	0.60			
# Lakes upstream	0.56	0.40				0.32	0.42	
% Other lakes	0.41	0.54					0.44	-0.32
% Stream fringe area	0.51		0.37	-0.54				

^aWetlands/watershed area; ^bAgriculture/wetlands; ^cAgriculture/urban-residential; ^dHerbaceous wetland type; ^eForest/soils; ^fDilution ratio; ^gOther lakes; ^hWatershed relief.

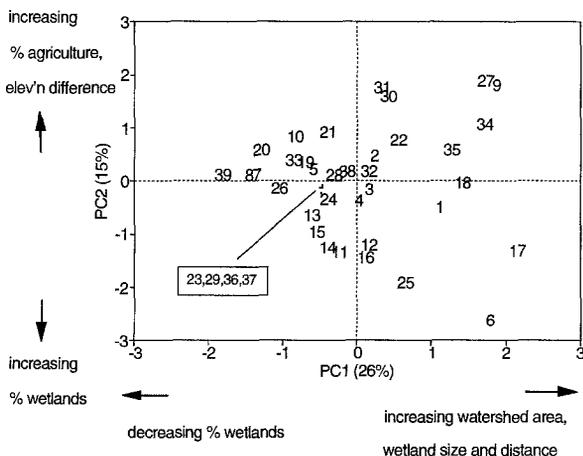


Fig. 2. Thirty-three lake watersheds (38 site-years) selected from

(i.e., cattail marshes). Eagle and Orchard Lakes, for example, had 6.1 and 6.0% coverage, respectively. In contrast Golden Lake, with a low PC4 score, had marshes covering only 1.0% of the watershed, and 18.8% coverage of herbaceous seasonally-flooded/saturated wetlands.

Two of the remaining PCs (PC3 and PC5) were related to land-use categories. PC3 represented the contrast between agricultural (+) and urban (-)

← within the Minneapolis-St. Paul metropolitan area graphed in landscape principal component space, PC1 (wetlands/watershed area) versus PC2 (agricultural/wetlands). See Table 1 for explanation of codes.

Table 6. Average, standard error, minimum, and maximum epilimnetic values of chemical and physical parameters for 38 lake water-quality observations within the Twin Cities metropolitan area, MN.

variable	abbrev	units	n	avg	std err	min	max
Total phosphorus	TP	mg P/L	38	0.08	0.017	0.01	0.60
Dissolved phosphorus	DP	mg P/L	25	0.04	0.014	0.01	0.36
Total nitrogen	TN	mg N/L	33	1.7	0.20	0.6	7.2
Organic nitrogen	ON	mg N/L	31	1.5	0.21	0.2	6.8
Nitrates + nitrites	NOx	mg N/L	34	0.06	0.012	0.01	0.33
Ammonium (NH ₄ -N)	NH ₄	mg N/L	32	0.14	0.022	0.02	0.47
Un-ionized ammonia	NH ₃	mg N/L	15	0.015	0.0025	0.006	0.031
Secchi depth	SECCHI	m	35	1.59	0.129	0.20	3.29
Chlorophyll a	CHLA	µg/L	30	49	12.5	6	309
Chl. a, corr'd	CHLACORR	µg/L	8	17	4.7	1	47
Color	COLOR	Pt-Co units	12	21	4.2	6	63
Turbidity	TURB	Hach FTU	8	3.7	0.64	1.1	5.8
Total suspended solids	TSS	mg/L	21	14	3.1	1	70
Volatile suspended solids	VSS	mg/L	20	12	3.0	1	66
Dissolved oxygen	DO	mg/L	34	8.6	0.25	4.2	11.5
Total hardness	HARD	mg/L CaCO ₂	20	134	8.4	68	234
Total alkalinity	TALK	mg/L CaCO ₂	33	118	4.3	71	162
Lab pH	PH	log [H ⁺]	33	8.3	0.15	4.7	9.5
Conductance at 25°C	COND	µMHO/cm	32	304	12.5	153	446
Chloride	CL	mg/L	24	32	6.2	4	144
Fecal coliform	FCOL	Colonies/100 mL	23	4	0.8	1	16
Arsenic	AS	µg/L	18	7.7	0.79	2.0	14.0
Total lead	PB	µg/L	18	2.4	0.23	0.8	4.7
Cadmium	CD	µg/L	19	0.26	0.03	0.04	0.62
Total mercury	HG	µg/L	18	0.17	0.018	0.05	0.30
Zinc	ZN	µg/L	19	10.9	1.3	1.0	24.0
DERIVED PARAMETERS							
Volatile/total SS	VSS/TSS	–	20	0.80	0.041	0.40	1.00
TN:TP	TNTP	–	33	27.5	1.79	6.4	46.1
Dissolved/total P	DP/TP	–	25	0.46	0.032	0.17	0.76
Organic N/Total N	ON/TN	–	31	0.83	0.028	0.24	0.98
NH ₄ -N/Total N	NH ₄ /TN	–	31	0.11	0.024	0.01	0.70
NO _x -N/Total N	NO _x /TN	–	33	0.04	0.08	0.01	0.19

land-use, but also was strongly correlated with soil erodibility. Watersheds with high PC3 values (Forest Lake 1957, Dutch Lake) were relatively undeveloped (AGR = 29–47%, FOR = 15–30%), while Crystal Lake (1966, 1980) with the lowest PC3 score had the highest percent urban/residential coverage (83%) of all watersheds. PC5 was positively related to forested area, forested lake fringe, and soil pH, and was weakly inversely related to surface soil phosphorus. Chub Lake, with 36% forested land, was distinct from the other watersheds with a high PC5 score.

The strong negative association between PC6 and

the dilution ratio, with only weak correlations with other landscape variables reflects the independence of lake morphometry from watershed characteristics. Chub and Bryant Lakes, with the highest values of PC6, have small to intermediate-size watersheds (6–12 km²) and are relatively small (0.8–10.0 km²) lakes. Waconia Lake, with the lowest value for PC6 has a large watershed (42 km²), and is the largest lake in our study (140 km²).

In the following discussion, the first six PCs will be referred to as the wetlands/watershed area PC (PC1), the agriculture/wetlands PC (PC2), the agriculture/urban PC (PC3), the herbaceous wet-

Table 7. Significant correlations between lake water quality variables and water-quality principal components (WQPC) for 28 Minneapolis/St. Paul metropolitan area sites represented in reduced data matrix ($p < 0.05$, $p < 0.01$).

variable	wqpc1 ^a	wqpc2 ^b	wqpc3 ^c
Dissolved oxygen	0.60		-0.36
Secchi depth	-0.87		
Log total phosphorus	0.90		
Log ammonium-N		0.93	
Log total nitrogen	0.96		
Log organic nitrogen	0.87	-0.35	
Log chlorophyll <i>a</i>	0.93		
Log (NO ₃ + NO ₂)		0.35	0.86

^aTrophic state component; ^bAmmonium component; ^cNitrate component.

land class PC (PC4), the forest/soils PC (PC5), and the dilution ratio PC (PC6) (Table 4).

3.3. Lake water quality

Study lakes in the Twin Cities metropolitan area (Table 6) fall within the classification of Group III lakes (specific conductance 141–501 $\mu\text{mhos}\cdot\text{cm}^{-1}$), which occur on calcareous substrates throughout most of Minnesota and are characterized by the deposition of marl to the sediments at conductance $> 190 \mu\text{mhos}\cdot\text{cm}^{-1}$ (Gorham *et al.* 1983). Our study lakes are typical of Twin Cities metropolitan area lakes, the majority of which are hardwater, alkaline (80–180 $\text{mg CaCO}_2\cdot\text{L}^{-1}$), and eutrophic ($> 10 \mu\text{g chl } a\cdot\text{L}^{-1}$, $< 1.5 \text{ m}$ Secchi depth, $> 30 \mu\text{g total P}\cdot\text{L}^{-1}$; Oberts 1981). Ratios of total N:total P suggest that most of the study lakes are phosphorus-limited; only 3 lakes (Cynthia, Golden, and Spring Lakes) have total N:total P levels less than 12, the boundary between N and P limitation (Dillon and Rigler 1974). Chloride levels were higher (4–144 $\text{mg}\cdot\text{L}^{-1}$) than is typical of Group III lakes (0.7–1.8 $\text{mg}\cdot\text{L}^{-1}$), suggesting the presence of contamination from road salt. Of the heavy metals measured, only zinc levels (1–24 $\mu\text{g}\cdot\text{L}^{-1}$) were well below the maximum allowable (270–520 $\mu\text{g}\cdot\text{L}^{-1}$) and short-term (47 $\mu\text{g}\cdot\text{L}^{-1}$) guidelines for protecting freshwater aquatic life (EPA 1980).

3.4. Principal components analysis of water quality

Principal components analysis of the reduced water quality matrix for 28 of the original 39 site-years identified three principal components which explained 84.1% of the variance. The first water quality principal component (WQPC1) was related to lake trophic state and was highly correlated positively with total P, total and organic N, and chlorophyll *a*, and negatively associated with Secchi depth ($p < .05$; Table 7). Diamond and Cynthia Lakes, with high positive WQPC1 values, were highly eutrophic (0.36–0.60 $\text{mg}\cdot\text{L}^{-1}$ total P, 4.0–7.2 $\text{mg}\cdot\text{L}^{-1}$ total N, 280–309 $\mu\text{g chl } a\cdot\text{L}^{-1}$, 0.2–0.4 m Secchi depth), as compared to White Bear Lake (1980, 1987) with a low value of WQPC1 (0.02 $\text{mg}\cdot\text{L}^{-1}$ total P, 0.64–0.68 $\text{mg}\cdot\text{L}^{-1}$ total N, 7–11 $\mu\text{g chl } a\cdot\text{L}^{-1}$, 3.1–3.2 m Secchi depth). The second PC (WQPC2) was significantly correlated with log NH₄, while WQPC3 was significantly correlated with log (NO₃ + NO₂) (Table 7). In the following text, WQPC1 will be referred to as lake trophic state.

3.5. Multiple regression and partial correlation analyses

Multiple regression analysis demonstrated that trophic state variables were correlated with watershed-scale (PC1), land-use (PC2, PC5), and wetland (PC4) components (Table 8). Positive correlations between trophic state and PC1 or PC2

Table 8. Results of multiple regressions with growing season epilimnetic water quality averages as dependent variables and landscape principal components plus mixing ratio as independent variables. Dependent variable abbreviations and units defined in Table 6. Trophic state variables were correlated with watershed-scale (PC1), land-use (PC2, PC5) and wetland (PC4) components.

dependent variable	adjusted		F-stat	regression constant	regression coefficients associated with independent variables***						
	n	r ²			pc1	pc2	pc3	pc4	pc5	pc6	mixratio
log ₁₀ total P	33	0.28	5.2**	-1.24	0.13	0.12		-0.12			
log ₁₀ total N	29	0.30	7.0**	0.17		0.07			-0.12		
log ₁₀ organic N	28	0.36	8.7**	0.08		0.11			-0.16		
arcsin (ON/TN)	28	0.25	5.4*	1.03		0.09			-0.10		
log ₁₀ (NO ₃ + NO ₂)	30	0.15	5.8*	-1.6							0.06
log ₁₀ (NO _x /TN)	31	0.14	6.0*	-1.8							0.07
log ₁₀ NH ₄ -N	13	0.39	8.7*	-1.97	0.14						
log ₁₀ NH ₄ -N/TN	28	0.40	10.0**	-1.14		-0.15			0.24		
total N:total P	29	0.28	6.5**	28	-5			3			
log ₁₀ chl. <i>a</i>	28	0.24	9.6**	1.48		0.20					
Secchi depth	32	0.23	5.7**	1.5		-0.3		0.3			
color	11	0.76	16.5**	20	8			-7			
log ₁₀ turbidity	8	0.48	7.5*	0.37						0.31	
log ₁₀ total SS	21	0.59	8.2**	1.4		0.13	0.24		-0.18		-0.15
log ₁₀ volatile SS	20	0.24	6.9*	0.89					-0.17		
log ₁₀ chloride	22	0.31	5.9**	1.41		0.14			-0.14		
log ₁₀ total lead	18	0.35	5.7*	0.35		0.11			-0.07		
zinc	19	0.29	8.4**	11			4				
WQPC1	28	0.49	9.8**	-0.2	0.3	0.4			-0.6		
WQPC3	28	0.23	9.3**	-0.9							0.25

* p < .05

** p < .01

*** PC1 = Wetlands/watershed area PC; PC2 = Agriculture/wetlands PC; PC3 = Agriculture/urban-residential PC; PC4 = Herbaceous wetland type; PC5 = Forest/soils PC; PC6 = Dilution ratio PC.

and the negative correlation between trophic state and PC5 were explained by the influence of agricultural or forested land-use, topography, and wetland position within the watershed. Lake trophic state was negatively correlated with forested land-use with other PC5-related variables held constant (Table 9). Trophic state was positively correlated with agricultural lake-fringe and maximum elevation difference when the number of lakes upstream and wetland extent were held constant. Lake trophic state also was positively correlated with wetland distance upstream with other factors influencing PC1 held constant (Table 9). Conversely, lakes with proximal wetlands, *i.e.* relatively close upstream, had a lower trophic state.

The relationship between lake total or organic N and PC2 also was explained by the influence of

agricultural land-use. The partial correlation between agricultural lake fringe and organic or total nitrogen was significant with other PC2-related variables held constant (Table 9). Total and organic nitrogen were both negatively correlated with the forest/soils component (PC5) but the effect of original variables related to PC5 could not be separated through partial correlation analysis. Elevation difference was significantly correlated with total phosphorus or chlorophyll *a* with other PC2-related variables held constant.

Our evidence for the effect of agriculture on lake trophic state in the Twin Cities metropolitan area is based strictly on significant correlations, and thus is subject to errors in our interpretation of cause/effect relationships. It is possible, for example, that agricultural zones remaining in the face of strong

Table 9. Partial correlations (rp) between lake water-quality variables and original watershed variables for 33 lake watersheds in Minneapolis-St. Paul metropolitan area (n = 38 site-year observations).

independent variables			
water-quality	watershed	partial correlation, r_p	original watershed variables held constant for partial correlation
WQPC1 (trophic state)	FOR	-0.43*	SOILP, SOILPH
WQPC1 (trophic state)	AGLKFR	0.49**	OLAKES, WTLND
WQPC1 (trophic state)	ELEVDIFF	0.47*	OLAKES, WTLND
WQPC1 (trophic state)	WTLDDIST	0.41*	WTLND, CAREA, AVWTLDSZ
Total nitrogen	AGLKFR	0.39*	OLAKES, WTLND, ELEVDIFF
Organic nitrogen	AGLKFR	0.45*	OLAKES, WTLND, ELEVDIFF
Total phosphorus	ELEVDIFF	0.36*	OLAKES, AGLKFR
Chlorophyll <i>a</i>	ELEVDIFF	0.50*	OLAKES, AGLKFR
Color	WTLND	0.80**	CAREA, WTLDDIST, AVWTLDSZ
Color	STRFRG	0.81**	HBSPLKFR, HRBSP
Secchi depth	STRFRG	0.50**	HBSPLKFR, HRBSP
Total suspended solids	OLAKES	-0.52*	AGLKFR, WTLND, ELEVDIFF
\log_{10} total lead	WTLD	-0.60*	ELEVDIFF, OLAKES, AGLKFR
\log_{10} total lead	FOR	-0.52*	SOILP, SOILPH

* $p < 0.05$, ** $p < 0.01$

developmental pressures are located on the most fertile land, and that lakes in these areas have a naturally high trophic state. We tested this hypothesis through partial correlation analysis. Agricultural lake-fringe area (Log AGRKFR) was significantly correlated with lake trophic state when available soil phosphorus was held constant ($p < .01$), but there was no significant effect of soil phosphorus on trophic state when agricultural lake fringe area was held constant ($p > .05$; Table 9).

Lake transparency was associated both with wetland/watershed area (PC1) and herbaceous wetland type (PC4) components. Color was positively correlated with wetland extent with other PC1-related variables held constant. Landscapes dominated by wet meadow or herbaceous seasonally-flooded wetland, and with extensive stream-fringe areas (high PC4) contributed more to lake color (and reduced Secchi depth) than did those dominated by cattail marshes. Percent stream-fringe was positively correlated with color and negatively correlated with Secchi depth with other PC4-related variables held constant (Table 9).

Chloride levels were influenced primarily by land-use components. Lakes within landscapes with a high proportion of agriculture relative to

wetlands (high PC2) or with sparse forest coverage (low PC5) had higher Cl levels.

Independent variables related to internal (mixing ratio) or external (dilution ratio) loading were significantly correlated with turbidity, total suspended solids, and nitrate. Lakes with low dilution ratios (high PC6) had high turbidity. Those lakes with a tendency for stable stratification periods (high mixing ratio) had high nitrate levels but low suspended solids. In addition, the number of other lakes upstream was negatively correlated with total suspended solids with other PC2-related variables held constant (Table 9).

Of the metals considered, only zinc or lead levels could be explained as a function of landscape components. Lakes in watersheds that were highly agricultural with little urban development (high PC3 values) had higher levels of zinc. However, zinc was significantly correlated with soil K-factor ($r = 0.47$; $p < .05$) and not with % urban or % agricultural land-use. Lakes within agricultural watersheds with sparse wetland coverage (high PC2) or low forest coverage (low PC5) had higher lead levels. The negative partial correlation between log total lead and wetland extent was significant when additional PC2-related variables were held

constant. Likewise, the negative partial correlation between total lead and forested land was significant (Table 9).

4. Discussion

4.1. Effect of landscape components on trophic state

The existence of three different land-use related principal components (PC2, PC3, and PC5) allowed us to examine the unique influence of agricultural land versus wetlands (PC2), agricultural land versus urban/residential land (PC3), and forest/soils interactions (PC5) on lake trophic state. Lakes within moderately forested watersheds (high PC5 values) had relatively low total or organic nitrogen and suspended solids concentrations, consistent with the role of riparian buffers in trapping sediment and reducing nitrate concentrations (Peterjohn and Correll 1984; Cooper *et al.* 1986; Whigham and Chitterling 1988). Our results also suggest that variation in trophic state among Twin Cities metropolitan area lakes is related to agricultural land-use, especially within landscapes with a high potential for erosion and rapid run-off (higher elevation difference), and that trophic state is lower in watersheds with a high coverage of forested land, or with wetlands concentrated in the lower portion of the watershed.

Paleoecological records provide additional evidence for the impact that land clearing and cultivation have had on the nutrient status of Twin Cities metropolitan area lakes. Diatom profiles indicate that Lake Minnetonka was oligotrophic prior to European settlement (Bradbury 1975). The period of land clearing in the late 1980's corresponded with an increase in phosphorus accumulation, blue-green algal pigments, and carbonate content of sediments as productivity increased (Engstrom and Swain 1986). Similarly, an increase in lake productivity, as evidenced by increased rates of phosphorus and CaCO_3 accumulation, coincided with the establishment of farming and commercial gardening on the south side of Twin Lake (Allott 1978).

Our results suggest that lake water quality is

higher (lower WQPC1) when wetlands are concentrated near the lake of interest (low WTLLDIST). These results are consistent with our earlier work showing that proximal wetlands were related to improved stream water quality (low inorganic suspended solids, nitrate, flow-weighted ammonium, flow-weighted total phosphorus, and dissolved P:total P ratios) in the Twin Cities metropolitan area (Johnston *et al.* 1990).

Our results potentially conflict with the views of Prentki *et al.* (1978), who suggest that lake-fringe wetlands (dominated by *Typha* spp.) are net exporters of nutrients, through net upward translocation of N and P from the sediments and the subsequent release of nutrients during litter decomposition. However, long-term studies of nutrient dynamics during litter decomposition have shown that an initial period of leaching is followed by a period of nutrient (N, P, Ca) immobilization by microbial communities on the leaf-litter surface (van der Valk *et al.* 1978; Davis and van der Valk 1978). Nutrient immobilization during litter decomposition is especially pronounced in litter from fibrous plants (*Typha*, *Scirpus*) with high C:N ratios and slow decomposition rates (half-life of 1–2 years), as compared to that of plants with softer tissue (reviewed by Davis and van der Valk 1978). Thus, there may be a net storage of nutrients within wetlands over the period of years in spite of periodic releases during periods of senescence.

Our data suggest that, at the landscape level, wet meadows and herbaceous seasonally-flooded wetlands remove less total P and reduce lake transparency to a greater extent than do marshes, although they do not contribute more to overall lake trophic state (WQPC1). The efficiency of wetlands in trapping phosphorus depends both on the predominant form of phosphorus in inputs and on the retention time of individual wetlands. Much of the phosphorus in agricultural and urban runoff is associated with fine particulates (Ahern *et al.* 1980). Retention of these fine particulates, which have low settling velocities, should be a function of water retention time within wetlands (Adamus and Stockwell 1983). Thus, semi-permanent wetlands, with a longer retention time, should have the ability to trap a greater fraction of particulate-associated

P than do seasonally-flooded/saturated wetlands. Brown (1985) compared nutrient budgets among four different Twin Cities metropolitan area wetlands, and determined that the one impounded wetland had the greatest removal efficiency for suspended solids, total P, and organic N. In addition, many of the streams in the Twin Cities metropolitan area have been channelized, thus reducing the degree of contact between water and stream-fringe wetlands and reducing the efficiency of stream-side wetlands in trapping suspended sediments and associated pollutants (Johnston *et al.* 1990).

Lake transparency (Secchi depth) was positively associated with the herbaceous wetlands component (PC4) as well as with PC2 (agriculture/wetlands). The association of seasonally-flooded/saturated herbaceous wetlands with low lake transparency and high color helps to explain why these wetlands are associated with higher lake total P levels, but not with a higher trophic state index. The release of organic acids could counteract the effect of higher P loading by limiting lake transparency and thus algal biomass. Among the lakes studied, the relationship between log Secchi depth and log color was significant ($r = -0.66$, $p < .05$), and the range of lake color observed (6–63 PCU) corresponded to a range of >2 meters in Secchi depth. Beaver and Crisman (1991) found that empirical equations predicting primary productivity of Florida lakes were improved by first separating clear-water lakes from colored lakes in the analysis. Annual areal gross production responded more to a given level of total phosphorus in clear lakes than in colored lakes (Beaver and Crisman 1991).

Levels of nitrate + nitrite and the fraction of nitrogen present as nitrate plus nitrite ($\log(\text{NO}_3 + \text{NO}_2)/\text{total N}$) were related only to the mixing ratio of lakes, but not to land-use components. The epilimnion of lakes with more stable stratification periods would have little input of ammonium from the hypolimnion, and ammonium present from external loadings would be readily nitrified under the aerobic conditions in these surface waters (Wetzel 1983).

4.2. Suspended solids

The total suspended solids concentrations in Twin Cities metropolitan area lakes was influenced by both internal (lake mixing ratio) and external (PC2, agricultural/urban PC3, forest/soils PC5) variables. The negative relationship between log (total suspended solids) and lake mixing ratio probably is the result of the resuspension of sediments during mixing events, which are less frequent in lakes with a high mixing ratio value (Osgood 1988). Highly erodible agricultural lands (high PC3) can contribute large sediment loadings to surface waters, whereas urban/residential lands contain more impervious surfaces and in the absence of construction activity contribute mainly fine particulates to surface waters (Novotny and Chesters 1981). The correlation between PC2 and total suspended solids probably was related to the ability of upstream lakes to act as settling basins.

Both total and volatile suspended solids were negatively related to PC5. Forested riparian zones can act as filters for sediment from agricultural runoff, retaining as much as 88% of sediment inputs from adjacent fields (Gilliam *et al.* 1986). Forested areas, in general, export less suspended solids than do agricultural or urban areas (Omernik 1976).

4.3. Major ions

Chloride was positively related to PC2. A similar relationship was demonstrated in our earlier study of the cumulative effect of wetlands on stream water quality (Johnston *et al.* 1990). The reduction in chloride in watersheds with more wetlands relative to agricultural land is probably the result of dilution by groundwater inputs, as well as the higher loading of fertilizer-derived Cl from agricultural lands (Prochazkova *et al.* 1983). Alternatively, Cl has been found to be retained within an Ontario bog (Bayley *et al.* 1987), and could be retained by Twin Cities metropolitan area wetlands as well, although it is generally considered to be a conservative element.

4.4. Metals

Lead as a nonpoint source pollutant is associated with areas of high traffic. The level of lead in Twin Cities metropolitan area lakes was related more to watershed sinks than sources, however. A similar negative relationship was found between lead and wetland extent in our previous study of stream watersheds (Johnston *et al.* 1989). The negative relationship between total lead and wetland extent probably is related to the ability of wetlands to retain up to 100% of particulate Pb inputs (Giblin 1985). Unlike many other metals, Pb is relatively immobile in wetland environments (Giblin 1985).

4.5. Color

Seventy-six percent of the variation in epilimnetic color was explained as a function of the wetlands/watershed area and herbaceous wetland type components. Lake color increased as the extent of wetlands (PC1) increased, and as the extent of herbaceous seasonally-flooded/saturated wetlands increased (PC4). Individual wetlands export soluble organic carbon (Kowalczewski 1978), in particular humic acids (McKnight *et al.* 1985).

Lake color has been related to the ratio of muskeg area to lake surface area in Nova Scotia lakes (Gorham *et al.* 1986). To our knowledge, the capacity of herbaceous seasonally-flooded/saturated wetlands to export more highly colored waters than do marshes has not been reported before. Typical marsh vegetation in herbaceous semi-permanent wetlands of the Twin Cities metropolitan area (*Typha* spp., *Phragmites* spp.) has a slow rate of litterfall (<5 to 23% of aboveground production; Mason and Bryant 1975; Gustafson 1976) and a slow decay rate (half-life of 1–2 years). In contrast, wetland vegetation with less supportive tissue, such as the sedges and grasses found in seasonally-flooded/saturated wetlands can be expected to have a higher rate of litterfall and decay rate (van der Valk *et al.* 1978). For example, *Carex aquatilis* litterfall is equal to 100% of net aboveground production and occurs continuously throughout the growing season (Bernard and

Gorham 1978). In addition, the longer period of standing water in marshes would expose internally-generated dissolved organic carbon to photolytic degradation for a longer period than in seasonally-flooded wetlands.

4.6. Success and limitations of the landscape-based multivariate approach

We were able to explain a statistically significant proportion of the variability in water quality of Twin Cities metropolitan area lakes for 13 variables and 4 derived variables as a function of six landscape components and the lake mixing regime. However, our ability to predict lake water quality (average $r^2 = 0.34$, $r^2 = 0.14$ – 0.76) was lower than our ability to predict summer stream water quality in the same region (average $r^2 = 0.74$, range = 0.17 – 0.88) using a similar approach (Johnston *et al.* 1990).

Because of the low flow rates and long water retention time for lakes as compared to streams, lake water quality is affected more by internal processes such as sedimentation, sediment resuspension, and nutrient transformations including regeneration from the sediments, and less by exchanges across the land/water interface than is stream water quality. This disparity increases as lakes become more eutrophic and anoxic sediments release increasing amounts of phosphorus. Thus, water quality reflects the history of nutrient loading to a lake as well as current land-use practices.

Empirical models to predict in-lake phosphorus concentrations have included not only a term for external loading, but also terms representing sedimentation and flushing rate (Vollenweider 1968). In lakes with similar morphology and small relatively homogeneous watersheds, the loading term predominates in this relationship. For example, Schindler (1971) was able to predict chlorophyll *a*, total P, and color of lakes in the Experimental Lakes Area simply as a function of volumetric loading: watershed area/lake volume. Similarly, total P loadings and in-lake concentrations have been successfully predicted as a function of the percentage of watershed developed for small

urban Twin Cities metropolitan area lakes (Ayers *et al.* 1980; Walker 1987).

In analyzing data from a range of oligotrophic to eutrophic lakes across North America, Canfield and Bachmann (1981) discovered that the sedimentation coefficient was itself a function of external loading rates. Our empirical models were constrained to those expressing additive linear effects of the principal components on (transformed) water quality variables. Thus we did not consider the possible interaction between external loading and lake morphometry in accelerating the process of lake eutrophication. In contrast, Canfield and Bachmann's model incorporates the decreasing efficiency of net phosphorus sedimentation with increased loading, as modified by lake morphometry.

The prediction of total P and chlorophyll *a* concentrations can be further confounded by the influence of trophic interactions (Carpenter *et al.* 1985). For example, Osgood (1988) noted that Twin Cities metropolitan area lakes containing flake-forming blue-green algae (*Aphanizomenon* spp.) had higher levels of total phosphorus than expected and suggested that these algae transport phosphorus to the epilimnion from the sediments. Wright and Shapiro (1984) have documented the role of large-bodied zooplankton in reducing epilimnetic P by transporting phosphorus downwards during vertical diel migrations. Within developing landscapes, lake trophic structure is often intentionally manipulated by rotenone treatment and/or fish stocking (Wright and Shapiro 1984). Prediction of lake water quality from watershed characteristics in these settings might be improved by first stratifying lakes according to a trophic structure classification (*e.g.* Paloheimo and Zimmerman 1983; Zimmerman *et al.* 1983).

Our multivariate landscape approach has proven to be a rapid, cost-effective means of exploring empirical relationships between lake water quality and watershed characteristics. We were able to explain up to 76% of the variation in individual water quality variables among the 33 lakes studied as a function of landscape components. We were also able to explain 49% of the variation in a derived trophic state index (WQPC1), even though most of the lakes examined were already highly eutrophic, and

thus were influenced by internal loading. Unlike the empirical (nonlinear) modelling approach described above, our technique has the advantage that it does not require extensive data on external loadings to lakes. Finally, by allowing us to reduce a multitude of landscape variables into a few independent principal components, this methodology has allowed us to evaluate how the extent and placement of wetlands and other landscape features affects lake water quality.

4.7. Implications for watershed management to protect lake water quality

Both the extent and position of wetlands in the landscape mosaic must be considered in developing watershed management plans to protect lake water quality. Within the Twin Cities metropolitan area, the proportion of lake fringe area in agriculture was significantly correlated with lake trophic status, particularly total and organic nitrogen levels. Conversely, urban lake fringe was not a good predictor of lake water-quality, possible because nonpoint source pollutants are routed into lakes through stormwater systems, circumventing the opportunity for riparian treatment of nonpoint source runoff. In both urban and rural landscapes, wetland extent can counteract the nonpoint source loadings of nitrogen, phosphorus, sediment, and lead and thus help to maintain lake ecosystem health.

The negative relationship between total lead and wetland extent in the watershed suggests that wetlands play a significant role in trapping and immobilizing particulate lead in urban runoff. In the Twin Cities metropolitan area, lakes in watersheds with less than 18% wetland area are predicted to have levels of lead exceeding the EPA criteria denoting short-term toxicity to freshwater aquatic life (Detenbeck *et al.* 1991). Wetlands should not be considered as permanent sustainable sinks for heavy metals such as lead in urban runoff, however, as little is known concerning the long-term potential for bioaccumulation by wetland biota (*e.g.* Horner 1988; Stockdale 1991).

Wetlands should be preserved throughout the

watershed, but when nonpoint source loading to a lake within the watershed is a problem, restored or created wetlands could be sited strategically in the lower reaches of a watershed close to the lake of interest. Natural wetlands situated closest to surface waters should receive special protection. Replacement of drained or filled wetlands in areas away from surface waters in the watershed will not achieve the same reduction in nonpoint source loadings to a lake. Although our results suggest that seasonally-flooded streamside wetlands or wet meadows are less effective than cattail marshes in reducing total phosphorus loadings to downstream lakes, these wetlands contribute to lake color, and thus may moderate the response of downstream lakes to a given level of loading by limiting transparency.

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Hydrologic Regimes Revealed Bundles and Tradeoffs Among Six Wetland Services

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ABSTRACT

Ecosystem services are often described as occurring together in bundles, or tending not to occur together, representing tradeoffs. We investigated patterns and potential linkages in the provision of six wetland services in three experimental wetlands by measuring: flow attenuation, as peak flow reduction; stormwater retention, as outflow volume reduction; net primary productivity (NPP), as plant biomass; diversity support, as plant species richness; erosion resistance, as stability of surface soils in a flow path; and water quality improvement, as nutrient and sediment removal. Levels of ecosystem services differed in our system because of differences in hydrologic regime brought on by natural variation in clay-rich subsoils. The fastest-draining wetland (with thin clay layer) provided five of six services at their highest level, but had lowest NPP. In contrast, a ponded wetland (with thick clay layer) that was dominated by cattail (*Typha* spp.) provided the highest level of NPP,

but lowest levels of all other services. Hence, in our site, drainage supported several bundled services, whereas ponding supported such high levels of NPP that other services appeared to be limited (suggesting tradeoffs). These outcomes show that high NPP has the potential to be a misleading indicator of overall ecosystem services. Rather than focusing on NPP, we suggest identifying and establishing hydrologic regimes that can support the services targeted for restoration in future projects. Further direct assessments of multiple services are needed to identify bundles and tradeoffs and provide guidance at the scale of local restoration projects.

Key words: ecosystem services; flow attenuation; nutrient removal; plant diversity; primary productivity; restoration; soil stabilization; stormwater retention; water quality improvement; wetland hydrology.

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INTRODUCTION

Ecosystem services support and regulate the natural processes that humans depend on. With many services declining (MEA 2005), the need for ecological restoration is growing (Rey Benayas and others 2009). It would be efficient to restore multiple services in a single site (Kusler 2004; Banerjee and others 2013). However, not all services co-oc-

cur as “bundles,” which were defined by (Raudsepp-Hearne and others 2010) as sets of ecosystem services that repeatedly co-occur across space or time. Some services such as agricultural production and water quality improvement might instead form “tradeoffs” (Rodriguez and others 2006). Most landscape analyses are based on indirect estimates of services and generally show that (1) services occur in characteristic bundles, and (2) no area maximizes all services, although the number that co-occur at high levels varies (Raudsepp-Hearne and others 2010; Eigenbrod and others 2010; Haase and others 2012; Miller and others 2012; Qiu and Turner 2013). The extent to which these arguments apply to direct measures of services or to individual wetland sites or restoration projects remains unclear.

Wetlands are noted for improving water quality, abating flood waters, supporting biodiversity, and storing carbon (MEA—Wetlands 2005; Zedler and Kercher 2005; Jordan and others 2011; Moreno-Mateos and others 2012), and recent guidance calls for watershed approaches to sustain wetland area and services (NRC 2001; US Army Corps of Engineers 2008; US EPA 2012). A recent watershed-approach study entailed mapping seven potentially restorable services within each of 17 subwatersheds (Miller and others 2012). There is further need to determine which services are co-restorable at individual sites, but testing the compatibility of particular services requires intensive measurement (for example, Acreman and others 2011). There is some evidence that ecosystem functions and services depend on levels of plant diversity or net primary productivity (NPP; McNaughton and others 1989; Zavaleta and others 2010; Cardinale and others 2012; Hooper and others 2012). Positive correlations between NPP and plant diversity and other services are common in grassland experiments. The same may not hold in wetlands, where correlations between NPP and diversity are often lacking or negative (for example, Moore and Keddy 1989; Gough and others 1994; Schultz and others 2011). Assessments of multiple ecosystem services can help clarify bundles and tradeoffs and suggest co-restorable wetland services.

Concerted efforts to measure many wetland processes are relatively rare because they require integration of hydrodynamics, ecology, and biogeochemistry (but see Zedler and others 1986; Odum and others 1995; Mitsch and others 2012). Here, we applied the “intensive small-n” approach geomorphologists use to investigate complex small-scale processes (Richards 1996; Spencer and Harvey 2012) to assess provision of multiple services within

three parallel constructed wetlands in the Yahara Watershed, in southern Wisconsin, USA.

Our three parallel wetlands had the same size, shape, elevation, topography, and soils, were planted with the same species, and received similar surface inflows; however, they drained differentially due to variation in subsurface clay thickness. Hydrologic regime is known to be a major determinant of wetland structure, function, and services (Brinson 1993; Brauman and others 2007). We capitalized on differences in drainage and hydrologic regime by assessing the differential development of structure and services in our wetlands over 3 years. Drainage rates differed visibly from the first rainfall following wetland excavation, and different vegetation established in year 1 (Boehm 2011). From 2010 to 2012, we monitored the development of two hydrologic services [flow attenuation (FA) and stormwater retention (SR), which could reduce erosion and flooding downstream], two vegetation-based services (NPP and plant diversity support, which could provide wildlife habitat and cultural services), and two water-quality based services (erosion resistance and water quality improvement, which could retain soils and reduce eutrophication downstream).

We addressed two questions underlying fundamental relationships among wetland hydrologic regimes and ecosystem services: (1) How did hydrologic regime affect six wetland services? (2) Which services formed bundles versus tradeoffs? We also indicate insights derived from our intensive small-n approach. To the best of our knowledge, ours are the first integrated measures of these services with the aim of identifying bundles and tradeoffs.

METHODS

Site Description and Set-up

Our wetlands (3 parallel swales; Figure 1) were excavated in 2008–2009 within the University of Wisconsin—Madison Arboretum, Madison, Wisconsin (43.04°N, 89.42°W) to treat stormwater from a 45.7-ha urban watershed. Stormwater flowed through a 0.10-ha forebay, a 0.17-ha retention pond, then through identical weirs into four swales (96-m long, 8.7-m wide at inlet and 14.7-m wide at outlet; slope: 0.06 cm/m) separated by 0.3-m high earthen berms. Outflows moved through identical weirs to a 0.13-ha collection swale, then to a 0.30-ha retention pond. Inlet weir inverts differed by no more than 0.01 mm in elevation and outlet weirs varied by no more than 0.02 mm in elevation

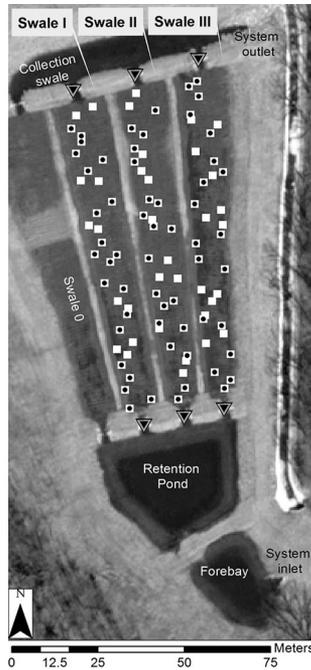


Figure 1. Map of our research site, with: *black and gray inverted triangles* representing inlet and outlet weirs of each swale (where water level and contaminant loads were measured), *white squares* representing vegetation plots (where plant abundance and diversity were sampled), and *black dots* overlaid on vegetation plots representing cohesive soil strength test sites; background image from WisconsinView (www.wisconsinview.org).

according to as-built surveys of the facility (Montgomery Associates, personal communication). Prior to planting, swales were capped with 15 cm of topsoil excavated from the site (six samples had means of: 28% sand, 59% silt, 14% clay, 40 ppm total phosphorus (P), 2033 ppm total nitrogen (N), and pH of 6.3; Montgomery Associates, personal communication). In November 2009, seed mixtures with 27 native wet prairie herbs were sown into Swales I, II, and III at a rate of 590 seeds/m² with the same 16 assemblages planted in 16 equal-area “sections” running the length of each swale. Swale 0 (Figure 1) was seeded differently and excluded from this study.

Regulators required that stormwater be diverted around all swales in 2010 while vegetation established and further required that inflows be increased in 2013; hence, we sampled hydrologic and water quality services primarily in 2011–2012 when we controlled inflows.

Hydrologic Sampling

We monitored surface water flows using six pressure transducers (HOBO water level loggers, Onset

Computer Corporation, Pocasset, Massachusetts, USA), which recorded water level every 60 s. Stilling wells constructed from polyvinyl chloride (PVC) pipe shielded the pressure transducers from sunlight and debris. At least biweekly we measured water level manually, reset the loggers to avoid sensor drift, and ensured that their sensor modules were clean.

We assessed the integrated effect of subsurface processes (loss by infiltration) on the surface water regime by measuring how quickly each swale’s surface water elevation decreased after storms. We measured this water level recession rate as the slope of the approximately linear portion of the water level time series, beginning once the storm passed and outflow over the weir ceased and ending either when the next storm arrived or when the water level receded below the sensor depth. This water level recession rate predominantly measures infiltration, but also includes a small evapotranspiration component that was likely similar in each swale.

Sharp-crested, aluminum 30° V-notch weirs at the inlet and outlet of each swale regulated flow through the system and allowed for flow measurement. A pressure transducer installed upstream of Swale III’s inlet measured water level in the forebay and provided the data needed to calculate flow into each swale. Pressure transducers installed near the outlet of each swale provided the data to calculate flow out of each swale. In addition, one pressure transducer just downstream of each Swale III weir verified that weirs were unsubmerged, with no backflow, and weir equations were valid for computing flow from water level. Flow through the sharp-crested, V-notch weirs can be expressed as

$$Q_V = C_1 H^{5/2}, \quad (1)$$

where C_1 is an experimentally determined constant and H is the depth of water above the invert of the weir (Ricketts and others 2004). From 27 May 2011 to 16 June 2011 and 12 September 2011 to 20 November 2011 (or, 8 of our 29 monitored storms), we attempted to control flows by sealing triangular PVC weir plates into weir V-notches, creating trapezoidal cross-sections with higher inverts. Flow through sharp-crested trapezoidal weirs can be expressed as

$$Q_T = C_2 H^{5/2} + C_3 H^{3/2}, \quad (2)$$

where C_2 and C_3 are also experimentally determined constants (Ricketts and others 2004). We experimentally determined weir coefficients in a flume using a replica of the weirs installed in the

stormwater management facility. When it became clear that drainage was affecting hydrologic regime more than weir plates (see “Results” section), we removed the plates. Thus, swales received equal inputs for all but 60 days during 2010–2012.

Using data from the water level loggers and weirs, we quantified two hydrologic ecosystem services: FA (a swale’s capacity to reduce peak stormflow rates) and SR (a swale’s capacity to reduce the volume of stormwater conveyed downstream). We calculated FA_S for each swale as

$$FA_S = 1 - \frac{1}{n} \sum_{j=1}^n \frac{\hat{Q}_{outs,j}}{\hat{Q}_{ins,j}}, \quad (3)$$

where $\hat{Q}_{ins,j}$ and $\hat{Q}_{outs,j}$ are the peak flows measured through the inlet and outlet weirs of swale S , respectively, during the j th storm. FA_S is equal to the average, over all storms, of peak FA expressed as a fraction of peak inflow. We calculated SR_S for each swale as

$$SR_S = 1 - \frac{\sum_{i=1}^m Q_{outs,i}}{\sum_{i=1}^m Q_{ins,i}}, \quad (4)$$

where $Q_{ins,i}$ and $Q_{outs,i}$ are the i th stormflow volumes measured through the inlet and outlet weirs of swale S , respectively, of the m measurements taken when all pressure transducers were sampling water depths. Thus, SR_S was a measure of the cumulative volume of surface water volume stored or removed during our monitoring period.

We considered higher scores on our FA and SR metrics to represent greater reduction in peak stormflows and stormwater discharge, respectively.

Vegetation Sampling

In 2010, Boehm (2011) sampled plant species richness and shoot biomass in 32 0.25-m² plots spaced uniformly throughout Swales I, II, and III. In 2011 and 2012, we sampled 1 m away from the previous year’s plot in a random direction to avoid previously disturbed vegetation (Figure 1). In May, July, and August of 2011 and 2012, we sampled: composition (presence of all vascular plant species rooted in each plot); maximum standing leaf height; leaf area index (LAI; using an Accupar-LP 80 ceptometer; Decagon Devices, Pullman, Washington, USA); moss cover (as percentage of centimeter with moss present along a 40-cm transect in the plot center); and presence of standing water at the plot center. In the last 2 weeks of August and first week of September we harvested: the year’s shoot biomass, litter mass (standing dead and loose litter from previous years), and root and rhizome

biomass (hereafter, root biomass). We clipped shoots of plants that were rooted within each plot at the soil surface, sorted them by species, and dried them at 70°C for 48 h; we collected and dried litter mass the same way. Root samples were collected as one 10-cm-deep by 10-cm-diameter core taken from the center of each plot. Cores were washed immediately or stored at –5°C (to prevent decomposition) for up to 4 weeks; we spray-washed cores over a 1-mm mesh removing adherent debris and soil by hand, and then dried and weighed root samples as with shoots and litter.

We used shoot biomass as an indicator of NPP because it represented annually produced material (not accumulated). We used species richness (derived from composition data) as an indicator of diversity support because Swales I–III received the same seed mixes and were open to colonization by the same naturally dispersed propagules.

Soil Stability and Water Quality Sampling

Soil Stability

We used a Cohesive Strength Meter (CSM; Model MKIV 60 psi, Partrac, Glasgow, UK) to measure critical shear stress as an indicator of surface soil stability. The CSM utilizes infrared optical sensors within a test chamber to measure water transparency after the soil surface is subjected to water pulses at increasing pressures to induce sediment detachment.

We sampled critical shear stress in a randomly chosen subset of vegetation plots (Figure 1), in September and November of 2010 and 2011, after collecting biomass. At each test site we categorized substrate surface as algal mat, moss mat, matted organic matter, bare soil, or muck soil; we defined bare soil as consolidated substrates that lack surface mats and muck soils as substrates with extremely low cohesion. We avoided obvious soil cracks and edges of algal mats. We discarded measurements with an initial beam transmission reading less than 70%, since this indicated prior surface particle disturbance. Multiple beam transmission measurements were averaged for each incremental pressure value. We converted vertically applied jet pressures to an equivalent horizontal bed shear stress (τ_o), defined by Tolhurst and others (1999) as

$$\tau_o = (67 - 67 \exp^{-\frac{x}{310}}) - (195 + 195 \exp^{-\frac{x}{1623}}), \quad (5)$$

where τ_o (N m⁻²) is bed shear stress and x (kPa) is eroding pressure. Critical shear stress (τ_c) was determined according to Black (2007). In some

instances of highly resistant surfaces, sediment did not detach under the maximum producible pressure. In these instances, we recorded a critical shear stress of 9.12 Pa, the stress equivalent of our device's maximum producible pressure. We considered swales with higher critical shear stress to have higher erosion resistance.

Water Quality

We collected stormwater samples over the course of the hydrograph for 13 selected storms from September 2011 to October 2012 using solar-powered Teledyne ISCO Portable Samplers (Model 6712 and 6715FR, Teledyne ISCO, Lincoln, Nebraska, USA); with those ISCO samplers we used a combination of Bubble Flow and Area Velocity Flow modules to measure water head above the weir inverts. Prior to each storm, modules were calibrated with manual measurement of the water level above the weir invert to avoid sensor drift. We used equations (1) and (2) to calculate flow rates, which we integrated over time to estimate the inflow and outflow volumes of each swale for each storm.

Each ISCO unit was programmed to collect samples in up to 24 1-l bottles per event on a volume pacing basis. Sample pacing ranged from 7.6 to 15.1 m³ of water flow between samples, depending on the anticipated storm event size. Sampling continued until the water level receded below the weir invert or change in flow rate plateaued. All samples were iced during collection and transport. Bottles from each swale position were composited by equal volumes into 3–6 composites per ISCO, based on the assessed hydrographs. Composites were analyzed by the Wisconsin State Laboratory of Hygiene, Madison, Wisconsin, for concentrations of total suspended solids (TSS), total nitrogen (TN), total phosphorus (TP), and total dissolved phosphorus (TDP). Samples for TP and TDP analysis were preserved with H₂SO₄ immediately after compositing.

We calculated total inflow and outflow stormwater volumes per rain event per swale using weir level data from the ISCO modules and HOBO pressure transducers. To calculate event loads (masses) of TSS, TN, TP, and TDP, we first multiplied sample concentrations by corresponding flow volumes to determine incremental loads, then we summed incremental loads into event loads. We calculated removal efficiencies (%) per event per swale as: removal efficiency = $((\text{inlet load} - \text{outlet load}) / \text{inlet load}) \times 100$, with inlet and outlet loads in g.

We considered higher contaminant removal efficiencies indicative of greater water quality improvement.

Comparison of Multiple Services

To facilitate comparisons of multiple services we normalized all swale means to the highest individual swale mean for each service. In the case of water quality improvement, which includes distinct component measurements, we first averaged the four contaminant removal efficiencies to create a more general water quality improvement score; to allow graphical comparison alongside other services we applied a linear transformation to water quality improvement scores such that all scores were positive prior to normalization.

Statistical Analysis

For plot-scale vegetation data in each year and for storm-derived measurements (recession rates, FA, and removal efficiencies) made discretely for each swale over the course of our monitoring period, we compared means with one-way ANOVAs followed by Tukey pairwise contrasts at $\alpha = 0.05$. For CSM measurements, we used the same procedure, but with ANOVA for unbalanced data. Vegetation parameters were measured in nearly the same location in each of the three growing seasons (2010–2012), so we also tested for effects among years and interactions between swale and year for those parameters, using repeated-measures ANOVA; to test for additional spatial variation we regressed vegetation parameters on plot position along the length of the swales. For all tests, we used R statistical package (R Core Team 2012). All error terms presented in the form mean \pm error are standard errors.

RESULTS

We accumulated 2.3 million measurements of water level, 912 of stormwater contaminant loads at swale inlets and outlets, 576 of plant abundance and diversity, and 141 of critical shear stress. Although constructed to be replicates, the wetlands developed different structures and services in relation to hydrologic regime.

Hydrologic Regimes

All swales received nearly the same inflows, but hydrologic regimes differed in association with subsurface heterogeneity (clay thickness; Montgomery Associates 2007). After storms, swale

drainage rates differed consistently (Figure 2): Swale II drained significantly faster (averaging 5.9 ± 0.6 cm of recession in water level per day) compared to Swales I and III, which did not differ from one another in drainage rate (averaging 1.7 ± 0.2 and 1.2 ± 0.1 cm of recession in water level per day, respectively; $n = 23$ storms for each mean swale drainage rate). However, Swale III was very different from Swale I and II in extent and duration of inundation: averaging results from six surveys of our 96 vegetation monitoring plots in 2011–2012, Swale III was highest in percentage of plots with standing water $76 \pm 10\%$, Swale I was intermediate ($27 \pm 12\%$), and Swale II was lowest ($19 \pm 9\%$). Though Swale III generally ponded water, one drawdown occurred during a severe drought in the summer of 2012. Over the monitored period (2011 and 2012), cumulative inflow was no greater in Swale III than in Swales I and II. In fact, our 60-day weir manipulation led Swale I to receive the greatest water volume, and Swale II and III to receive 91 and 84% as much, respectively. During our 29 monitored storms, Swale III always had an outflow, whereas Swales I and II each lacked outflow during three storms.

Hydrologic Services

On average, during monitoring, Swale I ($FA_I = 0.50$) and Swale II ($FA_{II} = 0.53$) attenuated flows significantly more than Swale III ($FA_{III} = 0.34$;

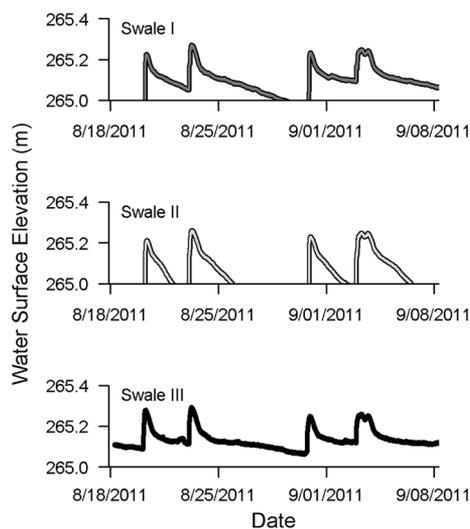


Figure 2. Representative time series of water surface elevation measured in each swale during four storms, showing consistently different water level recession rates between storms. Note that the gaps in data, in Swales I and II only, occurred when water levels dropped below the height of our data loggers.

Figure 3A); also, cumulatively, Swale II retained the largest fraction of incoming stormwater ($SR_{II} = 0.36$), Swale I was intermediate ($SR_I = 0.30$), and Swale III retained the least ($SR_{III} = 0.02$; Figure 3B).

Vegetation Structure

Vegetation composition, abundance, and diversity quickly differentiated, even though the three swales were seeded with the same 27 native species in the same proportions. Of those species, 18 occurred at least once in our 96 monitoring plots in 2010, 2011, or 2012 and 23 other species self-recruited (Online Appendix 1). The most frequent and abundant colonizers were cattails, *Typha latifolia*, *Typha angustifolia*, and their hybrid, *Typha × glauca* (hereafter “*Typha*”), especially in standing water. *Typha* occurred in over 80% of all plots and produced the majority of shoot biomass collected from all plots (55% in 2010, 87% in 2011, and 82% in 2012). In 2011, we found 29 plant species in Swale II, 19 in Swale I, and 9 in Swale III. In the same year, *Typha* was by far the tallest taxon and the most frequent, occurring in 100, 84, and 56% of plots in Swales III, I, and II, respectively. *Typha* was also the most abundant, comprising 99, 82, and 68% of shoot biomass collected from Swales III, I, and II, respectively (Online Appendix 1).

Additional variation in vegetation was visible along the lengths of Swales I and II in 2010. In both swales, areas near inlets were wetter and more invaded by *Typha* than areas farther down the

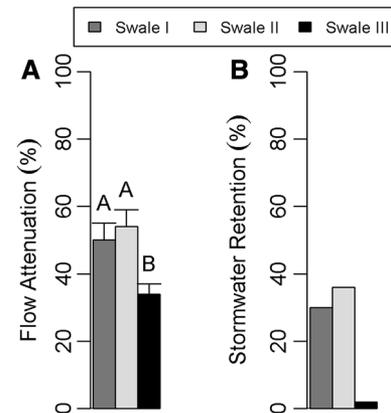


Figure 3. **A** Mean FA provided by the swales measured as a percentage of peak inflow. Bars indicate the value of FA_S , the FA metric. Error bars are standard errors and Tukey letters are derived from post-ANOVA pairwise contrasts with 95% confidence intervals, $n = 29$. **B** SR measured as the percent reduction in cumulative outflow volume relative to cumulative inflow volume during 2011–2012.

swale. Accordingly, shoot biomass was higher near inlets and species richness was lower ($P < 0.05$ for linear regressions on section number (that is, position along the swale)). No such trends occurred in Swale III, where inundation and *Typha* dominance were more uniform. In 2011 and 2012, swale ex-

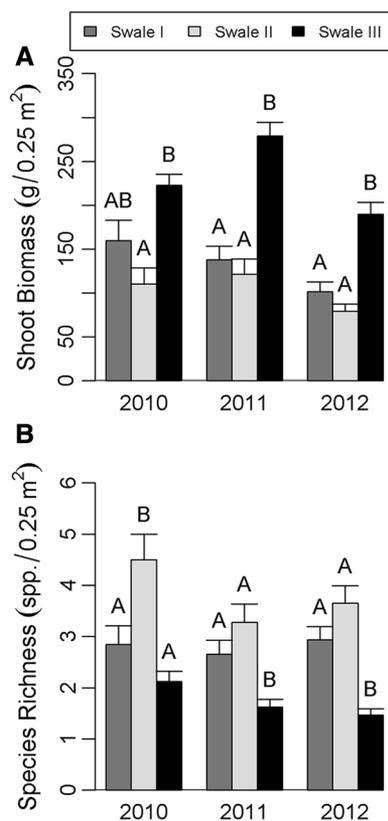


Figure 4. Mean levels of **A** shoot biomass and **B** species richness by swale and year. Error bars are standard errors and Tukey letters are derived from post-ANOVA pairwise contrasts with 95% confidence intervals, $n = 32$ for all bars.

plained at least 4× the variation in shoot biomass and species richness, compared to section number (based on ANOVA sums of squares). At the site scale (pooling Swales I–III, $n = 96$ plots), year had no effect on mean species richness, but shoot biomass was significantly lower during the 2012 drought than in 2010 and 2011 ($P < 0.05$, one-way ANOVA). Swales ranked the same in shoot biomass in all years with no interaction between swale and year ($P > 0.05$, repeated measures ANOVA); likewise, ranks for species richness were the same in all years and showed no swale–year interaction (Figure 4). Our indicators of plant abundance and diversity, shoot biomass and species richness, followed the same trends as alternative indicators (Table 1; Online Appendix 2).

Vegetation Services

During our sampling (2010–2012), Swale III consistently provided the highest level of NPP and Swale II the lowest, whereas Swale II provided the highest level of diversity support and Swale III the lowest; Swale I was intermediate in all cases and generally more similar to Swale II (Figure 4A, B).

Soil and Water

Soil Stability

Although all swales were capped with the same topsoil, they differed in cover of moss and algal mats and in soil stability. Moss and algal mats developed extensively in Swales I and II, where soils were not continuously inundated (Figure 2) and where more light penetrated the canopy (that is, lower LAI; Table 1). Mats were most frequent in Swale II, with 16 occurrences of moss mats and 18 of algal mats among the 50 plots sampled there for soil stability in 2010–2011. In contrast, there were zero occurrences of moss mats and three of algal

Table 1. Indicators of Plant Abundance

Indicators	2011			2012		
	Swale I	Swale II	Swale III	Swale I	Swale II	Swale III
Shoot biomass (g/0.25 m ²)	138 (15) a	122 (17) a	279 (16) b	102 (11) a	79 (8) a	190 (13) b
Litter mass (g/0.25 m ²)	102 (11) ab	80 (8) a	117 (14) b	89 (11) a	64 (12) a	183 (9) b
Root biomass (g/0.25 m ²)	120 (27) a	155 (46) a	207 (41) a	169 (25) a	118 (21) a	311 (63) b
Maximum leaf height (cm)	159 (8) a	118 (13) b	225 (4) c	112 (8) a	93 (9) a	181 (3) b
LAI (layers/m ²)	2.5 (0.2) a	2.6 (0.2) a	3.4 (0.2) b	1.6 (0.1) a	1.5 (0.1) a	2.4 (0.1) b

Means (and standard errors) of plant abundance parameters by swale in 2011 and 2012. Different letters following standard errors denote significant differences between swale means based on post-ANOVA Tukey contrasts, $n = 32$ for each mean, except for maximum leaf height and LAI, which had $n = 96$ (means were averaged over 3 measurements in each growing season).

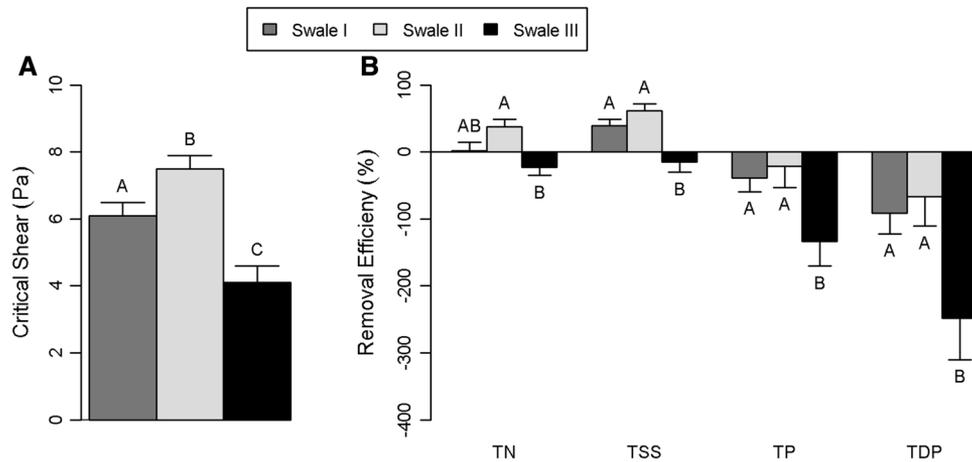


Figure 5. **A** Mean critical shear stress (erosion thresholds) for each swale. Error bars are standard errors and Tukey letters are derived from post-ANOVA pairwise contrasts with 95% confidence intervals, $n = 53$, 50, and 37 for Swales I, II, and III, respectively. **B** Mean removal efficiencies of TN, TSS, TP, and TDP by swale. Error bars and Tukey letters are as above, $n = 13$ for Swale I and III and $n = 12$ for Swale II.

mats among 37 plots sampled in Swale III in the same period. Matted organic matter, found in 21 of 37 plots, was the most frequent substrate in Swale III (where litter mass was high; Table 1); muck soils were second-most frequent, found in 7 of 37 plots.

Over all plots sampled for critical shear stress, muck soil was the most erodible substrate with an average τ_c of 1.8 Pa, followed by bare soil at 3.0 Pa, matted organic matter at 5.6 Pa, algal mat at least 7.4 Pa, and moss mat at least 8.6 Pa (Prellwitz and Thompson 2014); in several instances, the latter two exceeded the maximum producible shear stress of the CSM (9.12 Pa). Independent observations of moss cover in all vegetation plots during plant sampling affirmed patterns observed in the subset of plots sampled for soil stability: swale means of moss cover were 7, 11, and 2 cm (of 40-cm transects) for Swales I, II, and III, respectively, in 2011; and mosses were far less frequent throughout Swale III over six samples in 2011–2012 (Online Appendix 1).

Erosion Resistance

Swale II was most erosion resistant, Swale I was intermediate, and Swale III was least resistant (Figure 5A), based on critical shear stress measurements at the soil surface in 2010–2011 ($n = 53$, 50, and 37 for Swales I, II, and III, respectively). The artificial maximum shear stress (that is, maximum measureable) was reached 8 of 53 times in Swale I, 21 of 50 times in Swale II, and 4 of 37 times in Swale III. Thus, our critical shear stress data are conservative, especially for Swale II.

Water Quality

Contaminant loads were sampled at all swale inlets and outlets in 13 storms ranging from 5.6 to 64.9 mm of rainfall, excepting one storm in Swale II when equipment malfunctioned ($n = 12$ for all removal efficiencies in Swale II). The subset of storms sampled included 23 of the 111 dates with at least 1 mm of rainfall between 15 April and 8 November in 2011 and 2012 (some storms occurred over multiple dates; Online Appendix 3). During sampled storms, we recorded the following flow-weighted concentrations of contaminants averaged across all swale inflows: 7.3 mg/l of TSS, 0.82 mg/l of TN, 0.10 mg/l of TP, and 0.05 mg/l of TDP (Online Appendix 3). Cumulatively, the loads (masses) of contaminants entering all swales during storms were 60 kg of TSS, 6.6 kg of TN, 1.0 kg of TP, and 0.6 kg of TDP. In swales where downstream loads of some contaminants exceeded upstream loads, the “removal efficiency” was negative, that is, a net export of contaminants occurred.

The three swales differed significantly in removal of TSS, TN, TP, TDP (TDP = the dissolved portion of TP). Although the sign and magnitude of removal differed by contaminant, one trend was consistent for all contaminants: removal efficiency was highest in Swale II, intermediate in Swale I, and lowest in Swale III (Figure 5B). Based on cumulative inflow and outflow loads during the storms we sampled in 2011 and 2012, the three swales combined to remove 17.7 kg of TSS and 0.44 kg TN, but also combined to export 0.35 kg TP and 0.36 kg of TDP. Thus, removal efficiencies differed by swale and contaminant.

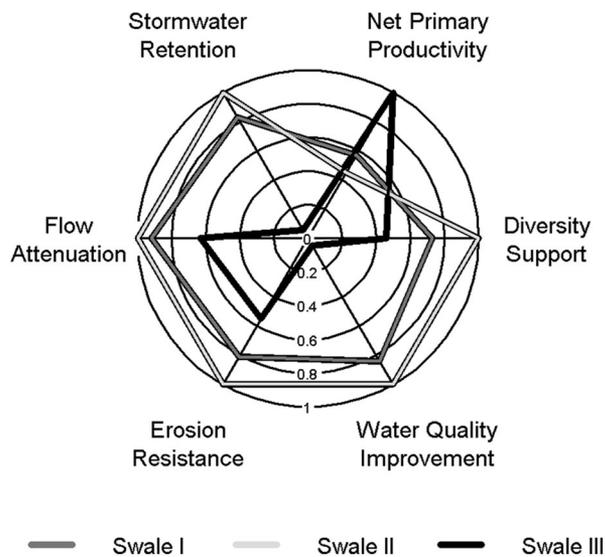


Figure 6. Relative provision of six ecosystem services for each swale. Data were normalized to the maximum swale value (1) for each parameter. For clarity, removal efficiencies of TSS, TN, TP, and TDP were averaged into a single water quality improvement parameter (Online Appendix 4).

Water Quality Improvement

None of the three swales provided substantial water quality improvement. Although negative removal efficiencies could be called an ecosystem disservice or lack of water quality improvement, swales did vary in their effect on water quality; Swale II had the most positive effect (some removal of TSS and TN and least discharge of TP and TDP), Swale I was intermediate, and Swale III had the most negative effect (some discharge of TSS and TN and most discharge of TP and TDP).

Overall Service Provision

Comparing all three wetlands for all six services measured over 2010–2012, Swale II ranked lowest in NPP and highest in FA, SR, diversity support, erosion resistance, and water quality improvement, whereas Swale III ranked highest in NPP and lowest in the other five services (Figure 6). Those patterns held in all years and for individual or averaged contaminant removal efficiencies (Online Appendix 4).

DISCUSSION

All Services Responded to Hydrologic Regime

Differences in levels of six wetland services were substantial, as indicated by ranges of means among

swales: $18.0\times$ in SR, $2.2\times$ in NPP, $2.2\times$ in diversity support, $1.8\times$ in erosion resistance, $1.6\times$ in FA, and from positive to negative water quality improvement. We attribute these differences principally to hydrologic regime, because the wetlands were initially replicates in size, shape, species planted, quality of inflowing water, and quantity of inflowing water (except 60 days with adjusted weir plates in 2011). It is recognized that hydrologic regime is a fundamental determinant of wetland characteristics (for example, Brinson 1993), and our study affirms that even small variations can have overarching effects on the development of wetland structure and services (Brauman and others 2007; Webb and others 2012). Differences in water recession rates (ranging $\sim 5\times$; from 1.2 cm/day in Swale III to 5.9 cm/day in Swale II) caused differences in swale water levels between every storm. Much greater variation in infiltration capacity (orders of magnitude) occurs among soils that differ in texture alone (Rawls and others 1983). Yet in swales with similar topsoil and inflows, differential thickness of a subsoil clay layer was enough to produce distinct hydrologic regimes.

Swales I and II drained between storms and provided similar levels of most services (Figures 2, 6). We hypothesize a sequence of cause–effect mechanisms as follows: greater infiltration and periodically dry soils slowed flows and removed large volumes of surface water from the system, increasing FA and SR. Fluctuating water levels facilitated more species of wet prairie and sedge meadow plants and restricted *Typha* dominance (Frieswyk and Zedler 2007). Occasional drying aided erosion resistance by ensuring consolidated surface soils (not erodible muck soils; Grabowski and others 2011) and by allowing moss rhizoids and mucilaginous algae to stabilize surface soil particles. In addition, TSS, N, and P, were “removed” (that is, pollutants were settled or infiltrated rather than discharged into downstream surface waters). These hypotheses are consistent with the idea that hydrologic services, plant diversity, and surface water quality improvement could co-occur in draining wetlands. We recommend further tests of those associations.

In contrast, we hypothesize that Swale III developed as follows: minimal infiltration led to prolonged inundation, which reduced the swale’s effective storage volume and allowed P to become soluble and exportable, as in other created or restored wetlands with similar hydrologic regimes (Aldous and others 2005; Boers and Zedler 2008; Montgomery and Eames 2008; Ardón and others 2010). Pounded water and available nutrients fa-

vored dominance by *Typha*, which is known to increase NPP and restrict plant diversity in natural and restored wetlands (Craft and others 2007; Frieswyk and others 2007; Boers and others 2007). Dense shade from *Typha* and its thick litter layer reduced light available to moss and algal mats on the soil surface, increasing the erodibility of surface soils. Again, we recommend direct tests of those proposed cause–effect mechanisms. Created sites offer the opportunity to perform such tests by manipulating vegetation and hydrologic regimes.

In experimental wetlands and mesocosms, pulsed or fluctuating water levels tend to favor greater N-removal than static water levels (Busnardo and others 1992; Phipps and Crumpton 1994; Tanner and others 1999; Mitsch and others 2012). Patterns of N-removal in our study match those results. It is possible that, alternating oxic and anoxic conditions in Swale II favored coupled nitrification–denitrification there (in addition to N-removal via infiltration), or that anoxic conditions and high nutrient availability allowed denitrification in Swale III that was outweighed by export of particulate N along with TSS; direct measurement of denitrification could clarify the mechanisms underlying differential N-removal. Also, because removal rates of N and other contaminants are largely dictated by loading rates (Jordan and others 2011), it may have been unusually difficult for our system to substantially reduce loads of through-flowing contaminants due to relatively high-quality inflows; inflowing concentrations of all the contaminants we measured were around the 25th percentile of those reported for similar treatment wetlands in the International Stormwater BMP Database (2012; Online Appendix 3).

However, relatively low inflows of P allowed us to recognize an important consequence of hydrologic regimes in our system: P-export. Specifically, near-continual inundation of Swale III was associated with much higher P-export compared to the periodically dry Swales I and II (Figure 5). Given that TDP loads increased to an even greater extent than TP loads between swale inlets and outlets, we conclude that exported P almost surely mobilized from soils and detritus when swales were inundated and anoxic, as in previous studies (for example, Aldous and others 2005).

Prolonged inundation commonly leads to productive monocultures of *Typha* or other wetland invaders (Kercher and others 2007; Boers and others 2007; Frieswyk and Zedler 2007; Boers and Zedler 2008; Hunt and others 2011). In studies of natural wetlands in the same watershed as our study site (the Yahara), Owen (1995) and Kurtz

and others (2007) observed links between hydrologic regime and vegetation similar to those in our swales: intermittent drainage leading to sedge meadow and ponded water leading to cattail dominance. Tight linkages between hydrologic regime and wetland attributes and services highlight the importance of establishing target regimes; natural variation in subsoils resulted in different levels of each service in our created wetlands. Further, if hydrologic regime is a consistent and comprehensive driver of wetland services, bundling of services should be widespread.

Bundled Services and Tradeoffs were Evident

In a landscape in Quebec, Canada, Raudsepp-Hearne and others (2010) estimated 12 services and found six types of bundles, but no site with all services at high levels. In our Yahara Watershed, Qiu and Turner (2013) estimated ten ecosystem services and found that high levels of multiple services often did not coincide. Our site-based results from intensive sampling are similar and suggest a subset of co-restorable services in our site.

Bundling of five of the six services we assessed was indicated by their co-occurrence at higher levels in two draining swales; these were FA, SR, diversity support, erosion resistance, and water quality improvement. In contrast, a tradeoff was suggested by the co-occurrence of the lowest levels of these services with prolonged inundation and very high NPP. The relationships among services were complex and were also affected by hydrologic regimes, but our detailed data helped us hypothesize mechanisms underlying bundles and tradeoffs.

We observed a positive association between erosion resistance and water quality improvement, but neither of those was positively correlated to NPP. In Swales I and II rapid drainage and short, sparse vegetation coincided with erosion-resistant surface soils and TSS removal. We propose that low vascular plant biomass allowed light to penetrate the canopy and soil-stabilizing moss and algal mats to expand (as in Bergamini and others 2001), and that mats helped prevent Swales I and II from contributing sediments downstream. In contrast, Swale III had the least moss and algal mat cover and was the only exporter of TSS. We sampled the cohesive strength of surface soils at small scales ($<0.01\text{ m}^2$), so it is unclear how the local condition of mat presence compared to whole-swale conditions (for example, periodic dryness of soils) as a determinant of sediment detachment and export. However, the very high level of NPP in Swale III did not ensure sediment retention and nutrient

removal, as is sometimes expected (Toet and others 2005; Quijas and others 2010; Mitsch and others 2012). From 2011 to 2012, NPP in Swale II was less than half that in Swale III, yet all plots in Swale II were vegetated and each plot produced at least 98 g of shoot biomass/m²/year. We speculate that the presence of moderately productive vegetation in Swales I and II was sufficient to limit erosion, and that very productive vegetation in Swale III indirectly contributed to sediment detachment and TSS export by shading out soil-stabilizing mats.

Similarly, very high NPP appeared to restrict plant diversity, as in other restored wetlands (Doherty and others 2011; Doherty and Zedler 2014) and in the experimental test of Kercher and others (2007) involving an invasive grass, *Phalaris arundinacea*. In the latter experiment, invasion and loss of resident species coincided with flooding, indicating an interaction between hydrologic regime and a highly productive plant. In natural wetlands as well, low NPP and high diversity co-occur where drainage is relatively fast, whereas high NPP and low diversity co-occur where drainage is slow (Moore and Keddy 1989; Amon and others 2002; Kurtz and others 2007; Acreman and others 2011; Webb and others 2012). In addition to NPP, leaf height and litter accumulation often confer competitive advantages in crowded plant communities (Grime 1979; Givnish 1982); the *Typha*-dominated vegetation in Swale III was taller and accumulated more litter than vegetation in Swales I and II (Table 1). In nutrient-rich wetlands, *Typha*, *P. arundinacea*, and other productive dominants are known to lower plant diversity by excluding other species (Green and Galatowitsch 2002; Craft and others 2007; Boers and others 2007; Jelinski and others 2011); though the same does not appear to be true in uplands (Adler and others 2011; Schultz and others 2011; Cardinale and others 2012). In wetlands, efforts to moderate NPP, for example, by not refilling treatment wetlands with nutrient-rich topsoil, could promote plant diversity.

Overall, our results fail to support the idea that levels of most ecosystem services track NPP (McNaughton and others 1989; MEA 2005; Zavala and others 2010; Cardinale and others 2012; Hooper and others 2012). Because plant cover was correlated with NPP, cover would also have been a misleading indicator of overall wetland service; we join others in cautioning against the use of plant cover as an indicator of overall wetland function or service (Cole 2002; Fennessy and others 2007; Matthews and Endress 2008; Moreno-Mateos and others 2012). For particular services, NPP and cover

should be used as indicators, for example, tall, dense vegetation can indicate salt marsh bird nesting (Zedler 1993), aboveground biomass can indicate potential biofuel yield or nutrient removal via harvest (Meerburg and others 2010), and large root systems can indicate potential to limit methane emissions by aerating anoxic sediments (Bouchard and others 2007; Fausser and others 2012). Some level of NPP is necessary to support other services (MEA 2005), but our data suggest that very high NPP can be detrimental. We hypothesize a hump-shaped curve for wetland ecosystem services versus NPP, just as intermediate levels of NPP support maximal diversity in some biotic communities (Mittelbach and others 2001).

Small-Scale, Integrated Assessments Provided New Insights

Large-scale maps drawn from available environmental or land cover data allow for spatially extensive characterization of ecosystem services (for example, Raudsepp-Hearne and others 2010; Miller and others 2012) but are more reliable if derived from primary data (Eigenbrod and others 2010) and ground-truthed (Qiu and Turner 2013). We were able to attribute overall differences in services to differential hydrologic regimes because our three swales (area ~0.12 ha each) were designed to hold wetland size, grade, geometry, soils, light levels, and inflows constant. That design, plus intensive direct measurements, allowed us to recognize patterns in service provision and to hypothesize specific cause-effect mechanisms.

Integration of hydrologists, ecologists, and engineers enhanced understanding of interrelationships among ecosystem services (Rice and others 2010; Spencer and Harvey 2012). Direct measurement of water level, LAI, and abundance of moss and algal mats helped us explain variation in surface soil stability (Prellwitz and Thompson 2014), which would have been overlooked by measuring only whole-swale TSS removal. Estimating erosion resistance by directly stressing surface soils to induce sediment detachment (Tolhurst and others 1999) indicated the importance of moss and algal mats. Had we relied instead on root biomass (Quijas and others 2010) or soil loss equations (for example, MUSLE; Williams 1975) to assay erosion resistance, we would have concluded that Swale III was most resistant. Instead, direct measurements of contaminant loads showed that Swale III exported TSS, and monitoring of surface soil stability, vegetation, and water levels helped explain the export of TSS and TN in Swale III and export of TP and

TDP from all three swales. Sampling TDP (not just TP; Toet and others 2005) showed that Swale III outflows had 2.5× the TDP load (in g) as its inflows, and earlier mechanistic studies on P-release (e.g., Boers and Zedler 2008) led us to conclude that topsoil P (and its co-precipitates) had become soluble during prolonged inundation. Further, TP and TDP export in Swales I and II would not have been evident from measurements of the particulate contaminant TSS alone (both swales removed TSS). We recommend more direct measures of erosion resistance, and measurements of dissolved and particulate nutrients and TSS to assess the efficacy of TSS as a general indicator of water quality (Collins and others 2010).

CONCLUSIONS

We found substantial variation in six wetland ecosystem services due to differences in the hydrologic regimes of three wetlands that were otherwise replicates. Ponding facilitated invasion and dominance by highly productive *Typha*, as well as mobilization and export of P. In comparison, drainage supported greater flood regulation, more diverse vegetation, a greater abundance of soil-stabilizing moss and algal mats, and cleaner water (Swales I and II discharged less contaminants than Swale III, though they exported some P). Associations between wetland hydrologic regime and services were strong, but services also appeared to be linked. The interactions among hydrologic regime and plant-based services gave rise to patterns like those seen in nearby natural wetlands (Kurtz and others 2007). If bundles of services occur reliably in wetlands, and certain bundles of services are co-restorable, restorationists will be able to set more achievable targets for individual sites. Identification and verification of such bundles require interdisciplinary research with direct measurement of multiple services. Clearer understanding of which services a given site (and its hydrologic regime) can support will enable restoration planners to locate projects in sites that offer complementary services or particular services that are needed based on large-scale assessments and watershed approaches (NRC 2009; Miller and others 2012; Wilkinson and others 2013).

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Vegetation Change in Great Lakes Coastal Wetlands: Deviation from the Historical Cycle

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ABSTRACT. Water-level change is integral to the structure and function of Great Lakes coastal wetlands, and many studies document predictable relationships between vegetation and water level. However, anthropogenic stressors, such as invasive species, land-use change, and water-level stabilization, interact to shift the historical cycle (of native vegetation migration up- and down-slope) toward dominance by invasive *Typha* species. Knowing from earlier studies that water-level stabilization alters the historical vegetation cycle, we asked if similar shifts can occur where water levels are not stabilized. Using historical aerial photographs of three coastal wetlands (in Lake Michigan's Green Bay, Wisconsin), we determined that habitat dominated by *Typha* species has expanded to eliminate wet meadow habitat. Between 1974 and 1992, linear regressions showed strong, significant relationships of both meadow area ($R^2 \geq 0.894$; $p < 0.02$) and marsh area ($R^2 \geq 0.784$; $p < 0.05$) to water level in all three wetlands. In 2000, meadow area was below that predicted by the historical pattern due to the landward advance of marsh habitat during a year of decreasing water levels. In the same period, land use in the wetland watersheds converted from agriculture to urban. Urbanization and the replacement of native *Typha latifolia* by the invasive hybrid *Typha xglauca* may have overwhelmed the beneficial impact of water-level fluctuation. The documentation of vegetation shifts, as herein, is an essential step in the process of preserving and restoring ecological integrity.

INDEX WORDS: Historical cycle, *Typha*, Great Lakes, wetlands, aerial photographs.

INTRODUCTION

Coastal wetlands of the Laurentian Great Lakes exemplify the integral role of water-level change in wetland structure and function (Planck 1993, Wilcox *et al.* 2005). High water levels renew structural complexity, restrict the advance of trees and shrubs, and keep the abundance of aggressive species in check (Keddy and Reznicek 1986, Planck 1993, Wilcox 2004). Low levels maintain patchiness, allow for the expansion of wet meadow areas, and renew the seed bank (Keddy and Reznicek 1986, Gottgens *et al.* 1998, Wilcox 2004, Wilcox *et al.* 2005). In fact, relationships between vegetation area and water level are quite predictable (Lyon and Drobney 1984, Williams and Lyon 1997, Chow-Fraser *et al.* 1998, Gottgens *et al.* 1998). Four habitat types of Great Lakes coastal wetlands,

shrub-carr, wet meadow, marsh, and aquatic (Harris *et al.* 1981, Kelley *et al.* 1984), also change in amount, kind and proportion (Guntenspergen 1985). In this "shifting mosaic" (Wilcox 2004), species and habitat types die back and reinvade based on their water depth affinities, with each type expanding as it moves lakeward (van der Valk 1981, Keddy and Reznicek 1986).

Water-level stabilization disrupts the historical cycle and is held responsible for promoting aggressive species (Wilcox 1993, Herrick and Wolf 2005). It converts formerly diverse, structurally complex wetlands to large areas of only a few species (Keddy and Reznicek 1986, Minc and Albert 1998) by eliminating the high and low water levels important to wetland regeneration, changing competitive interactions among plant species (Shay *et al.* 1999), and increasing phosphorus availability (Richardson and Vepraskas 2000, Boers 2006). For example, *Typha*-dominated habitat increased, displacing wet meadow habitat, in Lake Ontario coastal wetlands

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following the start of water-level regulation (Wilcox *et al.* 2005).

In addition to water-level stabilization, several other anthropogenic stresses have the potential to transform the historical cycle (Patterson and Whillans 1985, Chow-Fraser *et al.* 1998, Gottgens *et al.* 1998). These include land-use change, the introduction of invasive species, other hydrological alterations, and changes in sediment and nutrient loads, all of which can alter competitive relationships (Galatowitsch *et al.* 1999, Weller *et al.* 2003, Zedler and Kercher 2004).

We observed from Landsat TM imagery (30-m pixel) a vegetative trend similar to what occurs with stabilized water levels in a Green Bay, Lake Michigan wetland with natural water-level fluctuation. That is, wet meadow habitat was smaller relative to *Typha*-dominated marsh habitat in 2001 under low water levels than it was in 1994 when water levels were higher. In this interval, water level rose, peaking in 1997, then decreased, falling below the 1994 level by 1999. While some lag time between water-level change and vegetative response is expected, smaller meadow area at a lower water level was contrary to our expectation and prompted us to undertake a more detailed investigation of three Green Bay wetlands using aerial photographs. We examined the relationship of marsh and wet meadow habitat to water level to determine if the historical vegetation cycle has changed despite naturally fluctuating water levels. We hypothesized that (a) historically, both marsh and wet meadow habitats expanded predictably lakeward as water levels fell and wetland area increased, (b) during the most recent water level decline, marsh habitat area was greater and wet meadow habitat area was less than predicted by the historical trend, and (c) marsh habitat continued to expand landward during the most recent water level decline, contrary to the historical pattern.

METHODS

Study Area

We chose three wetlands and their associated upland areas along the western shore of Green Bay in Brown County, Wisconsin, to represent anthropogenically stressed, embayment wetlands of the Laurentian Great Lakes (Fig. 1). Atkinson Marsh (44°34'00"N/88°02'30"W), Peter's Marsh (44°35'15"N/88°01'30"W), and Long Tail Marsh (44°37'30"N/88°00'45"W) are all directly influenced by natural water-level changes in Lake

Michigan. Each one contains areas of shrub-carr dominated by *Salix* and *Cornus* spp., wet meadow dominated by *Carex* spp. and *Calamagrostis canadensis* (Michx.) Beauv., shallow marsh dominated by *Typha* spp., and deep marsh dominated by *Nymphaea odorata* Ait. and *Sagittaria* spp. or newly exposed sand flats dominated by *Juncus* spp. and *Schoenoplectus* spp. All were described by Herdendorf *et al.* (1981) as having low topography, direct exchange with the waters of Green Bay via seiche activity, important wildlife habitat, and surrounding areas undergoing urbanization. Prior to 1973, a chain of islands known as the Cat Islands stretched along the Green Bay coast offshore from Peter's Marsh and Atkinson Marsh. These islands were destroyed by rising water levels and severe storms in the early 1970s, reducing the area suitable for emergent vegetation and likely allowing greater impacts of waves on wetland shores.

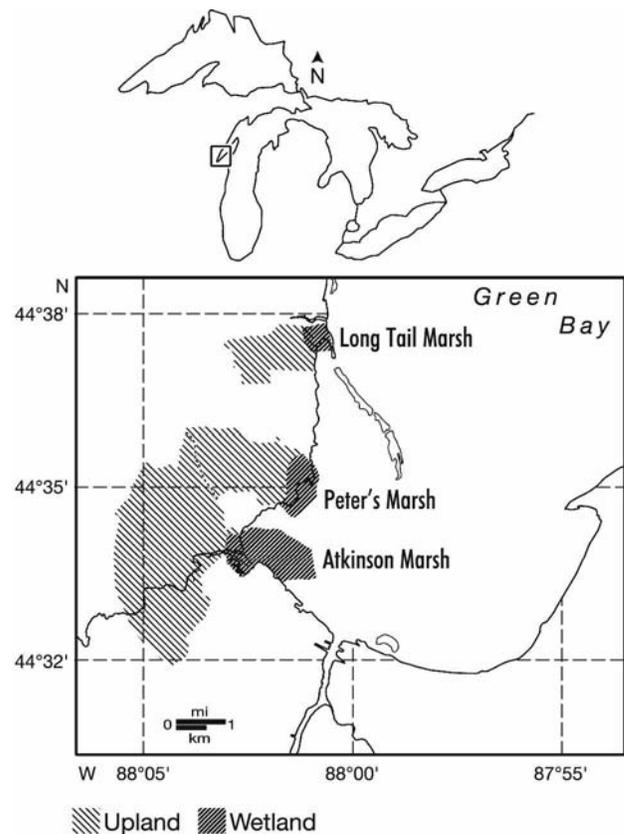


FIG. 1. Location of study sites along the coast of Green Bay, Lake Michigan in Brown County, Wisconsin, USA.

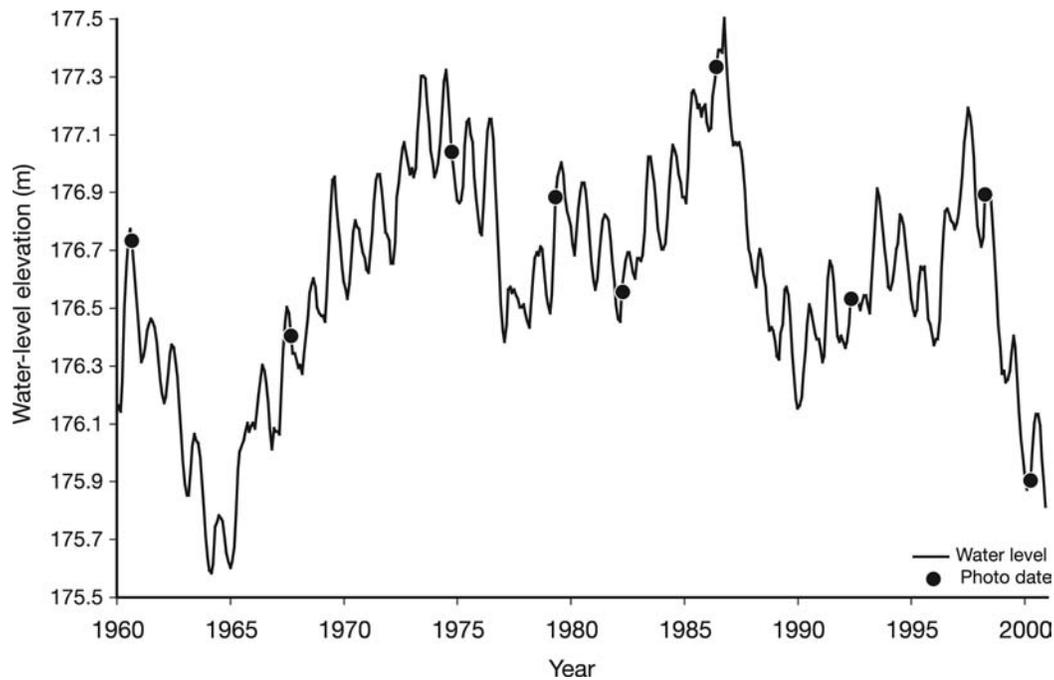


FIG. 2. Monthly average water-level elevation of Lake Michigan-Huron (meters above IGLD 1985) from the United States Army Corps of Engineers and aerial photograph dates.

Photo Interpretation

Historical air photo interpretation provides a quantitative method of examining changes in large areas across decades and has proven useful in other studies of Great Lakes coastal wetlands (Gottgens *et al.* 1998, Kowalski and Wilcox 1999). We selected aerial photographs from nine dates based on availability, distribution across the range of dates and water levels, photo quality, and similarity of photo attributes (Fig. 2, Table 1). Even though the water level was extremely low in 1965 (Fig. 2), no photograph was available for that date, and it was not included in this study.

We scanned photographs obtained as 9" × 9" contact prints using a Microtek ScanMaster 9600XL at 600 dpi (pixel size = 42 μm on the print and 0.84 m in the field for 1960 and 1967 and 1.64 m in the field for 1974). We then orthorectified the resulting digital images and those photographs obtained in digital form using OrthoMapper™ software (Image Processing Software, Inc.), in order to remove the innate distortion caused by topographic variation and camera angle (Wolf and Dewitt 2000). OrthoMapper™ uses algorithms to re-map a digital image pixel by pixel based on user-defined horizon-

tal control points, which represent the same geographic point in the image to be rectified and a previously orthorectified image, and a digital elevation model. Basing photo interpretation on orthophotographs reduces distortions in the shape and area of identified vegetation and land cover types and affords multi-date geographic registration, thereby improving the comparison of the areas across time.

Because the 2000 image was obtained as a digital orthophotograph (UTM zone 16, NAD83), we used it as the base image for orthorectifying images from previous years. Land-use changes due to the construction of Interstate 43 in 1967 made it difficult to identify control points for the 1967 and 1960 images in the 2000 image. Therefore, orthorectification of the 1967 image used the 1974 image as a base and orthorectification of the 1960 image used the 1967 image as a base. Despite a large number of control points (7–20), the positional error associated with the orthorectification, expressed as root mean square error (RMSE), ranged from 0.62 to 3.99 pixels, in many cases higher than the ideal of < 1 pixel. This may have been due to differences in photo shrinkage or expansion, irregularities in the scanner, or "drift" (slight distortion) over time in the road intersections used as control points. Posi-

TABLE 1. Summary of aerial photographs interpreted for analyses. Water level is the peak monthly water-level elevation of Lake Michigan-Huron (meters above IGLD 1985) during the previous growing season (May–September).

Date	Film Type	Scale of Original	Source	Original Format	Ortho Resolution	Water Level (m)
Sept. 1960	B&W	1:20000	Farm Service Agency*, USDA	9"×9" print (N = 7)	0.5-m pixels	176.77
Sept. 1967	B&W	1:20000	Farm Service Agency, USDA	9"×9" print (N = 7)	0.5-m pixels	176.50
Oct. 1974	B&W	1:40000	Farm Service Agency, USDA	9"×9" print (N = 4)	1-m pixels	177.32
May 1979	B&W	1:80000	Survey Photography, USDA	digital file (N = 1)	1-m pixels	176.71
April 1982	CIR	1:58200	National High Altitude Photography Program, USGS	digital file (N = 2)	1-m pixels	176.82
June 1986	CIR	1:58200	National High Altitude Photography Program, USGS	digital file (N = 3)	1-m pixels	177.25
May 1992	B&W	1:40000	National Aerial Photography Program, USGS	9"×9" print (N = 3)	1-m pixels	176.66
April 1998	B&W	1:40000	National Aerial Photography Program, USGS	9"×9" print (N = 3)	1-m pixels	177.19
April 2000	B&W	1:10080	Brown County Land Information Office	digital orthophoto (N = 1)	0.5-m pixels	176.40

*Known as the Agricultural Stabilization and Conservation Service (ASCS) at the time of photography.

tional error was taken into account during data analysis.

We held the area interpreted as wetland (as opposed to upland), including open water, constant across time and delimited it by approximately the furthest extent of wetland vegetation in any image on the eastern side, and anthropogenic land use or forest to the north, south, and west. We defined associated upland as the watershed of each wetland within 3 km of its upland boundary, which fully encompassed the watersheds of Peter's Marsh and Long Tail Marsh. Watersheds were based on topography and obtained from Danz *et al.* (2005). In each wetland and the associated upland, the boundaries of wetland vegetation and land-use classes were digitized on-screen to create shapefiles using ESRI software (ArcMap™ 9.0).

Wetland vegetation class polygons had a minimum mapping unit of 100 m² and were digitized at a 1:1,200 scale to standardize differences in resolution among images. We assigned the polygons thus delineated to one of eight wetland classes: Tree, Shrub, Meadow, Marsh, Mixed Vegetation, Bare soil/Rushes, or Water (Table 2). Other studies of

Great Lakes coastal wetlands have identified similar wetland classes from black and white aerial photographs (Harris *et al.* 1981, Kowalski and Wilcox 1999). Upland land-use classes were digitized at a 1:10,000 scale with a minimum mapping unit of 10,000 m² and assigned to the Urban, Agricultural, or Natural class (Table 2).

The shape, tone, and texture of the various wetland classes were determined by comparing the 2000 photo with field data collected in 2001 and 2002. In each wetland, transects were randomly placed perpendicular to the perceived water gradient, i.e., moving from water's edge to the upland. Plots, 1 m² in area, were then randomly placed along 20-m segments of these transects with a non-random plot at the "wet end" of the each transect. In each plot the species rooted within the plot were visually assigned one of six cover classes (< 1%, 1–5%, 6–25%, 26–50%, 51–75%, and > 75%) modified from Braun-Blanquet (1932). The number of plots sampled in each wetland was roughly proportional to the size of the wetland and 33, 58, and 16 plots were sampled in Atkinson, Peter's, and Long Tail marshes, respectively. In all, 15 plots were

TABLE 2. Description of wetland vegetation and land-use classes. Descriptions were based on a comparison of black and white images from 2000 and visually estimated species cover in 1-m² quadrats sampled in the field in July 2001/2002.

Class	Description
Water	Open water. Appears in photo in smooth dark tones, with light toned ripples or bright white.
Bare soil/Rushes	Total vegetation < 50% cover. <i>Schoenoplectus tabernaemontani</i> (K.C. Gmel.) Palla and/or <i>Juncus nodosus</i> L. have highest cover, <i>Eleocharis erythropoda</i> Steud. often present. Appears in photo a very smooth light tone along or close to water's edge
Marsh	At least 25% (often > 50%) cover m ⁻² cover by <i>Typha</i> spp. forming an obvious canopy; under-story often containing <i>Impatiens capensis</i> Meerb., <i>Urtica dioica</i> L., <i>Calamagrostis canadensis</i> (Michx.) Beauv., and <i>Leersia oryzoides</i> (L.) Sw. Appears in photo as mottled, mid-tone, clonal pattern (circles) often evident, may appear cloud-like.
Meadow	Grass (<i>Calamagrostis canadensis</i>) and/or sedge (<i>Carex lacustris</i> Willd., <i>Carex stricta</i> Lam.) at least 50% cover; dicots abundant. Appears a grainy, light tone often near and around shrubs
Mixed Vegetation	A mixture of <i>Typha</i> (5-50%) and Rush or Meadow vegetation. Appears in photo as mottled mixed tones between Marsh and Rushes or Meadow classes.
Shrub	<i>Salix</i> and <i>Cornus</i> shrubs making up at least 50% continuous cover, under-story of Meadow vegetation. Appears in photo in dark tones, distinguished from water by position, irregular shape and height.
Tree	Trees (e.g., <i>Populus</i>) making up at least 50% continuous cover, under-story of Meadow vegetation. Appears in photo in dark tones, distinguished from water by position, irregular shape and height, taller than shrubs.
Urban	Buildings, streets, parking lots, etc. and their associated landscaping, including artificial ponds.
Agricultural	Cropped land; fallow fields not distinguished from Natural.
Natural	Any area in the upland not included in Urban or Agriculture classes: forests, fallow fields, natural water, and grasslands.

characterized as Meadow, 56 as Marsh, 12 as Mixed Vegetation, and 16 as Bare soil/Rushes. This information was then used as a guide to interpret the historical photos.

Viewing stereo pairs of contact prints, vegetation maps of Peter's Marsh created by Harris *et al.* (1981) and a set of large scale, oblique, color photos of Peter's Marsh taken between 1974 and 1999 (obtained from G. Fewless, University of Wisconsin-Green Bay) also aided our interpretation of the historical photos. While *Typha x glauca* Godr. (pro sp.) dominated the Marsh vegetation in our 2001/2002 field data (Table 2), this class may have been dominated by other *Typha* species and/or other emergent species in the past. For example, Harris *et al.* (1981) showed *Scirpus* spp. dominating the marsh habitat of Peter's Marsh in 1978. We were unable to distinguish *Typha* and *Scirpus* in our 1979 photo.

The same interpreter (CBF) did all photo interpretation for consistency. For quality assurance, interpretation was duplicated by Aaron Boers, who

had experience delineating *Typha*-dominated areas from air photos, for the wetland area of Long Tail Marsh in a low water (1974) and high water (1982) image.

Data Analysis

Topology, which defines the spatial relationship among the polygons in the map, was created for the digitized wetland vegetation and land-use polygons (i.e., shapefiles were converted to coverages). This process also calculated the area and perimeter of each polygon. We analyzed vegetation change using the "overlay-union" tool in ESRI software (Arc Toolbox™ 9.0). This tool combined the land-cover information in two maps of consecutive dates into one "change" map. Each polygon in the change map has two land covers associated with it, one from the first date and one from the second. Thus, areas where vegetation or land use had changed have two different land-cover identities, and areas without change have two identical land-cover iden-

tities. To reduce positional errors, all polygons with an area less than the minimum mapping unit were excluded from analysis. This reduced the wetland area analyzed by no more than 1.5% and the upland area by no more than 0.4% in any image pair.

Water levels were obtained as coordinated monthly means for Lake Michigan-Huron (one lake hydrologically) from the United States Army Corp of Engineers. Whole-lake levels are coordinated from several gauging stations to create a complete record. These levels are on average 0.02 m below available levels recorded in Green Bay and are highly correlated with the partial Green Bay record ($r = 0.99$). Because peak water levels during the growing season drive herbaceous vegetation changes, we used the highest monthly mean of the growing season (May–September) preceding each map date for our analyses. Because longer term water-level history can also be important to vegetation dynamics (Gottgens *et al.* 1998, Wilcox *et al.* 2005), we followed the method of Williams and Lyon (1997) to determine the lag time in vegetative response to water-level change. This method uses successive trials of a weighted average of the water level of an increasing number of years preceding each image date.

We used linear regression to examine the relationships among water level, the area of wetland vegetation (hereafter Wetland area), and the area of the Marsh and Meadow classes. Data from the 1960 and 1967 land cover maps were not included in regressions on water level because in Atkinson Marsh and Peter's Marsh the presence of the Cat Islands buffered the wetlands from the open bay and likely affected the relationships under consideration by increasing the area suitable for the growth of vegetation at any given water level. In order to determine if the relationship of Marsh and Meadow areas to water level and Wetland area remained constant in recent years, we performed regressions on water level using data from the 1974–1992 maps and regressions on Wetland area using data from the 1960–1992 maps. Then, we compared Marsh and Meadow areas in 1998 and 2000 against the 95% prediction intervals.

Transition matrices created from the “change” maps were used to determine the direction of Marsh recruitment. Transitions from Meadow, Shrub, and Tree classes to Marsh indicated a landward recruitment, which we expected with water level rise, and transitions from Water or Bare soil/ Rushes to Marsh indicated lakeward recruitment, as we expected with water level fall. Because many factors

besides water-level change affect Marsh recruitment, some recruitment in both directions can be expected in most intervals. The ratio of lakeward-to-landward recruitment (lake:land) was used to indicate if recruitment occurred primarily lakeward (lake:land > 1), primarily landward (lake:land < 1), or equally in both directions (lake:land ≈ 1). The ratios were then compared to the direction of water-level change.

RESULTS

General Trends, 1960–2000

Land-use changes were similar among the three wetland watersheds. Natural area remained steady while Urban area increased and Agricultural area decreased. The Peter's Marsh watershed had the largest proportion of Natural area, mostly due to the Fort Howard Paper Foundation Wildlife Area. In Atkinson and Long Tail Marshes, nearly 50% of the Agriculture area converted to Urban area between 1992 and 2000 (Fig. 3).

Wetland area, the combined area of all wetland vegetation classes, was negatively correlated with peak water level of the previous growing season ($r = -0.617, -0.774, -0.787$ in Atkinson, Peter's and Long Tail marshes, respectively). Wetland area varied from 9.20 ha to 242.06 ha in Atkinson Marsh, 16.09 ha to 120.11 ha in Peter's Marsh, and 5.35 ha to 47.89 ha in Long Tail Marsh with coefficients of variation (CV) of 68.60, 19.22, and 6.61, respectively (Figs. 4 and 5).

Meadow and Marsh areas were also negatively correlated with water level (for Meadow $r = -0.466, -0.554, -0.544$; for Marsh $\rho = -0.622, -0.628, -0.745$). Meadow area ranged from 2.33 ha to 72.68 ha, 1.38 ha to 62.52 ha, and 0.00 ha to 26.99 ha in Atkinson, Peter's and Long Tail marshes, respectively. The Marsh class occupied a larger portion of the wetland, ranging from 0.64 ha to 163.73 ha, 0.39 ha to 53.20 ha, and 0.53 ha to 17.13 ha, respectively. Both classes had high CVs (for Meadow CV = 30.56, 14.46 and 6.80; for Marsh CV = 47.08, 12.41, and 3.21).

In a blind test, separate image interpretations by Frieswyk and Boers showed high concurrence on the wetland and habitat areas of Long Tail Marsh in the 1974 and 1982 images. Neither interpreter had consistently higher or lower habitat areas than the other. Coefficients of variation (CV) between interpreters ranged from 0.02 to 0.47 and were below the CVs for each vegetation class among images. Habitat areas of Boers' interpretation were within

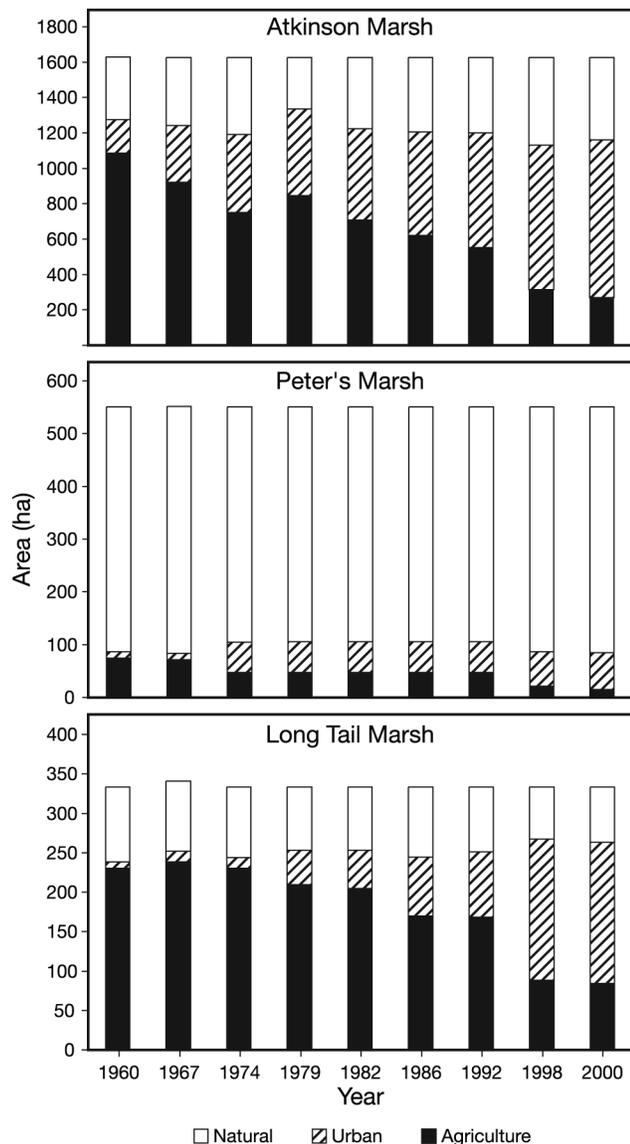


FIG. 3. Area of upland land-use classes in wetland watersheds as determined by air photo interpretation.

the 99% confidence intervals of regression analysis based on Frieswyk's interpretation.

Historical Patterns, pre 1992

Peak water level of the previous growing season was the best predictor of Wetland area using the weighted average method of Williams and Lyon (1997) to determine the lag time in vegetative response over the period 1974–1992. The regression fit (R^2) decreased for each additional year included in the weighted average of peak growing season

water levels up to 10 years in each of the three wetlands. Peak water level of the previous growing season was also the best predictor of Meadow area in Peter's and Long Tail marshes and of Marsh area in all three marshes. A weighted average of 6 yearly water levels was the best predictor of Meadow area in Atkinson Marsh.

As expected, we found predictable relationships among peak water level, Wetland area, Meadow area, and Marsh area during the historical period. Linear regressions over the period 1974–1992 showed the previous growing season's peak water level to be a strong and significant predictor of Wetland ($p < 0.02$ and $R^2 \geq 0.883$), Meadow ($p < 0.03$ and $R^2 \geq 0.845$), and Marsh areas ($p < 0.05$ and $R^2 \geq 0.784$). Wetland area was a stronger predictor than water level of Meadow ($p \leq 0.001$) and Marsh ($p \leq 0.001$) areas with similar regression fits for Meadow areas ($R^2 \geq 0.908$) and higher regression fits for Marsh areas ($R^2 \geq 0.900$) (Table 3).

Marsh recruitment, defined as the area that converted to Marsh from other habitat types between each sequential pair of images, followed a predictable pattern during the historical period. While at least some Marsh recruitment occurred in both the lakeward and landward direction between most images, recruitment ratios comparing lakeward to landward recruitment (lake:land) showed an overall pattern (Fig. 6). In the time intervals ending in 1967, 1979, and 1992, water levels experienced a net decrease and lake:land ratios were > 1 , indicating lakeward recruitment of Marsh. In intervals ending in 1974 and 1986, water levels rose and lake:land ratios were < 1 , indicating landward recruitment of Marsh. Variable Marsh recruitment between 1979 and 1982, a period with little net change in water level (Fig. 2), was reflected by lake:land ratios of approximately 1 in Atkinson and Long Tail marshes. In Peter's Marsh, Marsh recruited primarily landward in this interval (Fig. 6).

Deviation from Pattern, Post 1992

In examining how Meadow and Marsh areas deviated from historical patterns, we considered 95% prediction intervals around the regression line of Marsh and Meadow areas on either water level or Wetland area. Both predictors led to similar results, but we focus on those using Wetland areas as a predictor. Because this study focuses on the relationship between habitat types within the wetland area, we considered Wetland area preferable to water level for the prediction of Meadow and Marsh

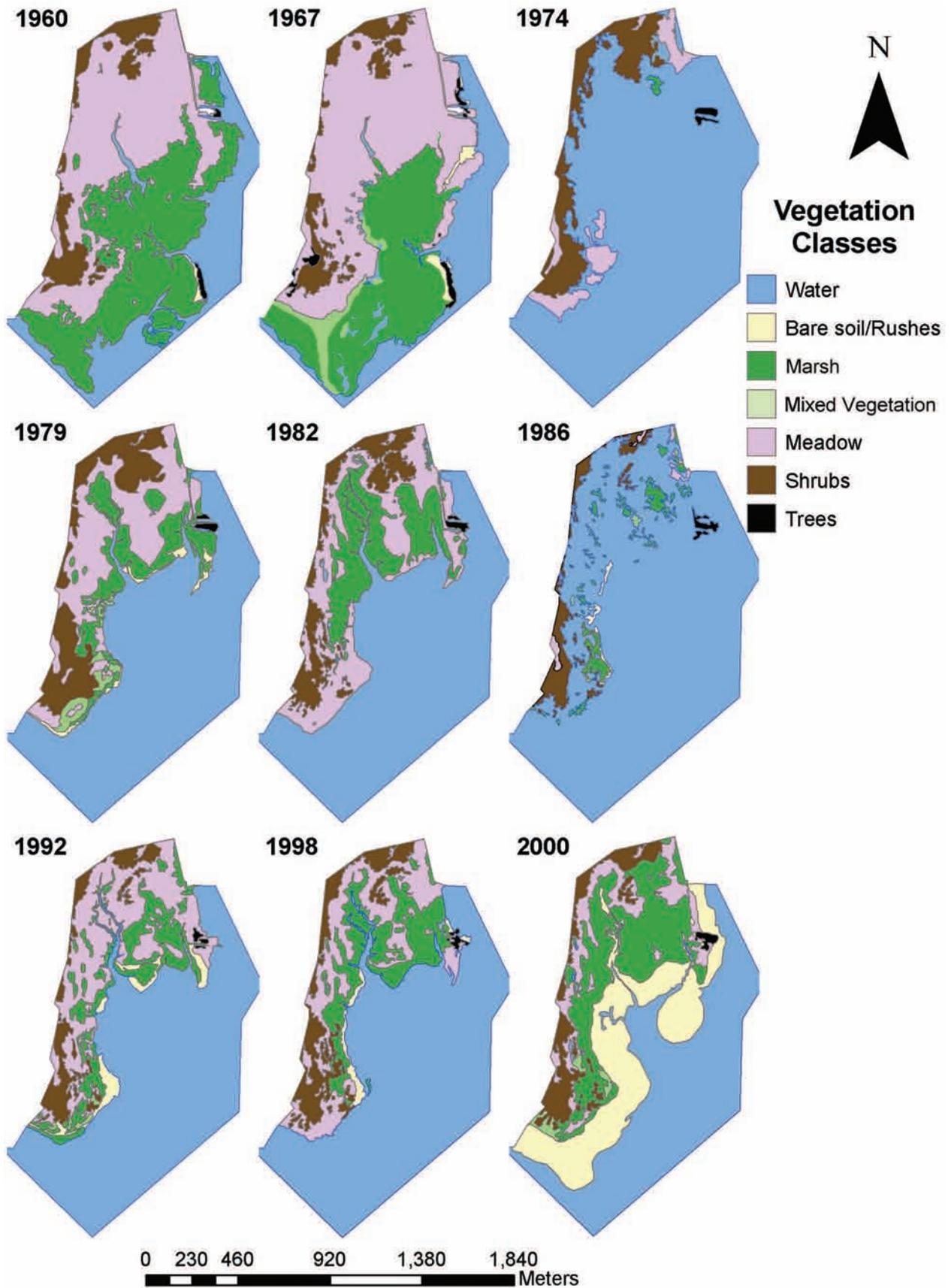


FIG. 4. Image interpretation maps showing changes in habitat areas between 1960 and 2000 in Peter's Marsh. Similar patterns occurred in Atkinson and Long Tail marshes.

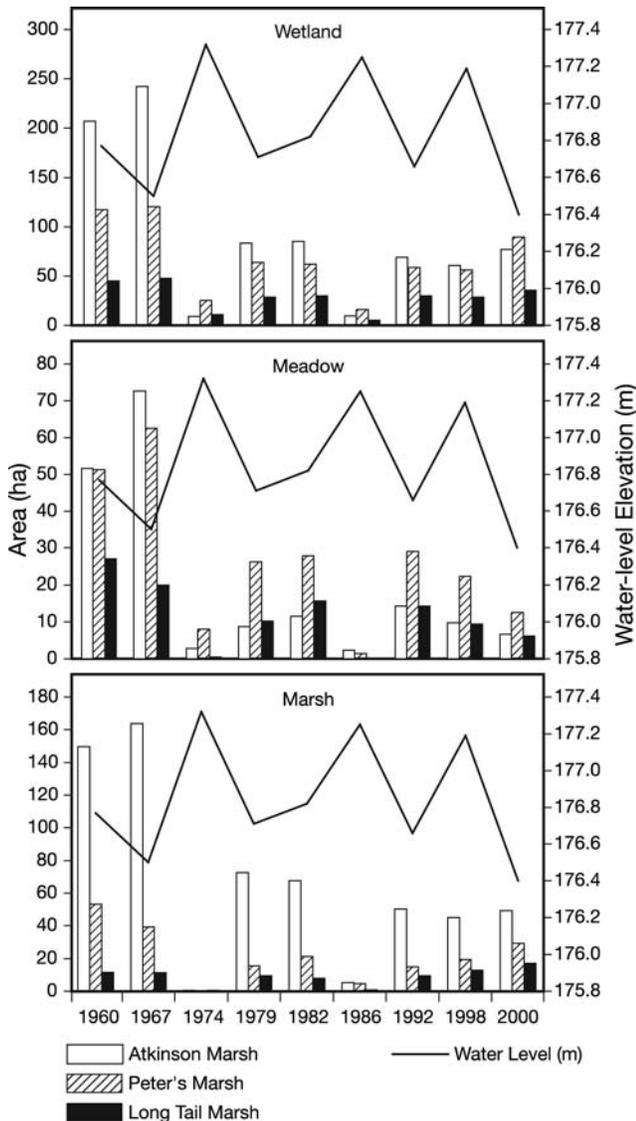


FIG. 5. Changes in habitat area with peak water level of the previous growing season (May - September).

areas. Wetland area also accounted for geomorphological changes resulting from the loss of the Cat Islands, so data from the 1960 and 1967 images were included in the regression model, which strengthened the model. In addition, wetland area was a better predictor of Meadow and Marsh area (Table 3), and lag time, which is not incorporated in Wetland area, was not a factor in this data set.

As expected, both Meadow and Marsh areas deviated from the historical pattern. When regressed against Wetland area, the Marsh area of Long Tail Marsh was above the prediction interval in 2000

TABLE 3. Historical relationships among peak water level of the previous growing season, wetland area, and habitat area. Regressions on water level based on interpretation of 1974–1992 images ($N = 5$); regressions on wetland area based on interpretation of 1960–1992 images ($N = 7$).

Regression	Coefficient	R ²	p-value
Wetland area (ha) on water level (m)			
Atkinson Marsh	-116.98	0.883	0.018
Peter's Marsh	-69.31	0.897	0.015
Long Tail Marsh	-36.40	0.902	0.013
Meadow area (ha) on water level (m)			
Atkinson Marsh	-15.85	0.861	0.023
Peter's Marsh	-39.26	0.900	0.014
Long Tail Marsh	-22.21	0.845	0.027
Meadow area (ha) on Wetland area (ha)			
Atkinson Marsh	0.29	0.937	< 0.001
Peter's Marsh	0.53	0.977	< 0.001
Long Tail Marsh	0.60	0.908	0.001
Marsh area (ha) on water-level (m)			
Atkinson Marsh	-102.06	0.859	0.024
Peter's Marsh	-24.48	0.784	0.046
Long Tail Marsh	-14.75	0.991	< 0.001
Marsh area (ha) on Wetland area (ha)			
Atkinson Marsh	0.70	0.987	< 0.001
Peter's Marsh	0.46	0.900	0.001
Long Tail Marsh	0.28	0.901	0.001

and Meadow area was below the prediction interval in 2000 for Peter's and Long Tail marshes. However, Marsh area in 1998 fell within the 95% prediction interval for all three marshes and within the prediction interval for Atkinson and Peter's marshes in 2000, and Meadow area fell within the 95% prediction interval in 1998 for all three marshes and in 2000 for Atkinson Marsh (Fig. 7). Results based on water level rather than Wetland area differed only in that, for Long Tail Marsh, Marsh area was above the prediction interval in 1998.

While the historical pattern of Marsh recruitment continued with a net rise in water level between 1992 and 1998, the pattern of Marsh recruitment changed during the most recent water level decline, as we hypothesized. Variable water levels with a net rise between 1992 and 1998 were associated with lake:land ratios > 1, indicating landward recruitment, as predicted by the historical pattern. During this time period, Marsh patches conglomerated and

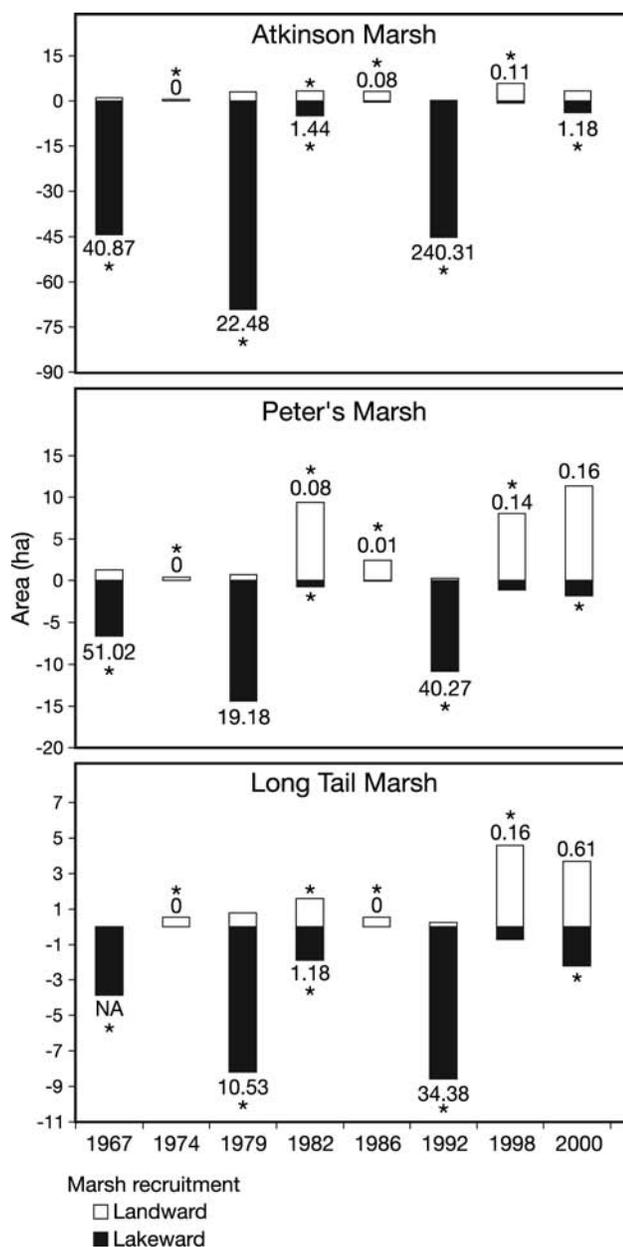


FIG. 6. Area of Marsh recruitment in the lakeward and landward directions. Lakeward recruitment is represented by negative areas and landward recruitment is represented by positive areas. The number displayed with each bar is the ratio of lakeward to landward recruitment (lake:land) and * indicates direction of Marsh recruitment expected based on water-level change. Note the different y-axis scales.

Meadow patches disappeared, although some areas of Marsh converted to Meadow. Despite a 0.8-m drop in water levels between 1998 and 2000, Marsh continued to recruit primarily landward or nearly equal in both directions, with lake:land ranging from 0.2 (Peter's) to 1.5 (Atkinson) as Marsh replaced Meadow, filled Meadow patches, and expanded along its landward border (Fig. 6).

DISCUSSION

Strong, linear relationships between area and water level supported our first hypothesis that wetland area, marsh, and wet meadow expanded historically as water levels fell and contracted as they rose (Table 3). This pattern is consistent with the contraction and expansion of emergent and wet meadow habitats seen in Pentwater Marsh, Lake Michigan, by Kelley *et al.* (1984) and the strong relationship found between wetland area and water level in other Great Lakes coastal wetlands (Lyon and Drobney 1984, Gottgens *et al.* 1998).

Supporting our second hypothesis, we found evidence that change in Marsh and Meadow area during the most recent water-level decline does not fit the historical pattern in Peter's and Long Tail marshes. In Long Tail Marsh, Marsh area exceeded the 95% prediction interval about the regression line in 2000. This overabundance of Marsh was balanced by lower than predicted Meadow area. In 2000, Meadow area was also lower than predicted in Peter's Marsh (Fig. 7). While we did not find deviation from the historical pattern in Atkinson Marsh, very little Meadow was present in 1998 and 2000. Even though Wetland area recovered after the high water level of 1974, the Meadow area remained small in Atkinson Marsh, which experienced the smallest changes in Meadow area of the three wetlands despite having the largest changes in Wetland area (Fig. 5).

Evidence also supports our third hypothesis that marsh habitat continued to expand landward during the most recent water level decline. The Marsh expansion helps explain the small Meadow areas observed in 2000. In the historical pattern, Marsh recruited primarily landward during rising water levels and primarily lakeward during falling water levels. While water levels began falling after 1997, landward recruitment of Marsh was greater between 1998 and 2000 than in any other interval of declining water levels, and lakeward:landward recruitment was less than or close to 1.

Our third hypothesis is further supported by field

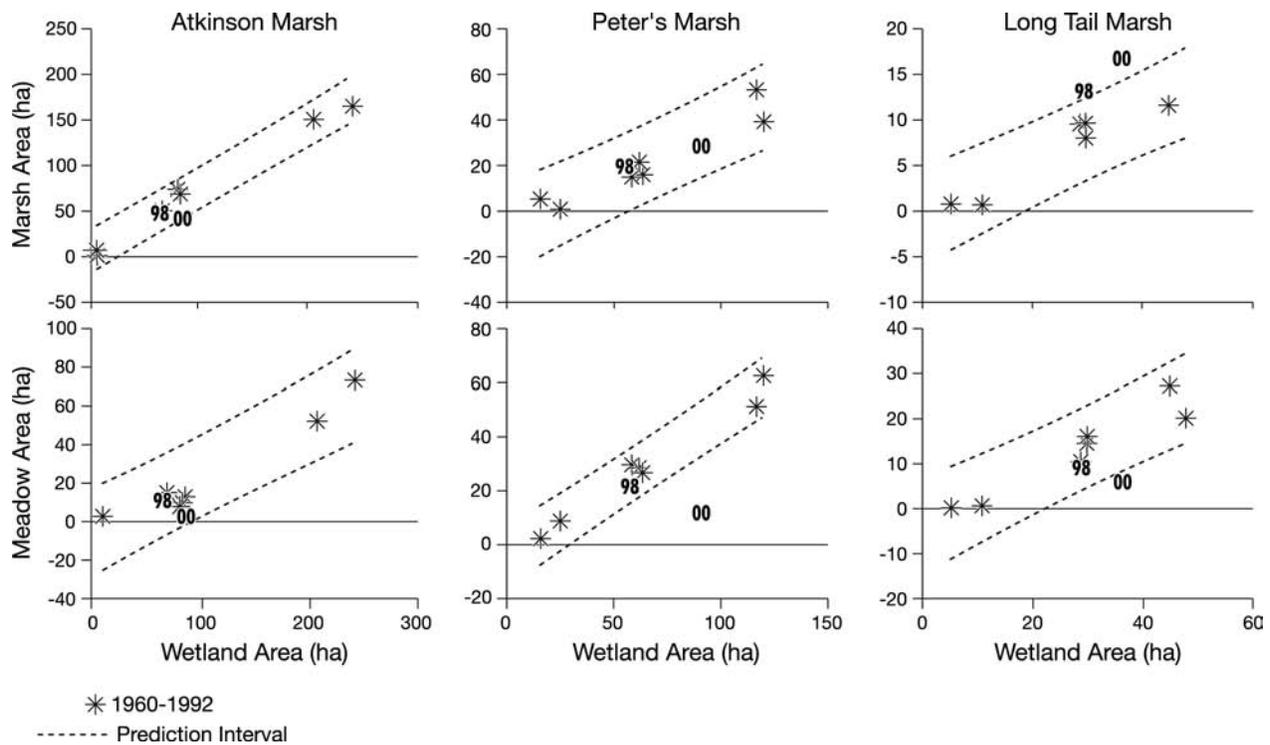


FIG. 7. *Ninety-five percent prediction intervals based on linear regressions of habitat area on wetland area. Stars represent areas used in the regression, two-digit years represent areas from the most recent period of water-level decline that were tested against the regression. Note the different y-axis scales.*

data collected after several years of sustained low water levels. In June 2003, we mapped the boundary between wet meadow habitat and *Typha* \times *glauca* Godr. (pro sp.)-dominated (marsh) habitat in each of the study marshes using a hand-held Garmin GPS unit (Frieswyk and Zedler in press). When this boundary was overlain on the 2000 map, we measured both landward and lakeward changes in the boundary position within each wetland. The boundary moved primarily landward, up to 30 m in some places; lakeward movement was never more than 15 m.

We recognize, however, that lag effects could be influencing our results. The decline in water level preceding the 2000 map, while large, occurred over a period of only two growing seasons, while water level declines preceding the 1967, 1979, and 1992 maps occurred over longer periods, giving the vegetation more time to respond. Data on the lag time between water level and vegetation change in Great Lakes coastal wetlands are inconsistent. Williams and Lyon (1997) found a lag time of 14 years for emergent wetlands along the St. Mary's River.

Using the same method, our data showed a 6-year lag time in the Meadow area of Atkinson Marsh, but no lag time for Meadow in the other two marshes or for Marsh in all three marshes. Hudon *et al.* (2005) found that broad classes of wetland vegetation (Meadows and mudflats, Marshes, and Shallow submerged) responded quickly to the water level of the current and previous growing seasons in Lake Saint-Pierre. In addition, while few data are available on the drought tolerance of marsh vegetation, Harris and Marshall (1963) found reduced *Typha* spp. density after only 1 year of drawdown in a Minnesota marsh.

Historically, the marsh zone of Green Bay coastal wetlands was dominated by the native *Typha latifolia* L. Today, *Typha* \times *glauca* and *Typha angustifolia* L. are expanding throughout the Great Lakes (Chow-Fraser *et al.* 1998), and these aggressive invaders are widely dominant (Frieswyk 2005). While *Typha* \times *glauca* has likely been present in Green Bay coastal marshes for the last 50 years, it became ecologically important in the late 1980s (Smith 1987). Our field data found *T. xglauca* to dominate

the marsh habitat in Green Bay coastal wetlands, while sparse *T. angustifolia* occurred in the bare sand/mud flat areas. *T. ×glauca* is more competitive and more tolerant of water level fluctuation (Galatowitsch *et al.* 1999), and it tolerates a wider range of water depths than *T. latifolia* (Waters and Shay 1990). Its wide tolerance range may be due to the production of both shallow and deep rhizomes (S.G. Smith, University of Wisconsin - Madison, pers. comm.). Its growth form is a dense canopy, due to short intervals between rhizome branches (Woo and Zedler 2002). As a hybrid of *T. latifolia* and *T. angustifolia*, *T. ×glauca* produces very few seeds and therefore reproduces primarily vegetatively (Smith 1987). Sexual reproduction occurs only in the presences of both parents (Chow-Fraser *et al.* 1998), but unlike most emergent species, seeds are able to germinate under water (Shay *et al.* 1999). *T. angustifolia*, on the other hand, is better able to disperse its seeds and colonize disturbed wetlands (Smith 1986) and tolerates deeper water (Grace and Wetzel 1982) than *T. latifolia*.

When water levels are low, the vegetation that develops on bare soil depends on germination from the seed bank (Keddy and Reznicek 1986), and the subsequent flooding regime influences establishment (Hudon *et al.* 2005). At the upslope edge, expansion of intact vegetation is limited by drying that shifts competitive advantage (Wilcox *et al.* 2005). Neither process operates when water levels are stabilized, so *Typha* spp. expand (as in Lake Ontario coastal wetlands; Wilcox *et al.* 2005) and wet meadow shrinks. Low water levels can reduce wet meadow habitat if *T. ×glauca* fails to migrate downslope by tolerating drier conditions. Resilience of wet meadow would then depend on the seed bank or dispersal from other wet meadows. Three factors reduce chances that wet meadow will persist unaided. First, the dense growth and thick litter of *T. ×glauca* inhibit germination from the seed bank (Frieswyk and Zedler 2006). Second, bare patches might be swamped by the abundant and widely dispersed seeds of *T. angustifolia*. Third, floating mats of *Typha* spp. could arrive on bare sand/mud flats as high waters recede, although we did not find such mats in our study wetlands. The potential for wet meadow vegetation to recover is far from certain, especially where invaders are able to become more aggressive.

While not a prerequisite for the expansion of *T. ×glauca*, the growth and spread of invasive species, including *T. ×glauca*, can be enhanced by an increase of urban and agricultural land use in water-

sheds (Galatowitsch *et al.* 1999, Boers 2006). Our results show that increased urbanization in the watersheds of the Green Bay coastal wetlands (Fig. 3) coincided with the loss of wet meadow habitat (Fig. 7). Similarly, Thibault and Zipperer (1994) found that as agricultural land was urbanized near Syracuse, New York, wet meadows converted to scrub-shrub or emergent cover in wetlands. The indirect effects of urbanization on Great Lakes coastal wetlands is poorly studied, but the changes in hydrology and sediment quality normally associated with urbanization (Lougheed *et al.* 2001, Paul and Meyer 2001, Choi and Bury 2003) could affect habitat dynamics and promote invasive species like *Typha ×glauca*, especially when lake levels are low. For example, Harris and Marshall (1963) found that during drawdown in Agassiz Refuge, Minnesota, the expansion and survival of emergents, including *Typha ×glauca*, depended in part on the sediment type, which is linked to the rate of drainage and soil chemistry.

In addition to undergoing changes in habitat area, the three study wetlands decreased in total area over time, not regaining their full extent following extreme high water levels (Fig. 5). A similar trend has been recognized in other Great Lakes coastal wetlands where recovery from high water levels has been incomplete in response to anthropogenic stresses such as shoreline armament, land-use change in the watershed, the introduction of common carp (*Cyprinus carpio*) and altered food webs (Chow-Fraser *et al.* 1998, Gottgens *et al.* 1998, Kowalski and Wilcox 1999). In lower Green Bay, long-term loss of wetland area was initiated by the loss of the Cat Islands, which occurred after severe spring storms and extreme high water levels in the spring of 1973. Plans to restore wetland area and provide wildlife habitat by restoring the Cat Island chain are already underway (V. Harris, Wisconsin Sea Grant, pers. comm.).

After we completed our field work, another invasive species, *Phragmites australis* (Cav.) Trin. ex Steud., began expanding in Green Bay. During the 2000 growing season, *Phragmites* formed substantial stands in Green Bay wetlands (G. Fewless, University of Wisconsin - Green Bay, pers. comm.). An ongoing study documented an increase in *Phragmites* cover of more than 100-fold between 2001 and 2004 in one Green Bay coastal wetland (M. Tulbure and C. Johnston, South Dakota State University, pers. comm.). Earlier, Wilcox *et al.* (2003) found that *Phragmites* was increasingly dominant in a Lake Erie wetland between 1995 and 1999, pri-

marily replacing wet meadow and marsh habitat. The long-term relative distributions of *Typha* spp. and *Phragmites* in Great Lakes coastal wetlands are uncertain, because each species can show competitive superiority depending on environmental conditions (Grosshans and Kenkel 1997, van der Putten *et al.* 1997, Shay *et al.* 1999). Grosshans and Kenkel (1997) found *Phragmites* to be less competitive while Shay *et al.* (1999) found *Phragmites* to be more competitive than *Typha* spp. under fluctuating water levels. However, the increasing invasion of Great Lakes coastal wetlands by *Phragmites* will further change habitat dynamics and contribute to the loss of wet meadow and biodiversity.

Because wet meadows are the most species-rich habitat type in Great Lakes coastal wetlands (Keddy and Reznicek 1986, Wilcox *et al.* 2005), their replacement by *Typha*-dominated (marsh) habitat threatens the ecological integrity of regional wetlands. Wet meadows contribute to wetland structural complexity (Wilcox *et al.* 2005) and support a wide range of wildlife, particularly birds (Riffell *et al.* 2001), while marshes dominated by *Typha*, and particularly *T. xglauca*, are known to be structurally uniform and monotypic (Smith 1986, Frieswyk 2005).

Our evidence indicates that *Typha*-dominated habitat can expand to eliminate wet meadow habitat during periods of low water levels. Although water-level variation sustains the structure and function of Great Lakes coastal wetlands (Planck 1993, Wilcox *et al.* 2005), ecological integrity remains at risk. The dual stresses of invasive species and land-use change could overwhelm the beneficial effects of water level fluctuation (Patterson and Whillans 1985) and allow wet meadow to be displaced by *Typha* spp. Fluctuating water levels are necessary but not sufficient to preserve and restore ecological integrity. Documenting shifts in vegetation before wet meadow is entirely eliminated gives managers cause for action, and we urge more widespread monitoring of vegetation change via historical air photo interpretation.

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Effects of *Phalaris arundinacea* and nitrate-N addition on the establishment of wetland plant communities

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Summary

1. Nutrient enrichment may adversely impact plant species richness in wetlands and enhance their susceptibility to colonization and dominance by invasive species. For North American prairie wetlands, enrichment by nitrate-N ($\text{NO}_3\text{-N}$) from agricultural runoff is thought to contribute to the increasing colonization and dominance of *Phalaris arundinacea* (reed canary grass), especially during restoration. If true, *P. arundinacea* might compromise the re-establishment of sedge meadow vegetation on sites reflooded with agricultural drainage water.

2. We tested this hypothesis using a fertilization experiment in wetlands with controlled hydrology. A community mixture comprising 11 species from native sedge meadow was seeded in mesocosms and grown under one of three $\text{NO}_3\text{-N}$ levels ($0 \text{ g m}^{-2} \text{ year}^{-1}$, $12 \text{ g m}^{-2} \text{ year}^{-1}$, $48 \text{ g m}^{-2} \text{ year}^{-1}$) with or without *P. arundinacea*. Above- and below-ground biomass were measured after two growing seasons to assess the response of vegetation to $\text{NO}_3\text{-N}$ and *P. arundinacea* treatments.

3. The total shoot biomass of the native community was suppressed in the presence of *P. arundinacea* at all $\text{NO}_3\text{-N}$ levels, but shoot suppression was significantly greater at the highest $\text{NO}_3\text{-N}$ dose level (48 g m^{-2}). Shoot growth of the native community was reduced by nearly one-half under these conditions.

4. The total root biomass of the community was also suppressed by *P. arundinacea* when no $\text{NO}_3\text{-N}$ was added.

5. As $\text{NO}_3\text{-N}$ increased, the relative abundance (shoot biomass) of native graminoids declined while native forbs increased in communities with and without *Phalaris*. The most common graminoid, *Glyceria grandis*, was suppressed by *P. arundinacea* at all levels, with suppression enhanced at the $48 \text{ g m}^{-2} \text{ NO}_3\text{-N}$ level. Three other species were suppressed at the highest $\text{NO}_3\text{-N}$ level, in the presence of *Phalaris*. The two most common forbs, *Asclepias incarnata* and *Sium suave*, exhibited a continual increase in growth with $\text{NO}_3\text{-N}$ additions along with overall suppression by *P. arundinacea*.

6. Community diversity and evenness declined with increasing $\text{NO}_3\text{-N}$ levels, whether or not *P. arundinacea* was present.

7. Our results demonstrate that if *P. arundinacea* is present, the restored sedge meadow community will not achieve levels of abundance that are possible when this species is absent, regardless of $\text{NO}_3\text{-N}$ enrichment conditions.

8. At the same time, the increased suppression by *P. arundinacea* at the $48 \text{ g m}^{-2} \text{ NO}_3\text{-N}$ dose level supports the hypothesis that the dominance of this species over the native sedge meadow community is enhanced by $\text{NO}_3\text{-N}$ inputs at levels that are common in agricultural landscapes.

9. Our results carry two implications for achieving biodiversity conservation in agricultural landscapes. First, reducing nitrate loads to wetland reserves is essential for minimizing declines in community diversity. Secondly, the use of *P. arundinacea* for soil conservation and other agri-environmental purposes should be curtailed because of the likelihood of off-site impacts to wetland biodiversity.

Key-words: agricultural impacts, ecological restoration, invasive species, prairie pothole wetland

Introduction

Wetlands are increasingly valued for ecosystem services, such as improving water quality through nutrient removal and filtration of sediments and chemicals, controlling and storing surface water, recharging groundwater, and providing wildlife habitat. In the prairie pothole region of North America thousands of wetlands have been restored in recent years, driven by the goal of improving or returning these ecosystem services to the landscape (Galatowitsch & van der Valk 1994). The prairie pothole region is an approximately 780 000 km² area in the central mid-continent where the vast majority of wetlands, once abundant landscape features, were drained for conversion to agricultural production (Kantrud, Krapu & Swanson 1989; Dahl & Johnson 1991). Knowledge is conspicuously lacking on how to recreate successfully the ecological structure and function of natural wetlands (Galatowitsch & van der Valk 1994; Crumpton & Goldsborough 1998; Murkin 1998). Restored wetlands often fail to resemble extant wetlands in vegetative structure and composition, and in plant and animal diversity (Mack 1985; Delphey & Dinsmore 1993; Reinartz & Warne 1993; Galatowitsch & van der Valk 1996a,b). Moreover, restored wetlands in the prairie pothole region are often dominated by a small number of invasive plant species (Galatowitsch, Anderson & Ascher 1999). Dominance by fewer species can profoundly alter ecosystem processes and reduce biotic diversity on a landscape scale (Drake *et al.* 1989; D'Antonio & Vitousek 1992; Vitousek & Hooper 1993; Gordon 1998).

The causes for the vulnerability of restored prairie pothole wetlands to plant invasions have not been thoroughly investigated. In general, landscape disturbance is believed to enhance the susceptibility of a site to invasion (Burke & Grime 1996; Galatowitsch, Anderson & Ascher 1999; Symstad 2000). In addition, it appears that plant invasions are most successful where disturbance coincides with increased fertility (Hobbs & Atkins 1988; Burke & Grime 1996). Situated in landscapes of intensive agricultural row crop production, restored prairie pothole wetlands are subject to high levels of nutrient enrichment from surface runoff and subsurface drainage, particularly enrichment by nitrate-N (NO₃-N) (Baker & Johnson 1981; Davis *et al.* 1981; Neely & Baker 1989; de Molenaar 1990). A strong correlation has been demonstrated between increased nutrient loads and shifts in wetland species composition and species dominance in ombrotrophic and minerotrophic fens in the Netherlands (Verhoeven *et al.* 1983; Vermeer & Berendse 1983; Vermeer & Verhoeven 1987; Verhoeven, Koerselman & Beltman

1988). A similar shift, along with overall reduced species richness, has been demonstrated in eutrophied aquatic systems (Wentz 1976; Whigham, Simpson & Lee 1980; Dolan *et al.* 1981; Tilman *et al.* 2001).

In the prairie pothole region, one of the chief invasive species is *Phalaris arundinacea* L. (reed canary grass), a cool season, perennial grass, believed to be indigenous to the North American continent but improved by selection (Galatowitsch, Anderson & Ascher 1999). *Phalaris arundinacea* grows under a wide range of environmental conditions and has been observed to colonize preferentially post-disturbance moist devegetated sites and achieve rapid and near-total dominance over native wetland plant communities (Hodgeson 1968; Comes 1971; Morrison & Molofsky 1998; Galatowitsch, Anderson & Ascher 1999). In restored wetlands, *P. arundinacea* was shown to preclude the establishment of a common meadow graminoid, *Carex lacustris* (Budelsky & Galatowitsch 2000). *Phalaris arundinacea* has shown dramatic increases in biomass in response to nitrogen fertilizer inputs (Mason & Miltimore 1970; Niehaus 1971; Dubois 1994; Figiel, Collins & Wein 1995). In a controlled greenhouse experiment, Green & Galatowitsch (2001) found, however, that *P. arundinacea* could suppress the native community regardless of nitrate level (0–40 mg l⁻¹).

Improving control strategies for *P. arundinacea* requires greater understanding of its mechanisms for colonization and dominance over native species, including both innate biological characteristics and environmental factors. Furthermore, because restored wetlands in the prairie pothole landscape are frequently intended to achieve multiple ecological goals, in particular vegetative diversity and water quality improvement, it is critical to improve understanding of the potential interaction and/or conflict between these goals. The primary objective of this research was to test the hypothesis that NO₃-N enrichment of a restored prairie pothole community would be associated with greater dominance by *P. arundinacea* over the native sedge meadow plant community after the first two growing seasons. We conducted a controlled field experiment designed to observe an experimental plant community's responses to specific nitrogen input levels in the presence and absence of *P. arundinacea*, as well as to test for the interaction between the effects of these factors.

Methods

EXPERIMENTAL DESIGN OVERVIEW

Native communities were grown in controlled mesocosms in a field setting and subjected to six treatments consisting of three NO₃-N addition levels (0, 12 and 48 g m⁻² year⁻¹ NO₃-N) and two invasion conditions [native community mixture (non-weed); native community plus *P. arundinacea* addition] (all species nomenclature follows Gleason & Cronquist 1991). The

experimental design was a randomized incomplete block with each treatment replicated 10 times.

STUDY SITE AND PREPARATION

The experiment was conducted at the University of Minnesota Horticultural Research Center in Carver County, Minnesota, USA, 44°51'45"N latitude, 93°36'00"W longitude. Historically a depressional wetland, the research area was drained and planted with grain crops during the first half of the 20th century. In 1974, the area was cleared, an irrigation and drainage system was installed, and the site used for research on *Zizania aquatica* L. (wild rice). In 1994, it was dedicated to wetland restoration research. The area was cleared once again and the land surface graded to form four rectangular basins separated by earthen dikes. Each basin was approximately 0.20 ha, with an approximate 5% slope on all sides and a 1.0-m depth at the centre. Each basin had a water inlet and adjustable drainage tile to allow for precise control of water levels during the growing season. The experiment was conducted on the western sides of two basins. In October 1997, the experimental sides were regraded to create even soil elevation throughout, and treated with Basamid® soil fumigant (Dazomet; BASF Corporation, Mt Olive, NJ) to eliminate the seed bank. The soil was a Glencoe clay loam (Cumulic Endoaquoll). Soil tests conducted by the University of Minnesota Research Analytical Laboratory in spring 1998, prior to the start of the experiment, indicated surface soil (0–10 cm) macronutrient levels were as follows (all measurements in mg kg⁻¹): 0.4–0.8 NO₃-N; 409–627 total P; 3602–4163 Ca; 756–839 Mg; 128–180 K; 42–49 Na. NO₃-N in basin water was 0.01–0.02 mg kg⁻¹. The pH (KCl) of all water samples was between 6.4 and 6.8. Nitrate for all samples was extracted with 0.01 M CaCl and measured using cadmium reduction colorimetry on an Alpkem Rapid Flow Analyser (Astoria of Pacific International, Klackamas, Oregon, USA) at 520 nm. Total phosphorus was measured using a microwave digestion method (EPA 3052, US Environmental Protection Agency) and subsequent analysis of the digestate with inductively coupled argon plasma (ICP, Fisons Instruments Division, Waltham, Massachusetts, USA) analysis. The remaining nutrients were measured using a 1-N ammonium acetate extract with ICP analysis.

In May 1998, 60 circular plots (1.13 m²) were established, 30 in each basin, in two rows per basin. Plot boundaries were formed with circles of 0.060 gauge plastic (0.61 m high, 1.2 m diameter), embedded in the soil to a depth of approximately 0.5 m, with a 1.0-m distance between every plot. Plot soil heights were surveyed before and after placement of plot boundaries and extensive effort was made to equalize soil height in every plot. Nevertheless, soil settling and microtopography resulted in some variance among plots. The range between the highest and lowest plot in the south basin was 4.6 cm (standard deviation = 0.99), while in

the north basin the range was 5.0 cm (standard deviation = 1.3). Additional survey measurements taken at the beginning of the second field season and at the end of both seasons verified that no additional soil settling occurred in the course of the research. Water levels in both basins were maintained constant throughout the experimental growing seasons at 2–3 cm below mean plot soil surface in each basin. Groundwater wells (2.54 cm diameter) were placed to a depth of 40 cm in each plot and between all plots to enable continual monitoring of water levels.

The native sedge meadow community mixture comprised 11 species that are abundant and widespread in prairie pothole wetlands in this region (Galatowitsch & van der Valk 1994) and that represent the two primary functional groups found in prairie wetlands: C₃ perennial graminoids and non-leguminous perennial forbs (see Table 2 for species list). All native community seeds were collected in 1996 or 1997 from wetlands in southern Minnesota or northern Iowa. *Phalaris arundinacea* seed from an open-pollinated population (i.e. not cultivars) was obtained through the University of Minnesota Department of Agronomy. Voucher specimens have been deposited at the University of Minnesota herbarium. Viability for each species' seed batch was estimated using a tetrazolium chloride test on a sample of 150–200 seeds per species (Grabe 1970).

The native community seed mixtures were created with equal viable densities of each species and a total native community viable seed density of 1500 seeds m⁻². The experimental density approximated actual densities found in wet meadow seed banks in prairie wetlands (van der Valk & Davis 1976, 1978; Weinhold & van der Valk 1989; Galatowitsch & Biederman 1998). Beginning in April 1998, the seed mixtures were placed in cold wet storage at 4 °C for 46 days to overcome seed dormancy. To prevent fungal infection during cold stratification, the mixtures were first soaked for 60 s in a 1 : 2 bleach and water solution and rinsed thoroughly.

EXPERIMENTAL TREATMENTS

Prior to cold stratification, *P. arundinacea* seed was added to 30 randomly chosen seed mixtures at a relative viable density equal to that of each individual species in the mixture, for a total viable seed density of 1636 m⁻² in *Phalaris*-addition plots.

Following the stratification period, the seed mixtures were sown with random assignments of treatments to plots within both basin and row blocks (15 plots per row in four row blocks, two rows per basin). Because the row blocks did not allow for three full replicates, the randomization process was as follows: two full replicates of the six treatment combinations plus three randomly selected treatments from a third replicate were assigned to one row block; the remaining three treatments from the incomplete replicate and another two full replicates were assigned to the second row block in the same basin. The process was repeated for the

second basin. Overall, the loss of statistical efficiency due to incomplete row blocks was minimized by the balancing of basin blocks.

NO₃-N treatment levels were as follows: control (0 g NO₃-N m⁻² year⁻¹), low (12 g NO₃-N m⁻² year⁻¹) and high (48 g NO₃-N m⁻² year⁻¹). The high NO₃-N level was chosen so that the resulting concentration would be comparable to above-average (but below maximum) values reported from tile drainage in the region (Davis *et al.* 1981; Neely & Baker 1989). Based on results from a greenhouse experiment (Green & Galatowitsch 2001) that showed greater treatment differences among low nitrate levels, the low NO₃-N level in this field study was selected to be 25% of the high level. Treatments consisted of calcium nitrate tetrahydrate [Ca(NO₃)₂·4H₂O] dissolved in water. Calcium nitrate was used for three reasons. First, this salt is very soluble in water so amenable to treatment application from stock solutions. Secondly, as the local soil is derived from highly calcareous glacial till, calcium is by far the dominant cation; use of this salt was less likely to change the ionic balance than other choices. Finally, nitrate is the predominant form of nitrogen that wetlands receive from tile runoff; ammonium is stable under anaerobic conditions so would not have readily nitrified. NO₃-N treatments were divided into two applications per field season, timed approximately 4 weeks and 9 weeks after plant emergence. Nitrogen solution was delivered to the plots using a fertilizer spreader with a manual control nozzle to minimize contact with plant tissue. Nitrogen applications were followed by 15 s of aerial water irrigation. Water from groundwater wells in each of the research plots was sampled, and nitrogen levels measured, 2 days and 4 weeks following NO₃-N treatment applications. Measurements were taken using a nitrate ion-selective electrode (HACH One Model 48680; HACH Company, Loveland, CO) in order to determine approximate range of NO₃-N levels experienced per treatment. During the first 6 weeks of the first field season, all plots were weeded weekly for all extraneous species, weeds consisting mainly of annual grasses. During the second field season, weeding was done only as needed to remove *P. arundinacea* from non-weed plots. Non-weed plots were carefully monitored throughout the field season for the presence of *P. arundinacea*, and weeding was required twice.

DATA COLLECTION

Plant material was harvested in late August 1999, 15 months after seeds were sown. Although an effort was made to time plant harvesting with the time of maximum standing crop for a majority of the species, it was impossible to correspond timing exactly for all species. Species that did not appear to be at maximum standing crop at the time of harvest were *Aster* spp., *Eleocharis palustris* and *Eupatorium purpureum*. Above-ground plant material was harvested from a 0.5-m² sampling area in each plot. Plant material was clipped

5 cm above the soil surface and sorted by species. After completion of above-ground harvest, below-ground plant material was taken from a 0.1-m² sampling area in plots of the south basin only. Below-ground plant material was removed with soil cores of 25 cm depth. The shallow depth to water table restricted roots to the top 25 cm of sediment.

The sampling areas for both above- and below-ground plant material were delineated by placing plastic hoops of the required size in the plot centre, equidistant from all edges, thereby avoiding edge growth in all plots. The below-ground material was rinsed thoroughly to remove soil, and sorted into groups of *P. arundinacea* and native community mixture. The 5-cm plant stem base was used to distinguish *P. arundinacea* and native community roots. Fine roots not attached to a plant stem base could not be reliably identified and were included in an 'unknown' group. All plant material was dried at 70 °C, for 48 h, and weighed.

STATISTICAL ANALYSES

Treatment effects on native community shoot, root and total biomass and total community evenness and diversity (Shannon's index) were analysed using the analysis of covariance (ANCOVA) procedures in MacAnova (University of Minnesota 1997). The model includes basin and row as fixed blocks and NO₃-N (0, 12 and 48 g m⁻² NO₃-N) and invasion condition (none and *Phalaris* addition) as fixed factors. The model assumes that row blocks may interact with factors whereas basin blocks do not. The difference in plot soil height from the basin-wide plot height mean was considered a covariate. The covariate did not contribute significantly to the observed variance of any dependent variable. Biomass data were logarithmically transformed in order to minimize heteroscedasticity (Sokal & Rohlf 1995). Means were compared using Tukey's honest significant difference (HSD) with $\alpha = 0.05$. In addition, ANCOVA procedures were used to analyse effects of NO₃-N treatments on the differences in shoot biomass for *P. arundinacea* and the non-weed native community. For all tests, differences were considered significant only if $P < 0.05$.

Results

NO₃-N levels declined from their application concentration to near 0 within 4 weeks following application (Table 1). Mean total community biomass increased with NO₃-N dose level ($F = 11.11$; d.f. = 2, 19; $P = 0.0006$). In the absence of *P. arundinacea*, mean total community biomass increased 27.8%, 3564.1 g m⁻²–4554.7 g m⁻², from 0 to 48 g m⁻² NO₃-N levels (Fig. 1). Mean total community biomass in *Phalaris*-addition plots was lower with no NO₃-N additions (3082.7 g m⁻²), but increased 53.2% to 4721.6 g m⁻² at the 48 g m⁻² level.

At all NO₃-N dose levels, total native community shoot biomass was significantly less in *Phalaris*-addition

Table 1. Changes in NO₃-N concentrations from time of application to 4 weeks following application. NO₃-N concentrations were measured from shallow wells within each research plot

Dose level	NO ₃ -N (mg l ⁻¹) post-application			
	Mean 2 days	SD 2 days	Mean 4 weeks	SD 4 weeks
0	0.3	0.6	0.03	0.1
12	5.9	6.0	0.05	0.1
48	28.8	21.0	0.5	1.2

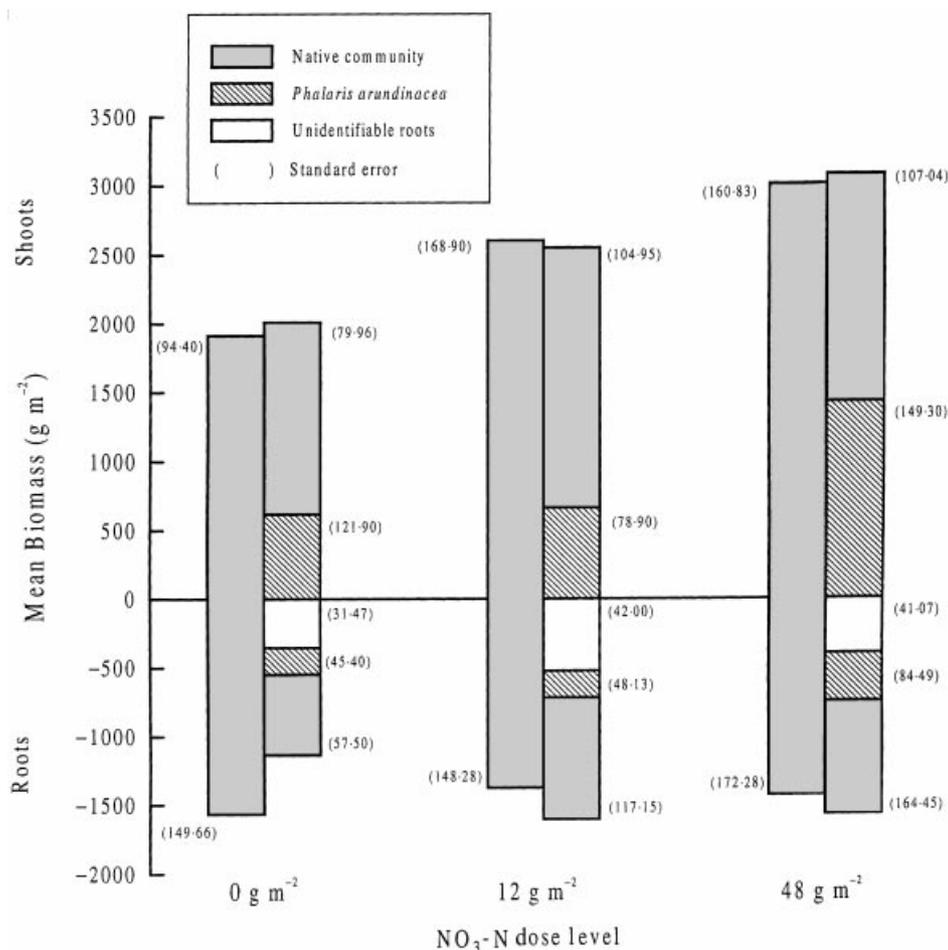


Fig. 1. Mean shoot and root biomass response of the native community and *Phalaris arundinacea* to NO₃-N treatments (0, 12 and 48 g m⁻²). Values are means ± 1 SE.

plots than in non-*Phalaris* plots ($F = 5.72$; d.f. = 1, 19; $P = 0.027$; Fig. 1). The analysis of covariance on total native community shoot biomass showed the NO₃-N-invasive interaction was significant ($F = 6.80$; d.f. = 2, 41; $P = 0.003$). In non-*Phalaris* plots the native shoot response to NO₃-N addition was a continuous increase in mean biomass from 1915.3 g m⁻² to 3010.0 g m⁻² in 0–48 g m⁻² NO₃-N-treated plots, respectively. In contrast, in *Phalaris*-treated plots native shoot biomass increased from 1392.2 g m⁻² to 1891.4 g m⁻² in 0–12 g m⁻² NO₃-N treatments, but then decreased to 1653.2 g m⁻² in 48 g m⁻² NO₃-N treatments.

NO₃-N additions enhanced shoot growth of *P. arundinacea* ($F = 16.82$; d.f. = 2, 17; $P < 0.0001$), its biomass more than doubling from 618.8 g m⁻² to

1426.0 g m⁻² over the range of NO₃-N treatments. The growth increase response occurred between 12 and 48 g m⁻² NO₃-N treatments, while there was no difference between 0 and 12 g m⁻² treatments (Fig. 1). At the highest NO₃-N dose level, the quantity of *P. arundinacea* shoot biomass (1426.0 g m⁻²) was similar ($t = 1.11$; $P = 0.15$) to that of the aggregate 11 species in the total native community (1653.2 g m⁻²).

Because the fraction of unknown roots was high (> 30% in all treatments) and not constant across NO₃-N treatment levels, characterizing differences in root growth between *P. arundinacea* and the native community was not possible. Comparing total root biomass between communities with and without *Phalaris* was informative. *Phalaris arundinacea* had a suppressing

Table 2. Shoot biomass response to NO₃-N treatments (0, 12 and 48 g m⁻²) for individual species in the seed mix. All species were planted at the same density: 9.1% of seed mix for plots without *Phalaris arundinacea* and 8.3% for plots with *P. arundinacea*. Percentages shown are based on total community biomass (+ < 1%)

NO ₃ -N treatments (g m ⁻²)	Shoot biomass (g m ⁻²) – plots without <i>Phalaris</i>									Shoot biomass (g m ⁻²) – plots with <i>Phalaris</i>								
	0			12			48			0			12			48		
	Mean	SE	%	Mean	SE	%	Mean	SE	%	Mean	SE	%	Mean	SE	%	Mean	SE	%
Native graminoids (total)	1251.6	72.8	65.3	1040.9	10.9	40.0	984.0	141.6	32.7	907.8	103.7	45.1	942.8	113.6	36.9	366.4	57.7	11.9
<i>Glyceria grandis</i> S. Wats.	509.1	117.1	26.6	416.9	64.3	16.0	681.1	164.0	22.6	323.0	65.0	16.1	355.8	50.4	13.9	248.0	48.9	8.1
<i>Scirpus atrovirens</i> Willd.	478.0	114.9	25.0	383.6	70.5	14.7	98.1	39.2	3.2	342.2	67.7	17.0	369.6	84.8	14.5	51.8	11.6	1.7
<i>Carex hystericina</i> F. Boott.	157.8	44.0	8.2	130.9	43.8	5.0	89.4	30.4	3.0	170.3	38.6	8.5	120.8	33.7	4.7	28.5	15.2	+
<i>Carex stricta</i> Lam.	82.0	25.8	4.3	67.9	19.4	2.6	88.9	26.1	2.9	55.4	16.9	2.8	73.0	18.5	2.9	25.7	10.5	+
<i>Calamagrostis canadensis</i> Michx.	18.2	3.5	+	39.4	9.5	1.5	25.7	6.7	+	16.0	6.85	+	22.0	3.4	+	11.3	6.0	+
<i>Eleocharis palustris</i> L.	6.5	2.4	+	2.4	1.2	+	0.9	0.5	+	1.0	0.3	+	1.8	0.9	+	1.0	0.8	+
Native forbs (total)	478.4	48.8	25.0	1372.1	183.3	52.7	1931.7	197.5	64.2	385.5	64.0	19.2	812.0	67.9	31.8	1169.7	112.7	38.0
<i>Asclepias incarnata</i> L.	140.8	23.3	7.4	627.3	106.1	24.1	1264.7	164.1	42.0	123.4	21.0	6.1	373.3	39.5	14.6	843.5	93.4	27.4
<i>Sium suave</i> Walter	107.5	31.5	5.6	233.7	54.5	9.9	394.3	71.7	13.1	111.7	44.9	5.6	166.6	33.2	6.5	222.8	35.5	7.2
<i>Aster</i> spp.	190.7	47.9	10.0	496.2	70.8	19.1	261.9	71.2	8.7	130.7	17.9	6.5	262.1	38.9	10.3	99.0	33.9	3.2
<i>Sagittaria latifolia</i> Willd.	39.0	21.7	2.0	13.9	5.2	+	4.3	2.1	+	19.3	12.0	+	9.7	5.7	+	4.3	3.2	+
<i>Eupatorium purpureum</i> L.	0.5	0.2	+	0.9	0.5	+	6.5	5.2	+	0.4	0.2	+	0.3	0.2	+	0.1	0.1	+
<i>Phalaris arundinacea</i> L.	–	–	–	–	–	–	–	–	–	618.8	121.9	30.8	663.0	78.9	26.0	1426.0	149.3	46.3
Unknown/other	185.2	42.8	9.7	191.4	40.2	7.3	94.4	33.7	3.1	98.93	24.97	4.9	136.6	18.6	5.3	117.12	28.62	3.8
Total community	1915.3	94.4		2604.5	168.9		3010.0	160.8		2011.0	117.0		2554.3	101.0		3079.2	159.1	

Table 3. Community diversity and evenness for NO₃-N and *Phalaris*-addition treatment combinations ($n = 10$ for each). Both evenness and diversity differed among NO₃-N treatment levels ($*P < 0.0001$) but not between *Phalaris*-addition and non-*Phalaris* plots ($P > 0.05$). Tukey HSD tests showed the high NO₃-N treatment level (b) differs from low and no NO₃-N levels (a) for both evenness and diversity ($P = 0.05$)

Nitrate treatments	Plots without <i>Phalaris</i>			Plots with <i>Phalaris</i>		
	Mean	SE	Range	Mean	SE	Range
Community diversity						
0 g m ⁻² *a	1.584	0.087	1.118–1.923	1.719	0.054	1.422–1.911
12 g m ⁻² *a	1.717	0.041	1.385–1.821	1.822	0.064	1.374–2.105
48 g m ⁻² *b	1.416	0.087	0.833–1.839	1.350	0.066	0.957–1.684
Community evenness						
0 g m ⁻² *a	0.700	0.031	0.538–0.826	0.721	0.019	0.618–0.797
12 g m ⁻² *a	0.755	0.017	0.666–0.818	0.769	0.025	0.597–0.878
48 g m ⁻² *b	0.637	0.036	0.379–0.798	0.605	0.026	0.436–0.702

effect on total community root growth when NO₃-N was not added, but not at 12 and 48 g m⁻² doses ($F = 18.06$; d.f. = 1,19; $P = 0.0004$). With no NO₃-N addition, total root biomass was 27.6% lower in invasive plots (1135.22 g m⁻²) than in those without the invader (1567.82 g m⁻²). With NO₃-N addition, the total root biomass of plots with *Phalaris* was slightly higher (1572.61 and 1606.14 g m⁻², for 48 and 12 g m⁻² levels) than in the absence of *Phalaris* (1374.70 and 1430.10 g m⁻² for 12 and 48 g m⁻² levels). NO₃-N treatments had no effect on native total community root growth and there were no significant differences among treatment group means at any NO₃-N dose level.

The native community in the absence of *Phalaris* exhibited a significant decrease in proportional allocation to below-ground biomass in response to NO₃-N levels between 0 and 12 g m⁻² (Fig. 1). Root : shoot ratios for the non-weed native community ranged from 0.82 at 0 g m⁻² NO₃-N to 0.48 at 48 g m⁻² NO₃-N, with no significant difference between ratios at 12 and 48 g m⁻² dose levels (Fig. 1). In contrast, the root : shoot ratio of plots with *P. arundinacea* was similar across all NO₃-N levels, from 0.51 to 0.63.

General shifts in floristic composition, between graminoids and forbs, in response to NO₃-N levels were similar in plots with and without *Phalaris*. As NO₃-N levels increased, the relative abundance (shoot biomass) of native graminoids declined while native forbs increased (Table 2). Three of six graminoids, *Carex stricta*, *Calamagrostis canadensis* and *Eleocharis palustris*, and two of five forbs, *Sagittaria latifolia* and *Eupatorium purpureum*, were of minor importance (< 2% of community biomass) in all treatment combinations.

Growth patterns and responses to experimental treatments by the other six individual species in the native community, however, differed substantially. The most abundant graminoid, *Glyceria grandis*, was suppressed by *P. arundinacea* at all levels, with suppression enhanced at the 48 g m⁻² NO₃-N level, the growth trend that strongly coincided with that of the overall native community. The two most common forbs, *Asclepias incarnata* and *Sium suave*, exhibited a continual

increase in growth (absolute and relative) with NO₃-N additions along with overall suppression by *P. arundinacea* (Table 2). The remaining three species, *Aster* spp., *Carex hystericina* and *Scirpus atrovirens* had diminished abundance at the 48 g m⁻² NO₃-N dose level in the presence of *P. arundinacea*. *Aster* spp. had a peak biomass at 12 g m⁻² NO₃-N in plots with and without *Phalaris*.

Both total community diversity ($F = 19.72$; d.f. = 2,42; $P < 0.0001$) and evenness ($F = 17.33$; d.f. = 2,42; $P < 0.0001$) were lower in high NO₃-N plots than in low or no NO₃-N plots (Table 3). In contrast, *Phalaris* addition did not significantly affect either diversity or evenness. In plots with no NO₃-N addition, two species (*Glyceria grandis* and *Scirpus atrovirens*) comprised 52% of the community biomass together in plots without *Phalaris*; individually each had a relative biomass (26.6% and 25%, respectively) comparable to *Phalaris* (30.8%) in plots where NO₃-N was added. At 12 g m⁻² NO₃-N levels, *Phalaris* was 26% of the total biomass, similar to *Asclepias incarnata* (24.1%), the most abundant species in plots where *Phalaris* was not added. Where NO₃-N levels were highest (48 g m⁻²), two species combined for approximately two-thirds of the overall biomass, regardless of *Phalaris* addition. *Asclepias incarnata* (42%) and *Glyceria grandis* (22.6%) dominated plots without *Phalaris*, whereas *Phalaris* (46.3%) and *Asclepias* (27.4%) did so in plots where it was added.

Discussion

Our results illustrate the dominance of *P. arundinacea* over the restored native sedge meadow community across the range of NO₃-N inputs used here. At the same time, the significance of the NO₃-N–competition interaction and the enhanced suppression of native community shoot biomass in *Phalaris*-treated plots at the 48 g m⁻² NO₃-N dose levels supports the hypothesis that an increase in NO₃-N inputs further enhances the competitive ability and dominance of *P. arundinacea* over the native community. The greater suppression of

community root growth by *P. arundinacea* at the 0 g m⁻² NO₃-N dose level shifts to greater suppression of shoots at the 48 g m⁻² NO₃-N level. Although diversity and evenness declined with increasing NO₃-N levels, this was not observed for *Phalaris* additions. *Phalaris arundinacea* essentially replaced one to two native species that dominated at each NO₃-N level.

The extraordinary capacity of *P. arundinacea* to use NO₃-N inputs for growth is illustrated in its doubling of shoot biomass in response to an NO₃-N dose level between 12 and 48 g m⁻². In comparison, the native sedge meadow community in non-weed plots demonstrated a steady increase in growth in response to NO₃-N inputs, with an overall proportional biomass increase of 1.6 over the range of treatments. None the less, the apparent equivalency of *P. arundinacea* shoot biomass and the total aggregate shoot biomass of 11 species at the 48 g m⁻² year⁻¹ NO₃-N dose level suggests an obvious advantage of the former in resource capture. Perry (2001) observed that the nitrogen-use efficiency of *P. arundinacea* increased with inorganic N concentrations while that of *Carex hystericina* declined, suggesting *Carex* is less likely to benefit from high N availability when competing with *Phalaris*.

We suspect that the extent of productivity increase we observed on the part of *P. arundinacea* may not be unusual in the North American prairie pothole region. Measurements of the range of NO₃-N conditions experienced just before and several weeks after treatment applications in this experiment coincide approximately with actual NO₃-N levels that have been measured in prairie wetlands or in agricultural drainage water entering wetlands. For example, data collected from 1976 to 1979 on influent waters at Eagle Lake Marsh in north-central Iowa showed a flow-weighted average of 13.0 mg l⁻¹ NO₃-N (Davis *et al.* 1981). In a review of literature from 1970 to 1979, Neely & Baker (1989) reported NO₃-N concentrations found in subsurface drainage associated with corn and soybean cropping systems to range from 5.8 to 61.2 mg l⁻¹, with a mean of 21.0 mg l⁻¹.

The overall suppression of native community growth across the range of NO₃-N treatments suggests that *P. arundinacea* must be controlled in restorations where an abundant native sedge meadow community is desired, regardless of NO₃-N input levels. At the same time, our results suggest that the abundance of the native community will be even further reduced in the presence of *P. arundinacea* given an increase in NO₃-N dose levels from 12 to 48 g m⁻². In both the enhanced suppression of the native community by *P. arundinacea* over a range of NO₃-N levels, and the significance of the NO₃-N-invasive interaction in explaining variance in native community biomass, our results concur with those of Wetzel & van der Valk (1998). They found that *P. arundinacea* suppressed growth of *Carex stricta* and *Typha latifolia* at both low and high levels of a combined N, P and K nutrient treatment and that the interaction of competition and

nutrient input factors contributed to the reduction in *Carex stricta* productivity.

This experiment was not designed to investigate the nature nor the mechanisms of competition between *P. arundinacea* and the native community. Nevertheless, the decline of root : shoot ratios with nitrogen addition suggests that, with reduced nitrogen limitation, competition for light was greater. How and why *Phalaris* addition resulted in greater nutrient limitation for the native community with increasing NO₃-N is less clear. With no nitrate addition, the native community produced less root biomass per shoot biomass in the presence of *Phalaris*. At the highest NO₃-N level, the native community produced more root biomass per shoot biomass with *Phalaris* addition. *Phalaris* can cause a light limitation for its competitors by growing much faster after seedling emergence (Perry 2001). If *Asclepias incarnata* and *Sium suave* grew even faster than *Phalaris* with NO₃-N addition, light would have been more limiting in the absence of *Phalaris*.

Our results suggest that the floristic composition of restored wetlands is primarily affected by nitrate additions rather than *P. arundinacea*, at least in the short term. Our findings are consistent with mounting evidence correlating eutrophication and species richness reductions (Willis 1963; Golley & Gentry 1966; Thurston 1969; Al Mufti *et al.* 1977; van den Bergh 1979; Willems 1980; Tilman 1982; Wilson & Keddy 1988; Wisheu *et al.* 1991). In our study, nitrate additions decreased diversity and evenness and favoured native forbs over native graminoids, whether or not *Phalaris* was part of the community. Like *Phalaris*, *Asclepias incarnata* and *Sium suave* both have a high capacity to increase production in response to NO₃-N additions. *Asclepias* exhibited nine- and sevenfold increases, with and without *Phalaris* additions, respectively; *Sium suave* had four- and threefold increases. In the absence of *Phalaris*, the community shifted from being dominated by two graminoids, *Glyceria grandis* and *Scirpus atrovirens*, to being dominated by a forb (*Asclepias incarnata*) and a graminoid (*Glyceria grandis*) at the 48 g m⁻² NO₃-N additions. Plots with *Phalaris* additions were likewise dominated by one to two species across the nutrient gradient: *Phalaris* dominated at no to low NO₃-N additions, while *Asclepias* co-dominated at the highest NO₃-N inputs. Diversity and evenness decrease with and without *Phalaris* additions because the proportion of the biomass contributed by the most abundant one to three species increases from approximately one-half to nearly three-fourths across the nitrate gradient. The combination of high nitrate levels and the presence of *Phalaris*, however, differentially suppressed four of the six common species (three graminoids and one forb) in this experiment. At least four of six planted native graminoids had relative biomass greater than 1% in all but the 48 g m⁻² NO₃-N level treatment with *Phalaris*. Only two graminoids achieved this abundance under the treatment combination of high nitrates with *Phalaris*.

Limitations in the experimental time period preclude determining whether forbs, such as *Asclepias incarnata*, that capitalize on nitrate inputs can coexist in the long term with *Phalaris*. Observations from wetland restorations within the region (Mulhouse & Galatowitsch 2001) lead us to hypothesize that presence of *P. arundinacea* in a restored prairie pothole wetland may lead to a reduction in diversity over the long-term. The overall productivity of this species in N-enriched conditions and the suppressive effect on the native community suggests an increase in plant-induced stress upon its competitors that is likely to have a positive feedback effect further enhancing the resource capture and growth potential of the dominant species (*sensu* Grime 1979). Positive correlations have been demonstrated between increases in herbaceous plant community biomass and shifts in species composition, and the composition shifts have been further correlated with a decrease in species richness at the community scale (Willis 1963; Grime 1973, 1978, 1979; Al Mufti *et al.* 1977; Wheeler & Giller 1982). Long-term research (e.g. greater than 3 years) is critical for understanding plant community dynamics, and the outcomes of interspecific competition may in fact be substantially different over varying time frames (Tilman 1986; Wilson 1988).

Our results have several implications for developing strategies to maintain biodiversity within agricultural landscapes; restoration of natural habitats is often an essential component of these schemes (Ostermann 1998; Ovenden, Swash & Smallshire 1998). First, substantially reducing nitrogen losses into wetland reserves is critical for minimizing losses of community diversity. The experimental communities we assembled for this study exhibited a significant loss of diversity within their first growing season. Unfortunately, schemes that rely on wetlands to achieve water quality improvement by intercepting agricultural drainage (Dubois 1994; Bernard & Lauve 1995) cannot assume coincidental biodiversity benefits. Within an agricultural landscape, some wetlands need to be restored that are not fed by enriched runoff, if diversity is a primary goal. Secondly, our results demonstrate that if the species *P. arundinacea* is present, wetland reserves will not achieve levels of biodiversity that are possible when the invader is absent. Moreover, if NO₃-N enrichment occurs to the extent that has been recorded in agricultural landscapes, the native community will be even further suppressed. Because *P. arundinacea* is widely used for pastures and soil-erosion prevention, this species is often considered part of sustainable agriculture (i.e. agri-environmental management) within the northern US. A belated recognition of the invasive potential that this species presents poses a special resource management problem: agencies primarily responsible for soil conservation include *Phalaris* on the list of recommended plants, while those concerned with wildlife habitat and species conservation prohibit its use and encourage eradication. Because native seed

banks are typically depauperate in newly restored wetlands in agricultural landscapes (Galatowitsch & van der Valk 1996b), the relative abundance of *Phalaris* seed dispersed from nearby sources could result in restored assemblages even more skewed to the invader than observed here.

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Constraints on Sedge Meadow Self-Restoration in Urban Wetlands

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Abstract

Invasive plants and urban run-off constrain efforts to restore sedge meadow wetlands. We asked if native graminoids can self-restore following the removal of *Typha × glauca* (hybrid cattail), and if not, what limits their recovery? After we harvested *Typha* and depleted its rhizome starch reserves, *Carex* spp. expanded vegetatively (approximately 1 m over 2 years) but not by recruiting seedlings. A seedling emergence experiment showed that seed banks were depleted where *Typha* had eliminated the sedge meadow over a decade ago (based on aerial photo analysis). *Carex* seedling emergence was 75–90% lower where *Carex* was absent than where it remained in the plant community, and at least 17 species that were abundant 30 years ago were absent from the seed bank and extant vegetation. By varying hydroperiod, we showed

that prolonged flooding prevented emergence of *Carex* seedlings and that a fluctuating hydroperiod reduced emergence and ultimately killed all *Carex* seedlings. In contrast, *Typha* seedlings emerged and survived regardless of hydroperiod. Thus, slow vegetative expansion by *Carex*, depauperate seed banks, and altered hydroperiods all constrain self-restoration. To compensate for multiple constraints on self-restoration, we recommend a long-term management approach that capitalizes on flooding and the capacity of *Carex* spp. to regrow vegetatively. We suggest annually harvesting swaths of *Typha* at the edges of clones, before or during flood events, to allow gradual, vegetative self-restoration of *Carex* spp.

Key words: *Carex*, hydroperiod, seed bank, self-design, *Typha × glauca*.

Introduction

In the upper Midwest, sedge meadows are targets for restoration because of their disproportionately high loss relative to other wetland types (Zedler & Potter 2008) and potentially high plant diversity (Curtis 1959; Peach & Zedler 2006). Yet, species-rich sedge meadow restorations are rare (Budelsky & Galatowitsch 2004), especially in urbanized landscapes. One constraint on restoring biodiversity is that invasive plants readily dominate wetlands with altered hydroperiods (Wilcox et al. 1985; Kercher et al. 2004; Boers et al. 2007).

The invasive *Typha × glauca* (hereafter *Typha*) is a hybrid that forms monotypes that displace native vegetation, especially in urban wetlands (e.g., Woo & Zedler 2002). Many restoration practitioners have focused on eliminating *Typha* to create mud flats for waterfowl (Beule & Hine 1979; Linz et al. 1999; Kostecke et al. 2004). Meanwhile, constraints on restoring native vegetation remain poorly understood. If managers can control *Typha*, we asked if sedge meadow vegetation could “self-restore.” We define self-restoration as the recovery of the target vegetation by reducing constraints (sensu Allen &

Starr 1982), such as invasive species, but not by deliberately replanting the desired native species. The related concept of “self-design” assumes that restoring hydrologic connectivity alone will generate diverse and sustainable wetland communities, all else being equal (Mitsch et al. 1998). For urban wetlands, we predict that recovery of diversity will encounter constraints in addition to insufficient hydrologic connectivity. Here, we test three factors that likely constrain self-restoration of sedge meadow: depleted soil seed banks, altered hydroperiod, and dominance by *Typha*.

Native species often recruit poorly in wetland restoration sites (Zedler 2000). *Carex* spp. dominate remnant sedge meadows, but they do not always recover in restored wetlands due to depleted seed banks and isolation from dispersal sources (Galatowitsch & van der Valk 1996). In contrast, *Typha* disperses widely and forms a prolific seed bank (van der Valk & Davis 1978). By invading and forming monotypes, *Typha* reduces native plant density and native seed production (Galatowitsch 2006; Frieswyk & Zedler 2006). As a result, native plant seed banks could become depleted, especially for *Carex* species that produce short-lived seeds (van der Valk et al. 1999). Even where viable seeds remain, hydrologic conditions might not match those of undisturbed sedge meadows, where water levels rise in spring and decrease over the summer (Budelsky & Galatowitsch 2004), allowing recruitment of flood-intolerant species. The prolonged or flashy hydroperiods characteristic of urban wetlands can further constrain self-restoration, because seeds of many species will

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not germinate under water (van der Valk & Davis 1978) and seedlings that do emerge are often more vulnerable to flooding than mature plants (e.g., Fraser & Karnezis 2005).

Given the potential constraints of seed bank depletion, altered hydroperiod, and *Typha* regrowth, we asked whether a historically diverse sedge meadow (Irwin 1973) could self-restore following the harvesting of *Typha* (cutting and removing leaves). Cutting *Typha* leaves underwater can kill *Typha* (e.g., Nelson & Dietz 1966) by depriving underground tissues of oxygen (Sale & Wetzel 1983). In the absence of flooding, repetitive harvesting could deplete rhizome carbohydrate reserves that subsidize shoot regrowth (Linde et al. 1976).

We hypothesized that (H1) harvesting *Typha* and depleting carbohydrate reserves would increase the cover of native graminoids (predominantly *Carex* spp.) by vegetative growth, because many *Carex* spp. expand rhizomatically (Bernard 1990); (H2) more seedlings of native species would emerge from soil collected within the sedge meadow than from soil in *Typha* monotypes; and (H3) graminoids would require a drawdown for emergence, whereas *Typha* would not. We tested H1 by sampling extant vegetation and the seed bank across the invasion front, which we mapped using historical aerial photographs. We tested H2 and H3 by comparing seedling emergence from soil samples under fluctuating, flooded, and drawdown hydroperiods in a growth chamber experiment.

Methods

Study Site

We conducted field experiments and sampled soil seed banks in Gardner Marsh in the University of Wisconsin—Madison Arboretum in Madison, Wisconsin (89°24'W, 43°3'N). Road construction, dredging, filling, and dams have altered the hydrology of Gardner Marsh, while impermeable surfaces within the urban watershed have increased run-off (Michaud 1994; WRM 2008). Local soil consists of marl deposited from glacial Lake Wingra overlain by a shallow (<5 cm) layer of peat. Surveys of Gardner Marsh conducted between 1970 and 1972 reported 108 plant species, including native forbs and sedge meadow graminoids (e.g., *Carex* spp., *Calamagrostis canadensis*, *Typha latifolia*); by that time, several rare species reported in the 1930s had disappeared (Irwin 1973). In recent decades, *Typha* × *glauca* replaced more than 12 ha of sedge meadow vegetation (WRM 2008).

Field Experiment

We established experimental plots along the ecotone between invading *Typha* and remnant sedge meadow in northern Gardner Marsh, where *Typha* clones had spread approximately 0.8 m/year (Fig. 1). We randomly assigned 40 contiguous 4 × 8-m plots to five treatments with eight

replicates, stratified into two blocks based on aspect (east-west and north-south). In May 2006, we positioned main plots such that *Typha* and native graminoids dominated half of each plot. Treatments were (1) selectively harvest (cut and remove) all *Typha* ramets in May 2006; (2) harvest *Typha* a second time after regrowth to 1 m in height; (3) harvest *Typha* four times consecutively after regrowth to 1 m; (4) herbicide *Typha* in May 2006 with glyphosate (0.75% solution of Monsanto's Rodeo with Dyne-amic surfactant) using a backpack sprayer; and (5) unmanipulated control. In the harvest treatments, we used a machete and cut ramets as close to the soil surface as possible (approximately 10 cm). During a prolonged flood in September 2007, we imposed an additional experiment on treatment 1 plots in order to compare the responses of *Typha* and native graminoids to a one-time harvest under inundated conditions. In these plots, we harvested all standing vegetation (*Typha* and native graminoids).

We positioned four 1-m² subplots uniformly along the central 8-m axis of each main plot; subplot 1 was closest to the sedge meadow and subplot 4 was closest to the *Typha* monotype. In each subplot, we recorded percent cover by species (using the classes 0, <1, 1–5, 6–25, 26–50, 51–75, and 76–100%). In addition, we recorded total cover of *Carex* spp. and total cover of native graminoids (Cyperaceae and Poaceae) using the same classes, collecting data before treatment in May 2006 and again in October 2006 and 2007. While implementing each harvesting treatment in 2006, we measured water depth in each subplot and averaged data within each plot to compare water depth among plots.

We harvested rhizomes in October 2006 (5 months after the initial harvest) to evaluate treatment effects on rhizome starch, the predominant storage carbohydrate in *Typha* (Kausch et al. 1981). At this time, ramets were mostly senesced, and rhizome starch concentrations were likely at their peak following carbohydrate recovery from leaves (Linde et al. 1976). From each of two replicate plots from each treatment in each block, we selected the tallest *Typha* ramets outside the 1-m² subplots. We excavated entire rhizomes by making a vertical circular cut with a machete through the soil around the base of the ramet. To achieve uniform samples, we trimmed rhizomes immediately above the uppermost lateral rhizome bud (approximately at the shoot base) and below the lowest lateral bud (where the rhizome base curves horizontally). We dried the rhizomes at 75°C until constant weight was achieved (2–3 days) and stored them at –10°C before analyzing starch concentrations colorimetrically (Hassid & Neufeld 1964) and converting concentrations to total starch mass per rhizome sample.

Seed Bank Experiment

We sampled the soil seed bank over a spatial gradient of *Typha* invasion after delineating historical and current *Typha* boundaries in a GIS (Arcview version 9.1) using six

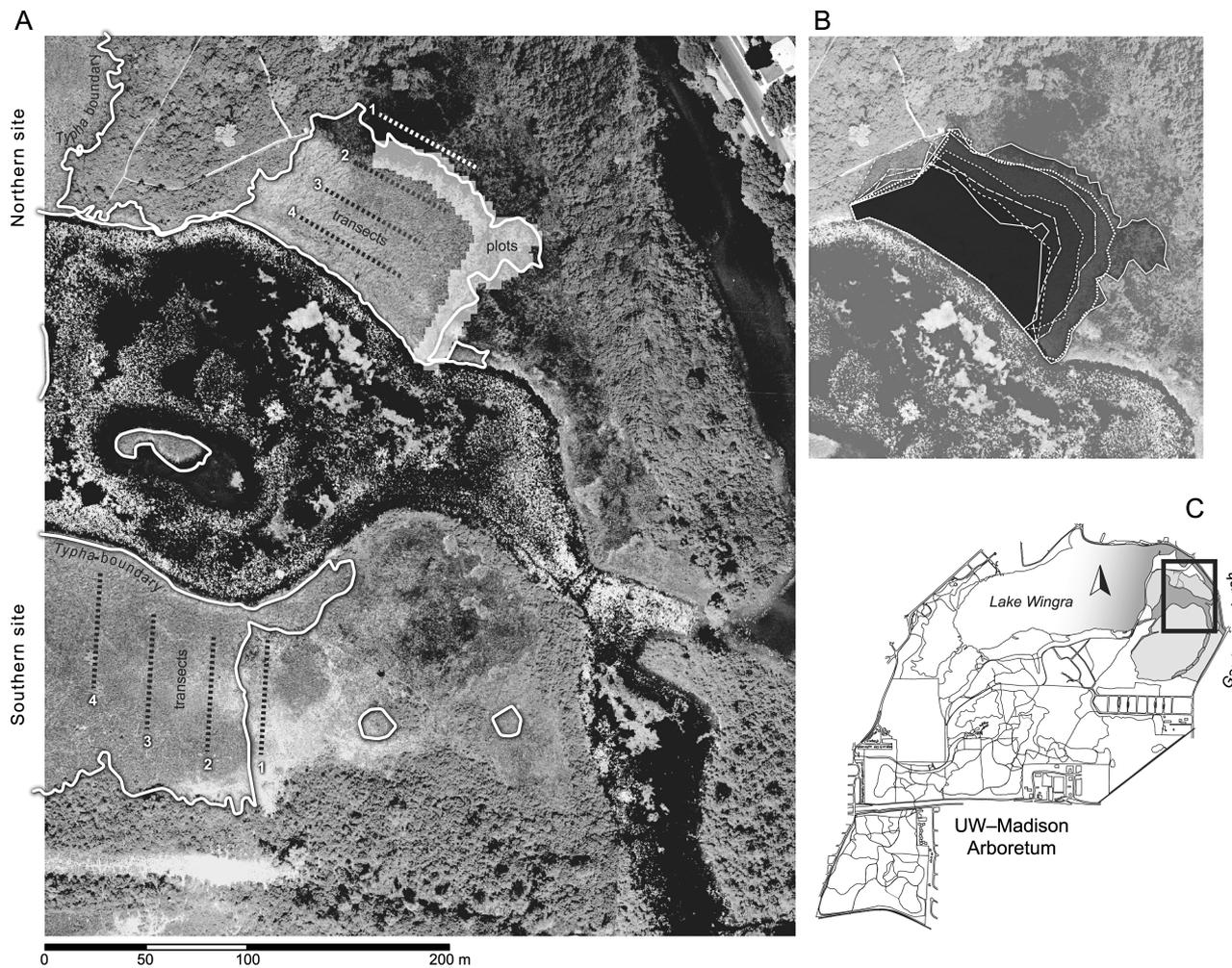


Figure 1. Study site in the University of Wisconsin—Madison Arboretum: (A) Northern Gardner Marsh. Dotted lines represent seed bank sampling transects, whereas the white shaded area in the northern site denotes contiguous 4×8 -m experimental plots on the *Typha*/sedge meadow ecotone. White lines mark boundaries between *Typha* and sedge meadow measured in February 2006. The four transects north and south of the lagoon comprise the northern and southern sites, respectively. (B) Polygons represent *Typha*'s expansion in the northern site, determined from ortho-rectified aerial photos from 1980 to 2004 and a field survey in 2006. (C) Gardner Marsh is on the edge of a 485-ha restoration site that is surrounded by urban land.

aerial photos from 1980 to 2004 and a field survey in February 2006 (Fig. 1). We ortho-rectified the photos to remove distortions using Ortho-Mapper software (F. Scarpace, University of Wisconsin—Madison) and defined four 25-m transects at 10-m intervals that paralleled the spread of *Typha* at each of two sites within Gardner Marsh. At each site, transect 1 ran through a noninvaded sedge meadow remnant, transect 2 had been invaded less than 5 years, transect 3 had been invaded 10–15 years, and transect 4 had been invaded for more than 25 years. Along each transect, we sampled 5-cm-diameter soil cores to a depth of 5 cm (approximately $100 \text{ cm}^3/\text{sample}$) at 1-m intervals for a total of 25 samples per transect. Because cold-moist stratification improves emergence of many *Carex* spp. (Kettenring & Galatowitsch 2007), we stratified our moist soil samples in sealed plastic bags in a freezer at -4°C for 8 weeks. After stratification, we homogenized all soil

samples within a transect using a kitchen mixer with dough hook, removed rhizomes, and spread soil in a layer 0.5 cm thick on top of 5 cm of autoclaved sand inside 1,000-mL clear plastic containers with a diameter of 10 cm.

We assigned containers from each transect to each of three hydroperiods. Containers under the flooded hydroperiod were watered weekly to 5 cm above the soil surface, whereas containers under the drawdown hydroperiod were watered weekly to 1 cm below the soil surface, and containers under the fluctuating hydroperiod were watered monthly to 5 cm above the soil surface. Under the fluctuating hydroperiod, water levels declined below the soil surface during the last week of every month. Each transect–hydroperiod combination was replicated in eight separate containers. We placed the containers inside two growth chambers with cool fluorescent

bulbs providing 16-hour days at 28°C and 8-hour nights at 16°C. This regime was similar to the 27/15°C regime that Kettenring and Galatowitsch (2007) found sufficient for germinating many *Carex* species, including *Carex utriculata*, *Car. lacustris*, *Car. pellita*, and *Car. stricta*, which were present at our site. Every 2 weeks, we completely randomized container location among chambers. We recorded seedling density by genus (and species when possible) monthly.

In the field, in September 2007, we sampled plant cover by species in 10 1-m² quadrats at 2.5-m intervals along each seed bank sampling transect in order to compare the composition of extant vegetation and the seed bank. To compare the vegetation at Gardner Marsh with historical data, we recorded species presence within 5 1 × 30-m belt transects in remnant sedge meadow near each seed bank sampling site in September 2006 and 2007.

Statistical Analysis

For the field experiment, we converted cover class data to percent cover using the midpoint of each cover class. We then used the software R (version 2.4.1) to generate linear models for *Carex* cover, with treatment, block, pre-treatment values, relative water depth, and subplots within plots as potential predictor variables. We used Tukey's honestly significant difference for multiple comparisons. To measure treatment effects on native species individually, we used the software PC-ORD (version 5.08) to perform indicator species analysis, a nonparametric test that compares observed with expected importance values calculated using species frequency and abundance (Dufrene & Legendre 1997). For the seed bank experiment, we used analysis of variance to compare seedling emergence density (log + 1 transformed to meet assumptions) among treatments.

Results

Sedge Meadow Composition

The sedge meadow remnant (subplots without *Typha*) averaged 4.9 ± 0.2 ($\bar{X} \pm \text{SE}$) species/m². Five species of *Carex* (*Carex aquatilis*, *Car. lasiocarpa*, *Car. lacustris*, *Car. pellita*, and *Car. utriculata*), the bulrush *Schoenoplectus acutus*, and the grass *Calamagrostis canadensis* had more than 50% cover in 1-m² subplots (Table 1 gives frequency data). Native graminoids had patchy distributions, and two or three species tended to form the canopy in each 1-m² subplot, whereas *Eleocharis erythropoda* was nearly ubiquitous in the subcanopy. Forbs were uncommon, except for *Lysimachia thyrsoflora* (present in 26 of 160 subplots).

Native Plant Response to *Typha* Harvest

After the first growing season, the four-harvest and glyphosate treatments reduced *Typha*'s rhizome starch mass to

30 and 50% of the control, respectively ($F_{[4,14]} = 5.7$, $p = 0.006$), whereas harvesting once or twice caused no reduction (Fig. 2). Cut ramets experienced prolonged submergence (>3 days) only during the fourth harvest. At the end of the second growing season, *Typha* density and vegetative spread remained reduced in the four-harvest treatment relative to the control (data in Hall 2008). Native graminoids responded to *Typha* harvest, increasing in cover by 230 and 170% in four-harvest and two-harvest plots, respectively, relative to the control and glyphosate plots, which had similar cover (Fig. 3). In four-harvest plots, native graminoids recovered to pre-invasion levels in subplot 3, expanding about 1 m, but they did not recover in subplot 4, closest to the *Typha* monotype (Fig. 3). Initial cover, water depth, subplot position, treatment, and block were all significant predictors in linear models (Table 2). Where all plants were harvested in September 2007 (total harvest), regrowth was slow, especially for native graminoids.

According to indicator species analysis, importance values of individual graminoid species did not significantly correlate with any treatment, although *Car. pellita* showed the strongest correlation with four-harvest plots ($p = 0.06$; all other species $p > 0.20$). *Eleocharis erythropoda* responded best in total-harvest plots from 2007 ($p = 0.08$; all other species $p > 0.20$). Considering species and subplots individually, *C. canadensis* responded best to the four-harvest treatment in the middle of the ecotone in subplots 2 ($p = 0.06$) and 3 ($p = 0.04$). We did not find *Carex* seedlings in any experimental plot in August or October of 2006 or 2007, but we found *Typha* seedlings in two plots from the four-harvest treatment in October 2006, and in October 2007, we found *Typha* seedlings in two plots from the glyphosate treatment.

Seed Bank Composition

In our seed bank experiment, 573 seedlings from 11 species survived after 4 months (Table 1). At 4 months, the 180 *Carex* and 251 *Typha* seedlings comprised 75% of all seedlings. Many *Carex* were not yet identifiable to species, but some individuals of *Car. aquatilis*, *Car. lacustris*, and *Car. lasiocarpa* were present. We recorded only 56 forb seedlings, 47 of which were *Lysimachia thyrsoflora*. Only two species that were not present in extant vegetation (*Eupatorium perfoliatum* and *Lycopus americanus*) emerged from seed bank samples.

Carex emergence differed by treatment, transect, and site, with significant two- and three-way interactions (Table 3). After 2 months, *Carex* emergence was greatest under the drawdown hydroperiod in soil from both the northern (1.8 ± 0.6 seedlings/container) and southern (4.3 ± 0.5 seedlings/container) sites, whereas *Carex* density was lower under the fluctuating hydroperiod (0.2 ± 0.4 and 0.3 ± 0.5 seedlings/container for the northern and southern sites, respectively). *Carex* did not emerge under the flooded hydroperiod. After 4 months, all *Carex* seedlings that

Table 1. Species list with presence and abundance data.

Species	Experimental Plot	Northern Site 2006–2007	Southern Site 2006–2007	Northern Site 1970–1972	Southern Site 1970–1972	Seed Bank
<i>Acer rubrum</i>	—	—	—	—	—	1
<i>Andropogon gerardii</i>	—	—	—	x	—	—
<i>Apocynum cannabinum</i>	—	—	x	—	—	—
<i>Asclepias incarnata</i>	—	—	x	—	—	—
<i>Aster</i> sp.	—	—	—	—	—	2
<i>Bidens cernua</i>	1	—	—	—	—	—
<i>Bidens coronata</i>	—	—	—	x	—	—
<i>Calamagrostis canadensis</i>	30	x	x	x	x	42
<i>Campanula aparinoides</i>	1	x	x	x	x	2
<i>Carex aquatilis</i>	34	x	x	—	—	x
<i>Car. flava</i>	—	—	—	x	x	—
<i>Car. lacustris</i>	69	x	x	x	—	x
<i>Car. lasiocarpa</i>	85	x	x	—	—	x
<i>Car. pellita</i>	30	x	—	—	—	—
<i>Carex</i> sp.	—	—	—	—	—	180
<i>Car. stricta</i>	—	x	x	—	—	—
<i>Car. utriculata</i>	19	x	x	—	—	—
<i>Cirsium arvense</i>	—	—	x	—	—	—
<i>Dichanthelium villosissimum</i>	—	—	—	x	x	—
<i>Eleocharis elliptica</i>	—	—	—	x	—	—
<i>E. erythropoda</i>	135	x	x	—	—	27
<i>Eupatorium perfoliatum</i>	—	—	—	x	x	2
<i>Euthamia graminifolia</i>	—	—	—	x	x	—
<i>Galium boreale</i>	9	x	x	—	x	—
<i>Geum</i> sp.	—	—	—	—	—	1
<i>Glyceria striata</i>	—	—	—	—	x	—
<i>Helianthus grosseserratus</i>	—	—	—	x	—	—
<i>Iris</i> sp.	—	—	x	—	—	—
<i>Juncus arcticus</i>	36	x	x	x	—	—
<i>J. canadensis</i>	—	x	x	—	—	—
<i>J. torreyi</i>	—	—	—	—	x	—
<i>Lycopus americanus</i>	—	—	—	x	x	1
<i>Lysimachia quadrifolia</i>	—	—	—	—	x	—
<i>L. thyrsoiflora</i>	27	x	x	x	—	47
<i>Lythrum alatum</i>	—	—	x	x	—	—
<i>Mentha arvensis</i>	—	—	x	x	—	—
<i>Mimulus ringens</i>	1	x	x	—	—	—
<i>Muhlenbergia</i> sp.	—	—	—	x	x	—
<i>Oligoneuron riddellii</i>	—	—	—	x	x	—
<i>Phalaris arundinacea</i>	—	x	—	—	—	—
<i>Phragmites australis</i>	—	x	x	—	x	—
<i>Pilea pumila</i>	—	—	x	—	—	—
<i>Polygonum hydropiper</i>	6	x	x	—	—	—
<i>Rosa blanda</i>	—	—	—	x	—	—
<i>Schoenoplectus acutus</i>	19	x	x	—	—	—
<i>S. fluviatilis</i>	2	x	x	x	—	—
<i>S. tabernaemontani</i>	—	—	—	—	x	—
<i>Solanum dulcamara</i>	—	—	—	x	—	—
<i>Sparganium eurycarpum</i>	—	—	—	x	—	—
<i>Spiraea alba</i>	1	x	—	—	—	—
<i>Symphotrichum pilosum</i>	—	—	—	x	—	—
<i>Teucrium canadense</i>	1	x	—	—	—	—
<i>Thelypteris palustris</i>	—	—	x	x	x	—
<i>Triadenum virginicum</i>	—	—	—	x	—	—
<i>Typha angustifolia</i>	—	x	—	x	x	—
<i>T. latifolia</i>	—	x	x	x	x	—
<i>Typha</i> × <i>glauca</i>	150	x	x	x	x	251
<i>Viola</i> sp.	—	—	—	x	x	—

“Experimental Plot” gives frequency by subplot (total $n = 160$) within the main experimental plots on the *Typha*/sedge meadow ecotone; boldface indicates species sampled in 2006 only. Species encountered in sedge meadow remnant sites north and south of the lagoon (Fig. 1) in 2006–2007 are denoted by “x” and are compared with data from 1970 to 1972 (Irwin 1973). “Seed Bank” gives total seedling emergence after 4 months from soil samples under the drawdown hydroperiod.

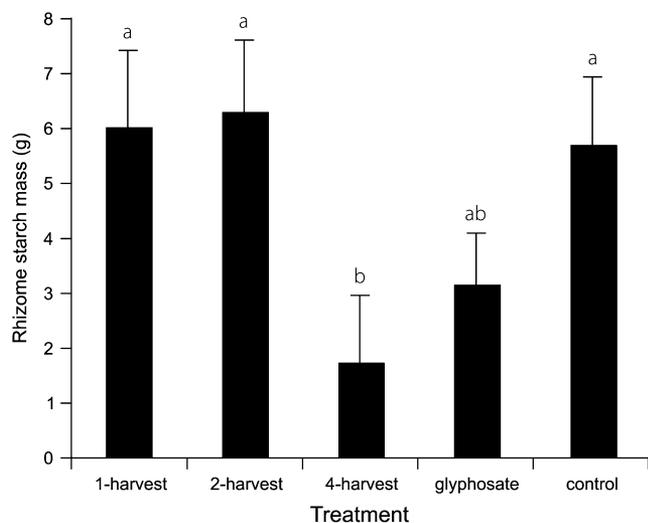


Figure 2. *Typha* rhizome starch mass \pm SE by treatment (1-harvest, 2-harvest, 4-harvest, glyphosate, and control) in October 2006; $n = 4$ for each treatment.

emerged under the fluctuating hydroperiod had died. *Calamagrostis canadensis* emerged only under the drawdown hydroperiod (42 seedlings). Forb emergence after 4 months was also greatest under the drawdown hydroperiod (Fig. 4), and emergence under the flooded and fluctuating hydroperiods was only 10% of that under the drawdown hydroperiod (hydroperiod effect, $F_{[2,84]} = 20.1$ and $F_{[2,84]} = 40.4$, respectively; $p < 0.001$ for both sites).

Typha seedling emergence patterns were similar after 2 and 4 months, so we present only the 4-month data. For the northern site, *Typha* emergence was significantly greater ($F_{[2,84]} = 7.5$, $p = 0.001$) under the drawdown hydroperiod (2.6 ± 0.5 seedlings/container) than under the fluctuating or flooded hydroperiods (1.4 ± 0.5 seedlings/container) (Fig. 4). For the southern site, emergence did not differ by hydroperiod ($F_{[2,84]} = 2.7$, $p = 0.07$) although tendencies were similar to those in the northern site (Fig. 4). *Typha* did not show flooding stress, because biomass per seedling did not differ for the flooded (0.005 ± 0.04 g), fluctuating (0.004 ± 0.03 g), and drawdown (0.002 ± 0.03 ; treatment effect, $\chi^2_{[2]} = 5.1$, $p = 0.08$) hydroperiods.

The extant vegetation of the northern site lacked *Carex* spp. in all invaded transects (2, 3, and 4). Where *Typha* occurred for more than 10 years (transects 3–4), *Carex* emergence was significantly lower (0.2 ± 0.2 seedlings/container) than where *Typha* had not invaded or invaded recently (transects 1–2; 1.9 ± 0.5 seedlings/container; transect effect, $F_{[3,84]} = 7.0$, $p = 0.0003$; Fig. 4). In the southern site, *Carex* was widespread in transects 2 and 3 (10 of 10 plots), albeit at low cover ($2.2\% \pm 0.7\%$), whereas it only occurred in one plot in transect 4. Soil from transects 2 and 3 had greater *Carex* emergence (5.9 ± 0.6 seedlings/container) than that from transect 4 (2.8 ± 0.4 seedlings/container; $F_{[3,84]} = 4.1$, $p = 0.01$; Fig. 4). *Typha* emergence differed by transect in the southern site ($F_{[3,84]} = 4.3$, $p =$

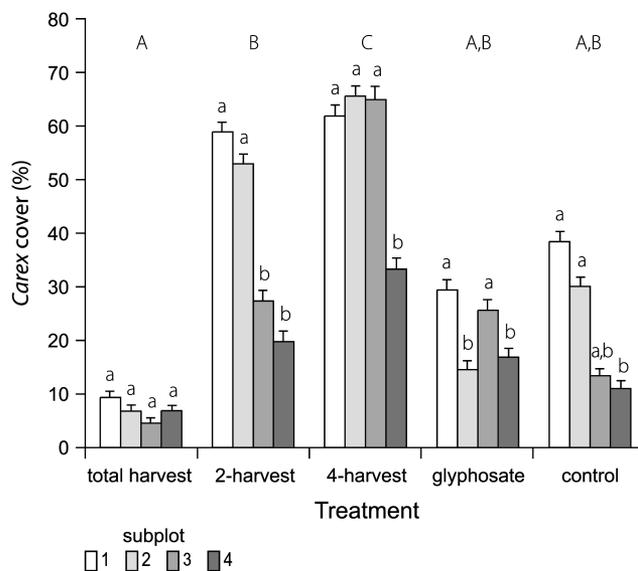


Figure 3. *Carex* cover \pm SE by treatment and subplot in October 2007; $n = 8$ for each treatment-subplot combination. Capital letters denote whole-plot treatment contrasts; lowercase letters denote subplot contrasts (within treatments only).

0.007) and was lowest in transect 1 (0.5 ± 0.3 seedlings/container vs. 1.0 ± 0.3 for the other transects; Fig. 4).

In the northern site, 1.0 ± 0.4 *Carex* seedlings/container emerged under the drawdown hydroperiod, which was only 25% of the emergence in samples from the southern site (4.6 ± 0.6 seedlings/container; site effect, $F_{[1,168]} = 60.9$, $p < 0.001$). In soil from the northern site, where *Typha* exceeded 75% cover in invaded transects, *Typha* seed bank emergence was twice as high (1.8 ± 0.5 seedlings/container) as that in soil from the southern site (0.9 ± 0.4 seedlings/container), where *Typha* had 54% \pm 1% cover (site effect, $F_{[1,168]} = 19.3$, $p < 0.001$). Forb emergence did not differ by transect ($F_{[3,84]} = 2.3$, $p = 0.08$ and $F_{[3,84]} = 1.9$, $p = 0.13$ for the northern and southern sites, respectively), but forb density was twice as high in the southern site as in the northern site (1.3 ± 0.4 seedlings/container vs. 0.6 ± 0.3 seedlings/container; site effect, $F_{[1,168]} = 9.0$, $p = 0.003$), even though no forbs were present among *Typha* (transects 2, 3, and 4) at either site.

Discussion

Ideally, restorationists could eradicate invasive species, and sedge meadows would self-restore. In reality, multiple factors, including the prolonged and erratic hydroperiods that favor dominance by *Typha*, constrain the restoration of native sedge meadow vegetation. Erratic hydroperiods do, however, provide a means for reducing *Typha* via underwater cutting. We hypothesized that native graminoids would increase in cover by vegetative growth following *Typha* harvest. Native graminoids did respond, albeit slowly, with a lateral expansion of approximately 1 m by

Table 2. Linear model (split plot) for total native graminoid cover (mostly *Carex* spp.) in October 2007.

	MS	df	F	p
Water depth (whole plot)	7,065	1	7.96	0.008
Initial <i>Carex</i> cover (whole plot)	9,370	1	10.6	0.003
Treatment	8,876	4	10.0	<0.0001
Block	6,579	1	7.4	0.01
Whole-plot residuals	888	32		
Water depth (subplot)	2,360	1	12.2	<0.0001
Initial <i>Carex</i> cover (subplot)	11,544	1	59.5	<0.0001
Subplot	655	3	3.4	0.02
Treatment × subplot	337	12	1.7	0.07
Subplot residuals	194	103		

Covariates (water depth, initial *Carex* cover) are included in both whole-plot and subplot levels. *df*, degree of freedom; MS, mean square.

the end of the second growing season. Over time, annual harvesting could shift the *Carex*/*Typha* ecotone. Notably, the graminoids did not expand to the edge of the plot, despite a dramatic reduction of *Typha* density and height attributable to depletion of starch reserves. Constraints on *Carex* expansion could have included an intrinsically slow growth rate, soil-related legacies of *Typha* invasion (Angeloni et al. 2006), or allelopathy (B. Cook 2008, Mankato State University, personal communication).

The absence of at least 17 forbs from the seed bank and extant vegetation of Gardner Marsh suggests that many forb species are not likely to self-restore following a reduction of *Typha*. Our sampling of extant vegetation was more intensive than that of Irwin (1973), so it is unlikely that we overlooked many species. The paucity of forbs in the seed bank contrasts with numerous other experiments, where forbs germinated abundantly from soil seed bank samples even when they were rare or absent in established vegetation (van der Valk & Davis 1978; Keddy & Reznicek 1982; Smith & Kadlec 1983; Galatowitsch 2006). Because a sedge meadow matrix persists outside the *Typha* monotypes in Gardner Marsh, we suggest that recent increases in water level (Hall 2008) relative to historical levels (Irwin 1973; Michaud 1994) limited forbs while allowing graminoids to persist. Characteristic sedge meadow forbs

Table 3. Model for *Carex* seed bank emergence (log + 1 transformed) using data from both sites.

	MS	df	F	p
Treatment	23.8	2	321.4	<0.0001
Transect	0.5	3	6.3	0.0005
Site	6.4	1	87.0	<0.0001
Treatment × transect	0.5	6	6.3	<0.0001
Treatment × site	6.4	2	87.0	<0.0001
Transect × site	0.3	3	4.6	0.0040
Treatment × transect × site	0.3	6	4.6	0.0002
Residuals	0.1	168		

df, degree of freedom; MS, mean square.

produce less root aerenchyma than graminoids and are less tolerant of flooding (Kercher & Zedler 2004). The few forbs still present at Gardner Marsh are either vigorous, flood-tolerant perennials, such as *Lysimachia thyriflora* and *Galium boreale* (S. Hall, personal observation), or annuals that flower and fruit even when the soil is flooded, e.g., *Mimulus ringens* (Fraser & Karnezis 2005). In addition to direct effects on forb recruitment and survival, prolonged hydroperiods could have decreased light availability for short-statured species by increasing the canopy height of native graminoids such as *Carex aquatilis* and *Schoenoplectus acutus*. These dominant graminoids were not recorded previously in Gardner Marsh (Irwin 1973) and could have suppressed less-competitive forbs (Keddy et al. 1998).

In support of our hypothesis that more native species would emerge in soil collected within remnant sedge meadow than in soil from *Typha* monotypes, we found a negative relationship between *Carex* emergence and *Typha* dominance and duration of invasion. That is, the longer *Typha* had occupied a site, the fewer *Carex* seedlings emerged from the seed bank. Where *Carex* persisted at low abundance despite dominance by *Typha*, emergence was substantially higher. Spatially uneven seedling emergence has also been shown in prairie potholes (van der Valk & Davis 1978), saline marshes (Smith & Kadlec 1983), freshwater tidal marshes (Leck & Graveline 1979), and Great Lakes coastal wetlands (Frieswyk & Zedler 2006). Data from both of our sites are consistent with dispersal limitation, although changes in soil chemistry (Leeds et al. 2006), granivory, or allelopathy (McNaughton 1968) could also explain reduced emergence in *Typha* monotypes. Possibly because *Carex* was not entirely eliminated and continued to supply seed after *Typha* invasion, our southern site could potentially support self-restoration of *Carex* given an appropriate hydroperiod.

Our data fully support our third hypothesis that graminoids would require a drawdown for emergence, whereas *Typha* would not. The dominant native graminoids (*Carex* spp. and *Calamagrostis canadensis*) emerged and survived only under the drawdown hydroperiod. *Carex* emerged under the fluctuating hydroperiod as water levels declined, but subsequent inundation killed seedlings. Even small fluctuations decreased emergence in a pilot study with weekly flooding to 1 cm followed by drawdown; *Carex* emergence dropped to 17% of that under a continuous drawdown (Hall 2008). The young seedlings in our experiment appeared more sensitive to inundation than older and larger *Carex* seedlings. In other studies, 2-week-old seedlings of four *Carex* species survived only 6 cm of inundation (Fraser & Karnezis 2005), whereas larger *Car. stricta* seedlings (35 ± 10 cm leaf length) tolerated 60 cm of water (Budelsky & Galatowitsch 2004). Although flooding appears to inhibit emergence and harm young seedlings of the common *Carex* spp. in Gardner Marsh, our results might not transfer to all congeners. For example, *Car. stipata* can emerge when inundated by 10 cm of

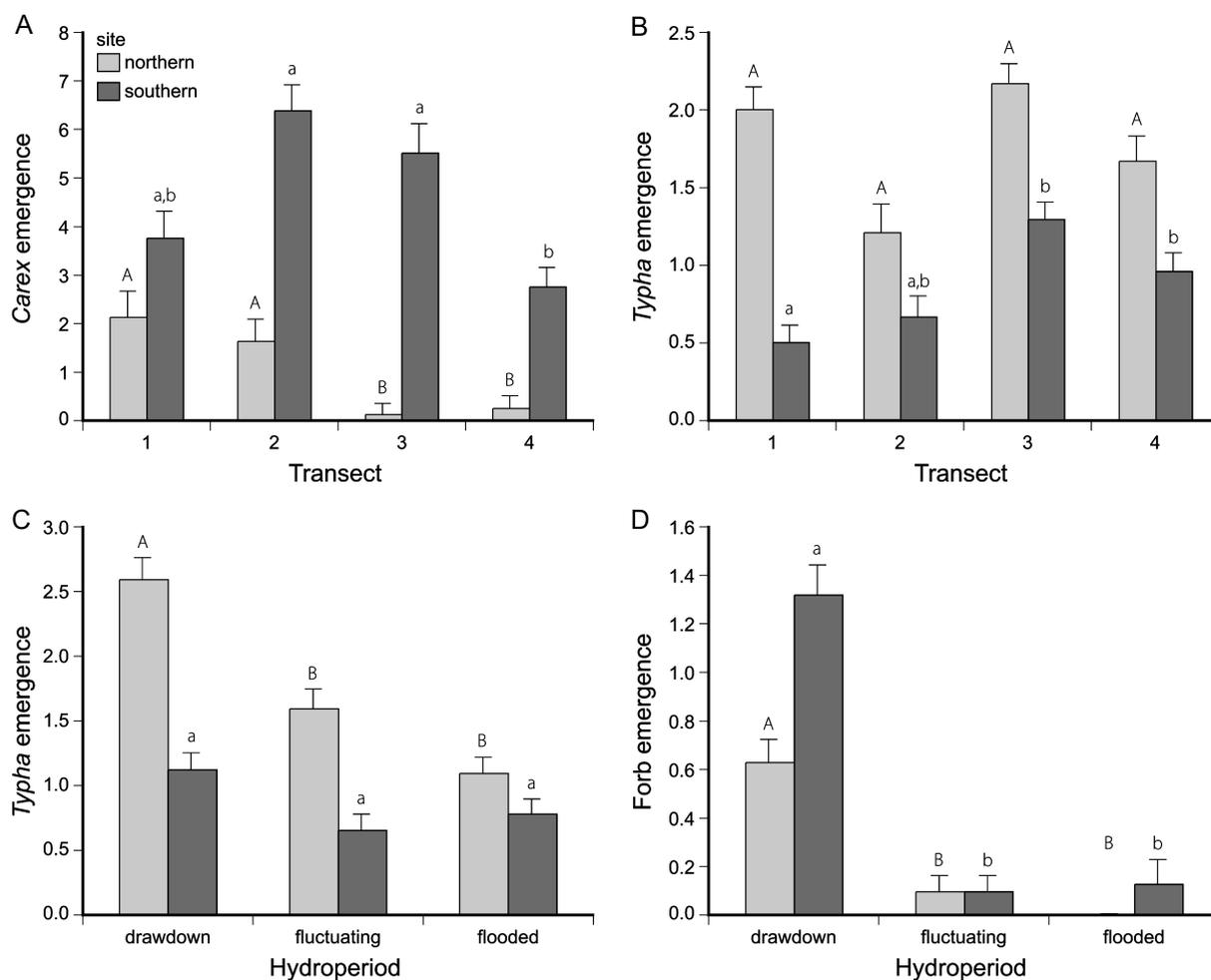


Figure 4. Seed bank emergence \pm SE by transect, hydroperiod, and site; $n = 8$ for each transect–site combination; $n = 32$ for each hydroperiod–site combination: (A) *Carex* emergence by transect and site from the low hydroperiod; (B) *Typha* emergence by transect and site averaged over all hydroperiods; (C) *Typha* emergence by hydroperiod and site; and (D) forb emergence by hydroperiod and site.

water (van der Valk et al. 1999). However, our results for *Typha* concur with those from a subtropical wetland, where flooding prevented emergence of all species except *T. domingensis* (Smith et al. 2002). In our study, *Typha* emerged and survived under all three hydroperiods, agreeing with the results of van der Valk and Davis (1978) and Smith and Kadlec (1983). *Typha* seedling recruitment is normally rare in undisturbed vegetation (Grace & Harrison 1986), but we found several *Typha* seedlings in experimental plots that had low vegetative cover. In the absence of management, these seedlings could form large clones within several years. For example, Boers and Zedler (2008) found that *Typha* \times *glauca* clones growing behind a dam expanded 4 m/year (average diameter increase).

Because *Carex* spp. appear to require a prolonged drawdown for emergence and survival, we speculate that flooding prevented recruitment in our harvested plots. However, *Carex* recruitment from seed appears rare even in undisturbed wetlands (Schmid 1984), and clonal spread

could explain dominance by *Carex* species (Kettenring & Galatowitsch 2007). Assuming that the hydroperiods we documented in 2006 and 2007 will recur well into the future, recovery of *Carex* after *Typha* control will depend on vegetative expansion of existing plants or the planting of mature propagules.

Where drawdowns are more predictable than in Gardner Marsh, restorationists can anticipate seasonal water levels and plant seed accordingly (e.g., Jones et al. 2004). In many areas, drawdown hydroperiods and propagule sources cannot be restored within the local hydrologic context (Bedford 1996; Galatowitsch 2006), because it is usually impractical to restore entire watersheds. Thus, we suggest a gradual, long-term program for restoring sedge meadow diversity that could be broadly applied in other systems dominated by clonal plants. To facilitate vegetative expansion of native species such as *Car. pellita* and *C. canadensis*, we recommend harvesting 3-m-wide swaths of *Typha* at the invasion front. This width is based on our findings that *Carex* spp. expanded vegetatively but slowly

(approximately 1 m radial expansion over 2 years) where *Typha* was harvested and that four harvests in one season shifted *Typha* approximately 1 m. Similar *Typha* reduction can be achieved by one harvest, if the ramets are cut under water (Hall 2008). Because harvesting with a machete is labor intensive (one person could harvest 64 m²/hour in this study), aquatic mowers could improve efficiency, although such harvesting would be nonselective. In a separate study, a nonselective harvest during a flood decreased regrowth of *Typha* but not native graminoids (Hall 2008), some of which appear to have greater anaerobic tolerance than *Typha* (McKee et al. 1988). Ideally, nonselective harvest could be timed to maximize carbohydrate depletion for *Typha* while minimizing depletion for *Carex* spp. Other studies showed that *Carex* spp. recovered leaf carbohydrates earlier in the summer (Steele et al. 1984) than did *Typha* (Linde et al. 1976), suggesting that a late-summer harvest would deplete *Typha* more than *Carex*. Self-restoration will not likely occur from the seed bank, but it can proceed vegetatively along the sedge meadow/*Typha* ecotone, with annual harvesting.

Implications for Practice

- Prolonged and flashy hydroperiods threaten the persistence of *Carex* and forb species in favor of monotypes of invasive *Typha*, which displace *Carex* spp. and native seed banks.
- Rapid reduction of *Typha* would likely create bare soil that would need to be planted with plugs (not seeds) of native species.
- Annual swath harvesting could promote sedge meadow self-restoration, although it might require 50 years for *Carex* spp. to expand 25 m.
- Nature reserves with a mission of biodiversity conservation could potentially sustain a long-term restoration effort by recruiting volunteers or artisans to harvest swaths of invasive *Typha* each year. Remnant graminoid populations would slowly expand, and flood-tolerant species could be added as plugs to increase sedge meadow diversity.

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SET-BACKS AND SURPRISES

Setbacks in Replacing *Phalaris arundinacea* Monotypes with Sedge Meadow Vegetation

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Abstract

Reed canary grass (*Phalaris arundinacea*) invades wetlands, forms monotypes, and resists control efforts, suggesting that strong feedbacks sustain its dominance, as in the alternative states model. In nine field experiments, we tested the hypothesis that applying a graminicide (sethoxydim) for three years would progressively reduce *Phalaris* abundance, and that seeding sedge meadow species (except grasses) would reestablish native plant dominance. The graminicide prevented *Phalaris* from flowering, reduced its height by 50% and reduced its cover, often to less than 40%. However, only two of the nine sites showed progressive declines over the three-year experiment. The first setback was that *Phalaris* recovered annually in nearly all treatment plots. A second setback was that seeding did not reestablish sedge meadow. In five sites, unseeded

plots had similar numbers of native species as those seeded with either forbs, forbs and graminoids, or graminoids. In four formerly agricultural sites, however, non-native weeds increased in species richness and cover (a third setback). In only one site did the graminicide's effect on *Phalaris* allow native species to increase in number and cover. But short-term gains were not long-lasting. In year four, three sites that developed high native-species cover were again strongly dominated by *Phalaris* (a fourth setback). The feedbacks that sustain this invader include resistance to the graminicide aboveground and rapid and robust regrowth from rhizomes and seeds belowground. The weak effect of this graminicide was a surprise; hence, we recommend stronger management actions to control *Phalaris*.

Key words: alternative states model, graminicide, herbicide, reed canary grass, wetland.

Introduction

Rapid invasions of native vegetation by clonal grasses are well described by the alternative states model (Hobbs & Suding 2009), especially where outcomes are difficult to reverse. Reed canary grass (*Phalaris arundinacea*, hereafter *Phalaris*) is a clonal species and a "model invader" with high competitive ability (Lavergne & Molofsky 2004). Rapid shifts from diverse native vegetation to a *Phalaris* monotype and difficulty reversing it (Herr-Turoff 2005) suggest the existence of strong feedbacks that maintain *Phalaris* dominance. One proposed feedback loop involves early growth of vertical stems, which branch in late summer and often recline to form a dense thatch; this reduces light and growth of competitors, thereby favoring vegetative regrowth of *Phalaris* (Zedler 2009). A management approach that could break such a feedback loop might employ a grass-specific herbicide (graminicide) and simultaneous restoration of native vegetation. Seeding of native species could accompany graminicide application if the target plant

community did not require immediate introduction of native grasses. Sedge meadows would be a suitable target for Upper Midwestern USA, where the dominants are forbs, sedges, and rushes, but few grasses (Curtis 1959; Peach & Zedler 2006).

Phalaris is a widespread invader in temperate North America (Galatowitsch et al. 1999; Lavoie et al. 2005; Perkins & Wilson 2005; Lavergne & Molofsky 2006). Its high competitive ability is related to its early spring sprouting, rapid height growth, clonal expansion, prolonged growing season, production of dense shade, and ability to obtain nutrients (Lavergne & Molofsky 2004). In addition, this C3 grass reproduces via seeds, rhizomes, and culm fragments, leading to broad dispersal, and its morphological plasticity allows it to dominate across a broad range of hydroperiods (Herr-Turoff & Zedler 2007). *Phalaris* has an additional competitive advantage in remaining green through October, after native species senesce. Its longer growing season also allows documentation of widespread dominance using late-season satellite imagery (e.g. it dominates 201,639 ha of Wisconsin wetlands; Hatch & Bernthal 2009).

Phalaris takes advantage of ample nutrients and quickly outgrows native plants (Green & Galatowitsch 2002; Kercher & Zedler 2004; Kercher et al. 2004). The shift from diverse native vegetation to a *Phalaris* monotype is especially rapid when nutrients and shallow water interact synergistically (Kercher et al. 2007). Once invaded by *Phalaris*, wetlands

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are very difficult to restore to native vegetation (Perry & Galatowitsch 2003; Foster & Wetzel 2005). Of the numerous approaches being used to control *Phalaris*, none has proven effective in the long term. Burning alone opens the canopy and favors *Phalaris* regrowth (Foster & Wetzel 2005; Wilcox et al. 2007) because increased light stimulates germination, seedling establishment, and vegetative expansion (Lindig-Cisneros & Zedler 2001, 2002a,b; Maurer & Zedler 2002; Kercher et al. 2004, 2007; Iannone & Galatowitsch 2008). Non-selective herbicides (e.g. glyphosate) kill all plant species aboveground, but leave the dormant rhizome buds and seed banks of *Phalaris* to regenerate. Grazing and mowing can reduce *Phalaris*' height during treatment, but *Phalaris* dominates when not mowed (Gillespie & Murn 1992). Removing sod and creating open water can suppress *Phalaris* regrowth (A. Kitchen 2005, USFWS, personal communication), but deep water is not a solution where the restoration target is a wet meadow. Likewise, overplanting with trees can outshade *Phalaris* (Hovick & Reinartz 2007), but the result is a woodland. Also, biocontrol is not an option, because *Phalaris* is used in pastures and biofuel production (Sahramaa et al. 2004; Casler & Undersander 2006; Casler et al. 2008).

In short-term trials, sethoxydim (Vantage[®]) reduced both biomass and panicle density of *Phalaris* (Annen et al. 2005), allowed some native species to establish (Wilcox et al. 2007), and did not harm sedges or forbs in mesocosms (Herr-Turoff 2005). Sethoxydim degrades rapidly in soil (Smith & Hsiao 1983; Shoaf & Carlson 1992), but its solvent (naphthalene) is toxic to aquatic animals and other wildlife, so it is not licensed for application over water (Durkin 2001, USEPA 2008). Because sedge meadows have short hydroperiods, sethoxydim can be applied after water recedes. Likewise, its sensitivity to UV light (Roberts et al. 1998; Matysiak &

Nalewaja 1999) can be mitigated by applying the graminicide on cloudy days or late afternoons and by adding methylated seed oil to the spray mixture.

Using a grass-specific herbicide, such as sethoxydim, management efforts could focus simultaneously on (1) breaking feedbacks that sustain the *Phalaris* monotype and (2) restoring non-grass native vegetation and reestablishing the feedbacks that sustain native plant communities (Zedler 2009). We expected the graminicide to reduce *Phalaris*' height and cover progressively over three years, with declining regrowth from rhizome buds and the seed bank. We expected restored natives to increase in diversity and cover and to develop their own positive feedbacks by producing shade that would reduce *Phalaris* regrowth (Zedler 2009). After three years, we planned to spot-spray the graminicide and add native grasses (e.g. *Bromus ciliatus*) to reestablish sedge meadow vegetation.

Methods

Experimental Design and Site Selection

We selected nine sites on five public and private lands between August 2004 and March 2005 (Table 1). All sites were in treeless wetlands that had >75% cover of *Phalaris* and near restoration projects that were threatened by this invader. One site (Brant) was on land of the Madison Audubon Society near Lake Mills, WI, surrounded by forest, agriculture, and low-density development. Two sites at Cherokee Marsh (CM) in Madison, WI, were surrounded by a suburban landscape. Two sites were located on the Wisconsin River floodplain at the Leopold Memorial Reserve in Baraboo, WI (hereafter LMR). Three sites at Goose Pond Sanctuary in Arlington, WI (GP), were within an agricultural landscape. One site (Z) was on private land near Oregon, WI, where *Phalaris* was likely planted decades ago.

Table 1. Site locations, surrounding landscape, seed mix, plot numbers, soil type, herbicide application dates, and burning dates.

	Brant	CM	LMR	GP	Z
Location of experiments	43°08'19.8"N 88°53'43.4"W	43°08'52.2"N 89°23'20.9"W; 43°08'51.4"N 89°23'18.6"W	43°33'36.7"N 89°39'14.1"W; 43°33'33.0"N 89°39'06.3"W	43°19'15.2"N 89°22'11.7"W; 43°19'14.9"N 89°22'12.8"W; 43°19'01.5"N, 89°22'04.8"W	42°58'34.8"N 89°21'56.7"W
Adjacent land use	Agriculture, forest, wetland	Suburban	Forest, wetland	Agriculture	Agriculture, prairie, wet meadow
Plot size	Not subdivided	8.6 × 5 m	8.6 × 5 m	8.6 × 5 m	6 × 5 m
Number of plots	Not subdivided	70	70	105	35
Soil type	Wacousta Silty Clay Loam	Adrian Muck	Adrian Muck	Ossian Silt Loam	Virgil Silt Loam
Glyphosate applied	None	None	9/27/04	None	None
Sethoxydim applied	5/21/07 6/04/06 6/08/05	4/28/07 6/03/06 6/03/05	5/28/2007 6/02/2006 6/02/2005	5/28/07 6/02/06 6/07/05	5/28/07 6/04/06 6/08/05
Burned	4/14/07 4/05/06 4/16/05	4/25/05 10/*/06 *Date uncertain	10/25/04	4/16/05	4/25/05

For seed mixes, F = forbs; G = graminoids (not grasses). Species in seed mixes are listed in Appendix.

Our experiments tested three seeding treatments (forbs, forbs and graminoids, and graminoids; Appendix), each with and without the graminicide (sethoxydim as Vantage®). An additional treatment had the graminicide with no seeding, for a total of seven treatments ($= 3 \times 2 + 1$). We did not intersperse control plots (no graminicide, no seeding) because related studies (Wilcox et al. 2007; Healy 2008) provided ample evidence that *Phalaris* monotypes persist when not treated, and the surroundings of each experiment allowed observation of untreated monotypes. We randomly stratified the seven treatments (one per each of five blocks) in rows, to facilitate graminicide application.

We tailored the basic design to meet concerns of each land steward. Local seeds were required at Brant, and none were available, so we did not test seeding or subdivide that site into plots. We applied glyphosate at LMR in autumn 2004 to initiate *Phalaris* mortality and prepare the site for seeding native species; however, we were not permitted to use this broad-spectrum herbicide at other sites. Overall, we employed 280 plots (of which 240 were seeded and 160 were graminicided; Table 1).

We burned all sites prior to seeding to remove thatch to expose the soil to light and facilitate germination and seedling recruitment (Wilcox et al. 2007) and to remove standing dead material that would otherwise intercept the graminicide. Burning dates differed slightly due to weather and availability of fire crews; also, standing water sometimes delayed the application of sethoxydim.

Graminicide Treatments

A separate test of timing indicated that sethoxydim had greater effect when applied in spring than summer (Healy 2008). We applied the graminicide in late May or early June of each year (2005–2007) when *Phalaris* was 30–100-cm tall, had ample leaf area to intercept the graminicide, and had begun to develop inflorescences, but had not formed seeds. We applied sethoxydim in the evening or during overcast periods to avoid UV damage and during minimal wind to avoid spray drift. We used a Solo 475 backpack sprayer with a flat-fan nozzle (Solo Inc., Newport News, VA, U.S.A.) to apply 2.25% v/v sethoxydim (Vantage®, 13% active ingredient sethoxydim, MicroFlo Company LLC, Memphis, TN, U.S.A.), at a rate of 4.4 L/ha. We added a 1% v/v ammonium sulfate water conditioner (Request®, Helena Chemical Company, Collierville, TN, U.S.A.) and a 1% v/v non-ionic sticker-spreader that includes methylated seed oil (Dyne-Amic®, Helena Chemical Company) to enhance the effectiveness of the graminicide (Matysiak & Nalewaja 1999a,b). We sprayed the top leaves of *Phalaris*, verified visibly by including 0.33% v/v dye in the tank mix. At our Brant site and on one date (on or about May 21, 2007), the land steward applied 2.25% v/v sethoxydim (Sethoxydim E-Pro®, Etigra LLC, Cary, NC, U.S.A.; personal communication, D. Musolf 6/4/2007 and C. Annen 7/20/2007). The tank mix during this application included the same 1% non-ionic sticker spreader used at our other sites,

Dyne-Amic®. A water conditioner was not added to the mix, as the applicator used soft water.

Seeding Treatments

After burning, we sowed the three seed mixes (13–16 native species per mix, Appendix) at eight sites, using seeds collected within Wisconsin. For LMR1 and LRM2, we obtained seeds from Murn Environmental, Inc. (Beloit, WI, U.S.A.) in June 2004 and stored them dry at 3°C. In fall, we mixed seeds with sand and hand-sowed each mixture on November 26, 2004. For the other sites, we purchased seeds during 2004 and 2005 from Murn Environmental, Inc., Prairie Moon Nursery (Winona, MN, U.S.A.) and Agrecol Inc. (Madison, WI, U.S.A.) and cold-moist stratified the seed mixes in sand for at least 6 weeks prior to sowing. We sowed the treatment plots in mid-May 2005 (Table 1).

We seeded at a rate of 1,300 seeds/m², or 81 seeds/species/m² (nearly twice that recommended by the seed supplier) as in previous work (Wilcox et al. 2007). We chose species for their wetland indicator status, height when mature, historical presence in wet meadows (Curtis 1959), and ability to coexist with *Phalaris* in flooded conditions (Kercher and Zedler 2004). To assemble the seed mixes, we weighed each species independently, using seed numbers/wt determined by suppliers.

Vegetation Sampling

We marked the central square meter of each plot with stakes and recorded coordinates using a high-precision Leica SR500 GPS (Leica Geosystems AG, St. Gallen, Switzerland). In June 2007, we collected a 30-cm-deep soil sample from the center of each plot in each research site, using a 2.5 × 30-cm stainless-steel piston step corer. We characterized the soil properties of one sample per site (a composite of the 35 cores). We froze all soil samples and had the University of Wisconsin Soil and Plant Analysis Lab analyze them for soil texture, pH, organic matter, exchangeable nutrients (calcium, magnesium, phosphorus, and potassium), and nitrogen (ammonium-N, nitrate-N, and total N).

During our 2007 survey (late August), we measured the leaf area index (LAI) and light penetration (τ) in each plot using an Li-COR PAR ceptometer with 80 sensors mounted to a 0.9-m-long aluminum wand (Li-COR Biosciences, Lincoln, NE, U.S.A.). At the end of each field season (late August and early September of 2005–2007), we sampled the central 1-m² of all plots for composition, canopy cover, and height of the tallest individual of *Phalaris*. We estimated cover of each species in seven classes (0, <1, 1–5, 6–25, 26–50, 51–75, and 76–100%) and measured plant height from the soil surface to the tip of the inflorescence or the stretched leaf, whichever was taller. We included the flowering stalk in height data because it facilitates lodging, which smothers other species. In September 2008, we revisited three sites to observe post-treatment outcomes.

Two observers collected plant data. At every seventh quadrat, we quality-controlled cover estimates by having each

observer estimate independently. When estimates differed by a cover class, the observers agreed upon a cover class. We photographed sampling quadrats and collected unknowns for comparison with specimens at the Wisconsin State Herbarium.

Statistical Analyses

To quantify the effects of seeding and graminicide treatments, we separated plant cover data for natives, natives in the seed mix, non-natives excluding *Phalaris*, and *Phalaris*. We used cover-class midpoints to obtain average cover and plotted cover over time by treatment using the Lattice package.

We employed the software R, versions 2.6.0–2.8.1 (R Development Core Team 2007–2008), for linear mixed effects models and repeated measures analysis of variance (ANOVA) of data across sites and site-by-site analysis. Because we observed dependence among the residuals plotted against the fitted value in our model, we calculated *p*-values based on randomization tests. Generating a randomization of treatments allowed us to construct a sampling distribution that allowed testing of differences between treatments. We conducted pairwise multiple comparisons of plots that did and did not receive sethoxydim and seeding treatments, while correcting for repeated measurements in permanent quadrats. Repeated measurements were accounted for by adding the quadrat location as a mixed effect to our linear mixed effects model. The linear mixed effect model contained the parameter of interest as the response variable (*Phalaris*' height or cover), with herbicide application, seed treatments, and year as variables in the model. We used the conservative Bonferroni correction for *p*-values for multiple comparisons. We determined *p*-values for comparisons of the response variable of interest by comparing the observed sample means with the mean of the distribution created from our data at random. This sampling distribution was generated by taking 10,000 random samples from our dataset, using the Markov Chain Monte Carlo (mcmc-samp) algorithm within the "arm" and "lmer" packages with R. We used JMP® (2005) to compare species richness with and without graminicide among eight sites (two-way ANOVA on untransformed count data, as residuals were normal) and to

compare LAI and tau for all plots with and without graminicide (*t* tests).

Results

Environmental Conditions

Calendar-year rainfall totaled 78 cm in 2005, 112 cm in 2006, 124 cm in 2007, and 112 cm in 2008; monthly rainfall was near normal except in August 2007 and June 2008, each of which was 3 times the norm (Lindbergh Field weather station, Madison, WI, U.S.A.). These extreme rainfall events created unusual flood times. Sedge meadows usually experience high water in spring during snow melt and late summer drawdowns (Amon et al. 2002). Cherokee Marsh was our wettest site, with standing water in both CM1 and CM2 in summer 2007.

Soils of CM1, CM2, GP1, and GP2 were similar in sand, silt, and clay fractions (Table 2). LMR2, on the Wisconsin River floodplain, had high sand content. Soils of all sites were similar in pH (near neutral), organic matter (between 2 and 3%), and nutrients (Table 2). Concentrations of calcium and magnesium were high in wetlands with considerable groundwater influence (CM and Z; McDermott Kurtz et al. 2007). The GP sites, which were near agricultural fields, were high in potassium and phosphorus. The LMR sites had high inorganic nitrogen levels (Table 2).

Effect of the Graminicide on *Phalaris*

Phalaris was graminicided as it was developing flowers; this halted growth of the flowering stalk and reduced maximum height. At Brant, where we graminicided but did not seed natives, sethoxydim reduced *Phalaris*' maximum height to 50% of that in control plots (approximately 200 cm) in all three years of treatment ($p < 0.001$). The other eight sites had similar reductions in *Phalaris*' height due to graminicide (Fig. 1). Mean maximum heights over three years ranged from 78 to 125 cm with graminicide and 141 to 218 cm without. The tallest plants were in CM1 and CM2, where nitrate levels were high (Table 2).

Table 2. Soil attributes for sites at CM, LMR, GP and Z.

	CM1	CM2	LMR1	LMR2	GP1	GP2	Z
Sand (%)	15	9	ND	49	15	15	ND
Silt (%)	57	63	ND	37	65	67	ND
Clay (%)	28	65	ND	14	20	18	ND
pH	6.6	6.3	5.4	5.3	6.1	6.1	7.4
OM (%)	2.3	2.6	7.1	2.9	2.9	2.8	7.8
Ca (ppm)	3151	2163	1107	1685	1693	1682	3340
Mg (ppm)	755	462	232	386	444	462	632
P (ppm)	33	62	11	17	75	15	24
K (ppm)	61	75	48	65	496	564	51
NH ₄ -N(ppm)	14.42	12.6	34.3	39.46	9.12	15.38	18.2
NO ₃ -N (ppm)	35.96	40.58	<0.01	40.6	8.12	22.36	23.01
Total N (%)	0.6	0.37	0.41	0.39	0.28	0.28	0.45
N:P (wt:wt)	1.8	0.9	7.4	7.2	0.4	3.5	2.5

Each value is from a composite of 35 sample cores. ND = no data.

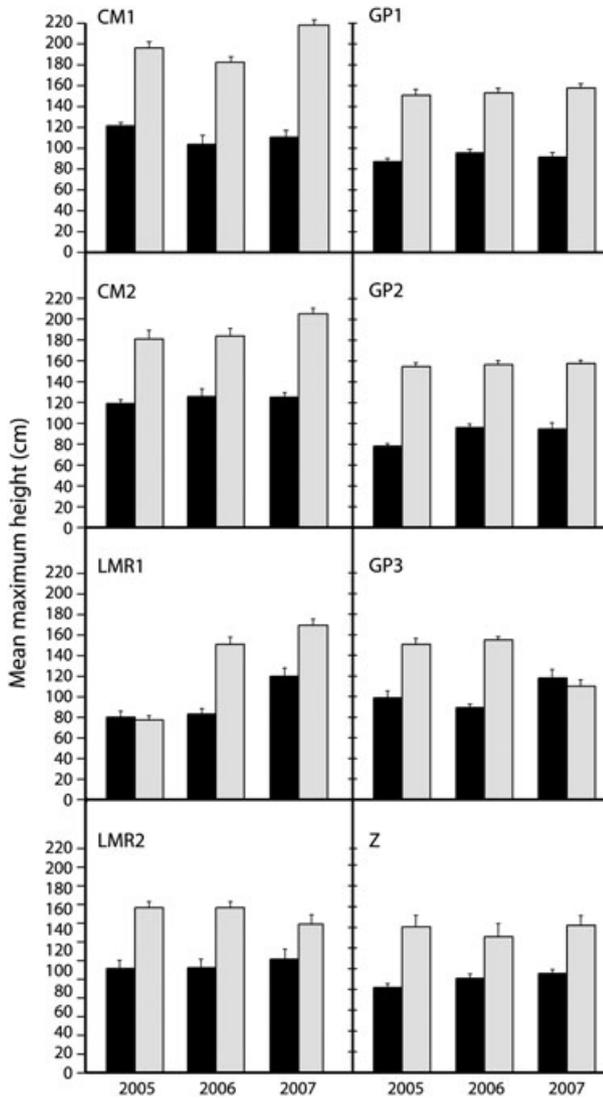


Figure 1. Mean maximum height of *Phalaris* with (dark bars) and without (light bars) graminicide (sethoxydim). Error bars are +1 SE. Site codes: CM = Cherokee Marsh; LMR = Leopold Memorial Reserve; GP = Goose Pond; Z = private land.

In the absence of graminicide, *Phalaris* consistently produced approximately 100% cover, and cover class midpoints averaged 88%. Sethoxydim tended to reduce cover, but the pattern varied with site. At Brant, *Phalaris* cover was similar (approximately 65%) for control and graminicided plots in 2005, but sethoxydim reduced cover to 35 and 40% in 2006 and 2007 ($p < 0.001$). In six sites (CM1, CM2, LMR1, LMR2, GP1, and GP2), cover was significantly reduced (often to less than 40%) in 2006 and 2007 (Fig. 2, graphs on right). Cover remained high in GP3 and Z. Only GP1 and GP2 showed clear progressive declines in *Phalaris* cover for the three-year treatment period. In CM1 and CM2, *Phalaris* cover increased substantially in 2007, coincident with standing water. Even after three years of sethoxydim treatment (2005–2007), mean *Phalaris* cover remained >20% in all sites. The two sites where we applied the broad-spectrum herbicide (glyphosate)

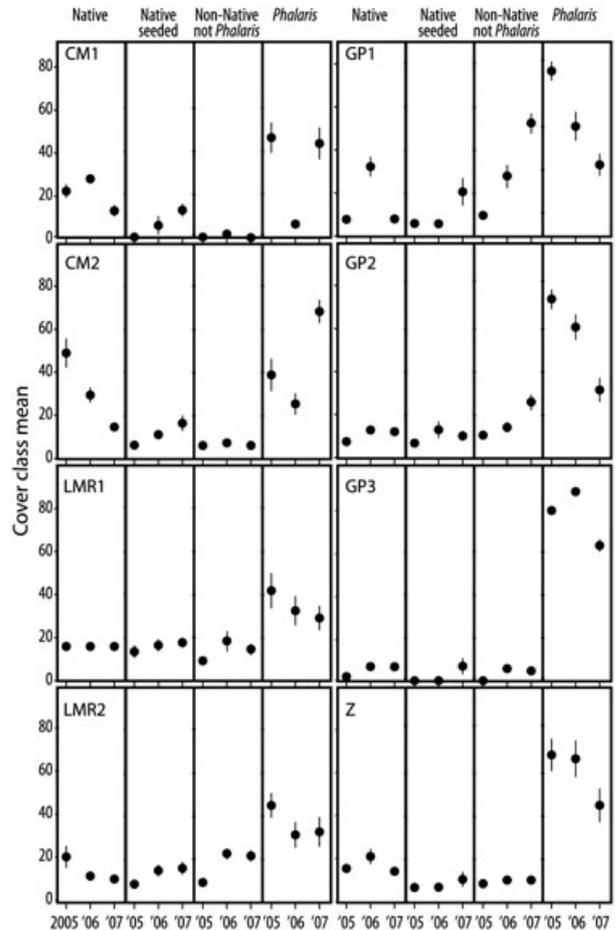


Figure 2. Mean percent cover (average of cover class midpoints) by species groups (native unseeded, native seeded, non-native but not *Phalaris*, and *Phalaris*) over three years for eight experimental sites. Data are for all graminicided plots. Sites without graminicide consistently had 75–100% cover. Bars are ± 1 SE; some are smaller than the dot. Site codes as in Figure 1.

in fall 2004 (LMR1, LMR2) showed no greater evidence of *Phalaris* mortality than the other seven sites.

Despite differences in height and cover, treated and untreated *Phalaris* canopies differed only slightly in LAI in August 2007 (LAI = 4.24 ± 0.14 SE with and 5.32 ± 0.14 without graminicide; $t = 5.1$; $p < 0.0001$). While LAI increased with maximum height of *Phalaris* (LAI = $0.0223 \times \text{max ht in cm} + 1.8$; $r^2 = 0.325$, $n = 270$), even where the canopy was <1-m tall, LAI ranged from 1 to 7, in part because dead leaves remained attached to vertical stems. Overall, little light penetrated the canopy and litter, although mean tau was slightly higher for graminicided plots (0.068 ± 0.004) than untreated plots (0.045 ± 0.005 ; $t = 3.3$, $p < 0.0001$). Other species were few in number (Fig. 3) and low in cover (Fig. 2).

Effect of Sowing Species-rich Mixtures

Seeding had its strongest effect at Goose Pond, where seeded native species appeared in plots that were seeded but did

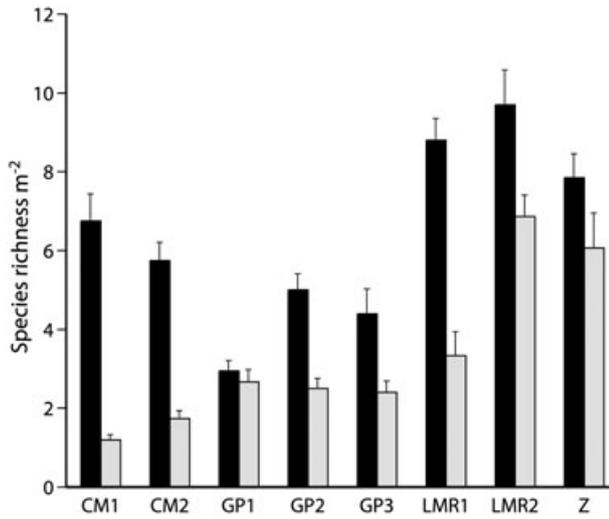


Figure 3. Species richness (per square meter, including non-native species) with graminicide (black bars) and without graminicide (gray bars). Data are means +SE at eight sites in August 2007. Species richness increased significantly with three years of graminicide application at CM1, CM2, LMR1, and LMR2 (Tukey HSD, $p < 0.5$). Site codes as in Figure 1.

not emerge from seed banks in unseeded plots (Fig. 4). Elsewhere, species richness was similar with and without seeding. Native species cover did not follow the expected pattern of a direct increase in native species due to seeding or an indirect increase of unseeded native species due to reduced cover of *Phalaris*. Increases were modest, and mean cover of native-seeded species never exceeded 20% in graminicided plots of the eight seeded sites, and only CM1 and CM2 increased progressively (Fig. 2). Mean cover of unseeded native species was as high or higher than that of seeded natives. In CM2, unseeded natives had 50% cover in graminicided plots in 2005, but the overall pattern was a progressive decline, the opposite of expectations (Fig. 2).

A number of species responded more positively to graminicide (two-way ANOVA for treatment and site; $F_{1,7} = 24.4$, $p < 0.001$). Species richness was greater in CM1, CM2, LMR1, and LMR2, but not in GP1, GP2, GP3, or Z (Tukey HSD, $p < 0.05$; Fig. 3). After three years of graminicide application, the four sites that increased in species richness averaged 7.8 ± 0.42 species/m² compared to 3.3 ± 0.35 species/m² without graminicide. Some of these species were non-native weeds, however. In August 2007, the eight main study sites had 120 species, of which 13 are classified as invasive by the Wisconsin State Herbarium. In 2007, only one site lacked non-native species other than *Phalaris* (CM1) and one had low cover of other non-natives (CM2). Neither CM1 nor CM2 was cultivated historically (Bedford et al. 1974), whereas other sites had previous agricultural use. The latter had measurable cover of non-native species in addition to *Phalaris*. In GP1 and GP2, non-native, agricultural weeds (e.g. *Cirsium arvense*) increased over time (Fig. 2).

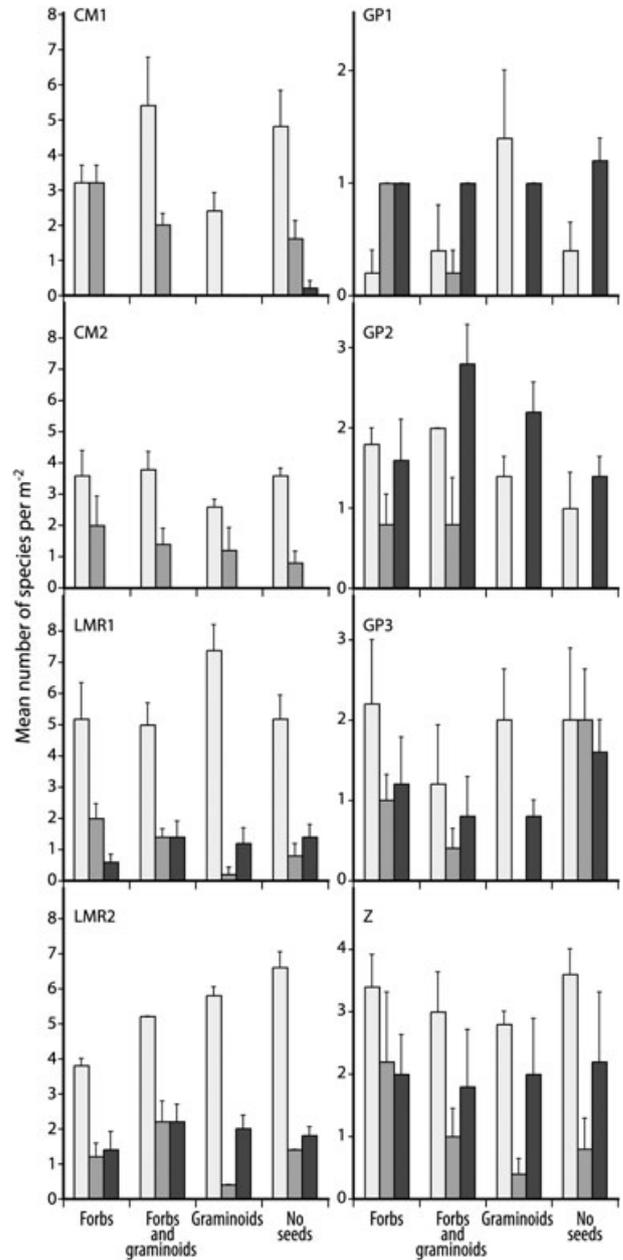


Figure 4. Number of species per square meter of non-seeded natives (clear bars), seeded natives (gray bars), and non-natives excluding *Phalaris* (darkest bars) found for each of the four seed addition treatments (x-axis; note that “Graminoids” did not include grasses). Data are August 2007 means +1SE in graminicided plots ($n = 5$). Site codes as in Figure 1.

The vegetation was not resilient to reinvasion once sethoxydim treatment ceased. Gains in native species richness and cover were short-lived and dependent on continued use of the graminicide. After treatment, the three sites we resampled (CM1, LMR1, LMR2) were all reverting to a *Phalaris* monotype with maximum heights approaching those of the ungraminicided plots. In September 2008, the mean maximum heights of *Phalaris* with and without prior graminicide

treatment were: 163 ± 6.6 cm versus 175 ± 9.2 cm at CM1 (no legacy; $t = 1.05$, $p = 0.30$); 147 ± 6.9 cm versus 178 ± 3.7 cm at LMR1 ($t = 3.96$, $p < 0.01$), and 136 ± 7.3 cm versus 159 ± 5.3 cm at LMR2 ($t = 2.49$, $p = 0.02$). Across all three resampled sites, *Phalaris* averaged 170-cm tall with $88 \pm 0.0\%$ cover (all plots with 75–100% cover class) where it was never graminicided and 149-cm tall with $81 \pm 3.1\%$ cover in previously graminicided plots.

Discussion

Consistent with the alternative states model (Hobbs & Suding 2009), *Phalaris* has challenged eradication efforts across North America (Bernthal & Willis 2004; Tu & Salzer 2005; Reinhardt Adams & Galatowitsch 2006), and our test of a graminicide plus seeding of native species did not restore any site to sedge meadow vegetation. One aspect of the proposed feedback loop (early growth of vertical stems) occurred prior to graminicide application; after treatment, however, *Phalaris*' height was consistently reduced and cover was sometimes reduced. Still, the stunted canopies (<1 m tall) had sufficient leaf area to reduce light by 85% (Healy 2008) and favor vegetative regrowth of *Phalaris*. Our treatments did not break the proposed feedback loop.

We experienced four setbacks in our attempt to replace *Phalaris* with native sedge meadow. First, the graminicide did not progressively decrease dominance by *Phalaris* over the three-year experiment, and *Phalaris* persisted in nearly all 160 treated plots. This was not entirely surprising, as other tests on perennial grasses suggest that sethoxydim is less effective than broad-spectrum herbicides (Roberts et al. 1998; Lingenfelter & Curran 2007), and our earlier use of glyphosate (one application) had not controlled *Phalaris* (Herr-Turoff 2005; Wilcox et al. 2007). The surprise was that three years of sethoxydim application had so little effect on *Phalaris* growth, both in duration and magnitude. Most effects did not persist beyond the year of application, as there was no greater reduction in year 2 or 3 except at LMR1 and LMR2. *Phalaris*' height reduction (approximately 50%) was fairly consistent despite variability in site conditions (sand, N, K, Ca, and Mg). Cover reduction was more variable (<50%). The two sites that showed progressive reduction (LMR1, LMR2) were sandy sites on the Wisconsin River floodplain. *Phalaris* also performed poorly in sand-filled microcosms, even with nitrogen additions (Herr-Turoff unpublished data). If the sandy soil impaired nitrogen uptake, efforts to control *Phalaris* could be more effective under such conditions.

While spring application of the graminicide inhibited flowering, *Phalaris* retained its ability to resprout and recruit from the accumulated seed bank. These results are consistent with sethoxydim's mode of action on grasses, namely, interfering with cell-wall formation (Stoltenberg et al. 1989). It is now clear that sethoxydim did not kill *Phalaris*; it only stunted stems. A broad-spectrum herbicide (glyphosate), which we applied to the LMR sites once in fall 2004, killed *Phalaris* aboveground, but strong resilience came from seed bank regeneration and regrowth of rhizome buds, some of which might

have been dormant and unaffected by sethoxydim at the time of application (Annen 2008).

Our second setback was the limited response to seeding, that is we did not greatly augment diversity or provide the dense canopy that is needed to suppress *Phalaris* resprouts and seedlings (Lindig-Cisneros & Zedler 2002a,b). In most sites, many of the species we seeded were also found in unseeded plots. This suggests that the species we seeded were already present in the seed bank and/or that seeds we sowed were moved around by wind, water, or wildlife. The responses to seeding were also inconsistent. At CM1, CM2, LMR1, GP1, GP2, and Z, we found more native species where we seeded forbs than in unseeded plots, but seeding graminoids had no such effect, and seeding both forbs and graminoids tended to dilute the effect of forb-seeding alone. The clearest response was in GP1 and GP2, where native species appeared in seeded but not unseeded plots. Even there, seeding produced only 0.5–1.0 species/m². Because those sites were recently cultivated, their native-species seed banks were likely depleted, and our addition of seeds clearly led to a small increase. But despite those modest gains, cover of seeded native species never exceeded 20%. We were unable to establish a native plant canopy that could resist reinvasion by *Phalaris* or other non-native species.

The "release" of non-native species in formerly agricultural lands (LMR, GP, Z) was our third setback. Graminicide plots produced *Cirsium arvense*, *Pastinaca sativa*, and *Cirsium vulgare*, all of which are invasive agricultural weeds. It is unclear why sethoxydim increased weed species richness but not native species. Perhaps the dense *Phalaris* canopy, with its high LAI and high light interception, suppressed all but the most aggressive species (notably non-native agricultural weeds) by the end of the growing season.

Our fourth setback was that the positive effects of sethoxydim (reduced flowering, height, and cover of *Phalaris*) were short-lived. *Phalaris* plots that had been treated from 2005 to 2007 all regrew tall, dense canopies that approached those of untreated plots in height and cover by September 2008. This outcome was not surprising, given that *Phalaris* had rebounded in spring 2006 and spring 2007, following graminicide in each previous year.

The minimal legacy of multi-year graminicide application (slight reduction in maximum height with resumption of flowering in 2008) supports the existence of strong feedbacks that sustain *Phalaris*. In the alternative states model, a system shifts from one state to another when a controlling variable exceeds some threshold and feedbacks in the native state are overcome (Hobbs & Suding 2009). For *Phalaris*, four controlling variables are nutrients, flooding, hydrological alterations such as wetland drainage or increased stormwater inflows, and light, via disturbances that create openings in native plant canopies (Lindig-Cisneros & Zedler 2002a,b; Green & Galatowitsch 2002; Kercher & Zedler 2004; Kercher et al. 2004, 2007). We did not manipulate these controlling variables in our field experiments, although flooding in 2007 at CM sites coincided with, and probably caused, increased *Phalaris* cover. In nearby Minnesota, Perry and Galatowitsch (2003) and Inannone et al.

(2008) explored ways to reduce light (by adding cover crops) and nitrogen (by amending the soil with organic matter to stimulate microbial sequestration of nutrients). The gains were short-lived and their management tools would be difficult to use in large restoration sites, where a single flood can re-introduce nutrients and smother cover crops, while adding propagules of unwanted invaders.

Because controlling variables are so difficult to manipulate, we tested the ability to remove the dense *Phalaris* canopy and prevent its thatch and seed banks from accumulating, expecting that breaking these strong feedbacks would release native species from shading (Zedler 2009). However, *Phalaris* continued to produce canopies with high LAI and low light transmission. The monotype also resisted restoration of diverse sedge meadow vegetation, as sowing species-rich seed mixtures of forbs and graminoids could not outcompete the resilient *Phalaris*. Greater control of *Phalaris* would be expected from an herbicide that targets the rhizomes. To date, no graminicide is consistently effective on *Phalaris*. The widely used broad-spectrum herbicide, glyphosate, has at least three shortcomings: dormant buds of *Phalaris* can survive belowground; most or all native species will also be killed; and amphibians and other wildlife can be harmed (Relyea 2005). Our improved understanding of the strengths of the feedbacks that sustain *Phalaris* leads us to recommend tests of other measures to control monotypes of this widespread invader (WRCGMWG 2009).

Implications for practice

- We rejected the use of sethoxydim for controlling *Phalaris* monotypes, although trials on sandy soil are warranted.
- The reduction in flowering and seed production could ultimately reduce the *Phalaris* seed bank, but only in sites that have minimal seed importation and for an unknown time period (seeds could remain viable for many years).
- Using sethoxydim for more than three years might eventually reduce *Phalaris*, but this graminicide is not licensed for aquatic conditions and a single year of no application could negate early gains, as in our study.
- Seeding of native species to restore sedge meadow vegetation produced minimal gains under a persistent, dense overstory of *Phalaris*, even with annual spring burning to remove standing dead and thatch. We suggest waiting to add seed until *Phalaris* is reduced in cover.
- Where seed banks include agricultural weeds, burning and graminiciding can release unwanted forbs, requiring follow-up management.
- Until a graminicide becomes available to kill (not just stunt) *Phalaris*, we suggest treating monotypes with a broad-spectrum herbicide for multiple years while delaying the restoration of native species. After *Phalaris* no longer emerges, burning and seeding of natives would more likely achieve the desired outcome. Field staff at

the UW-Madison Arboretum are currently applying this approach in Curtis Prairie.

- Long-term surveillance and spot treatment of *Phalaris* will be needed wherever controlling variables (nutrients, flooding) threaten natural wetlands.

Acknowledgments

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Appendix. Native plant species in three seed mix treatments (F = forbs; G = graminoids, omitting grasses; F + G = forbs and graminoids). Due to limited seed availability, the treatment was slightly different for Leopold Memorial Reserve (LMR) than for Cherokee Marsh (CM), Goose Pond (GP) and the private land (Z).

Species	F	G	F + G	LMR	CM, GP, Z
<i>Alisma subcordatum</i>	X				X
<i>Angelica atropurpurea</i>	X				X
<i>Asclepias incarnata</i>	X				X
<i>Aster novae-angliae</i>	X		X	X	X

Appendix. Continued.

<i>Species</i>	<i>F</i>	<i>G</i>	<i>F + G</i>	<i>LMR</i>	<i>CM, GP, Z</i>
<i>Aster puniceus</i>	X		X	X	X
<i>Aster umbellatus</i>	X		X	X	X
<i>Carex aquatilis</i>		X	X	X	
<i>Carex bebbii</i>		X	X	X	X
<i>Carex comosa</i>		X	X	X	X
<i>Carex crinita</i>		X		X	X
<i>Carex hystericina</i>		X		X	X
<i>Carex lacustris</i>		X	X	X	X
<i>Carex squarrosa</i>		X	X		X
<i>Carex stipata</i>		X	X	X	X
<i>Carex vulpinoidea</i>		X	X	X	X
<i>Cirsium muticum</i>	X			X	
<i>Eupatorium maculatum</i>	X			X	X
<i>Eupatorium perfoliatum</i>	X			X	X
<i>Euthamia graminifolia</i>	X			X	X
<i>Helenium autumnale</i>	X		X	X	X
<i>Helianthus grosseserratus</i>	X				X
<i>Hypericum pyramidatum</i>	X		X	X	X
<i>Juncus dudleyi</i>		X		X	X
<i>Juncus effusus</i>		X	X	X	X
<i>Juncus interior</i>		X			X
<i>Juncus tenuis</i>		X		X	X
<i>Juncus torreyi</i>		X		X	
<i>Pycnanthemum virginianum</i>	X		X	X	X
<i>Rumex orbiculatus</i>	X				X
<i>Rumex verticillatus</i>	X			X	
<i>Scirpus atrovirens</i>		X	X	X	X
<i>Scirpus cyperinus</i>		X			X
<i>Scirpus microcarpus</i>		X			X
<i>Scirpus validus</i>		X			X
<i>Solidago riddellii</i>	X		X	X	X
<i>Verbena hastata</i>	X		X	X	X



Does wet prairie vegetation retain more nitrogen with or without *Phalaris arundinacea* invasion?

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Abstract

Elevated nitrogen (N) levels accelerate expansion of *Phalaris arundinacea* L. (reed canary grass), a highly aggressive invader that displaces native vegetation and forms monotypes. Hence, *Phalaris* is commonly presumed to have high nutrient uptake that contributes to higher N retention in a wetland. We compared the capability of wet prairie vegetation with and without invading *Phalaris* under low-N and high-N treatments to (1) accumulate N in plant tissues, (2) retain N in soil and (3) remove N from water flowing through mesocosms. With high-N treatment, above-ground biomass increased by >90% ($P < 0.0004$; yrs. 1–2) and percent total N in above-ground tissues increased by >46% ($P = 0.0005$; yrs. 1–2). Consequently, there was ~3 times as much total N accumulation in above-ground tissue (calculated from biomass and percent total N in tissues) with high-N treatment vs. low-N treatment ($P < 0.0001$; yrs. 1–2). Without invading *Phalaris*, wet prairie vegetation produced over 49% more above-ground biomass ($P \leq 0.022$; yrs. 1–2) and accumulated over 38% more N in its above-ground tissues ($P = 0.009$; yrs. 1–2), compared to invaded mesocosms. The high-N treatment increased concentrations of soil ammonium ($\text{NH}_4\text{-N}$) up to 157% ($P = 0.0001$) and soil nitrate ($\text{NO}_3\text{-N}$) up to 549% ($P < 0.001$). After N treatments began, we found no differences in total N or $\text{NO}_3\text{-N}$ in soils ($P > 0.05$) or in concentrations of $\text{NH}_4\text{-N}$ or $\text{NO}_3\text{-N}$ released in the discharged water ($P > 0.1$) from wet prairie mesocosms with and without invading *Phalaris*. Soil $\text{NH}_4\text{-N}$ did not differ between the wet prairie mesocosms with and without *Phalaris* invasions on five dates ($P > 0.05$); the one exception was in August 2004 (27% greater with invasion; $P = 0.02$). Our results from wet prairie mesocosms do not support the presumption that *Phalaris* retains more N than native plant assemblages.

Abbreviations: $\text{NH}_4\text{-N}$ – ammonium–nitrogen; $\text{NO}_3\text{-N}$ – nitrate–nitrogen; N – nitrogen

Introduction

The conversion of native wetland vegetation to an invasive species following eutrophication (Green and Galatowitsch, 2002; Kadlec and Bevis, 1990; Kercher and Zedler, 2004; Maurer

and Zedler, 2002; Miao and Sklar, 1998; Windham and Ehrenfeld, 2003) suggests that the invader can take up more nutrients than the displaced resident species. Although aggressive invaders are recommended for use in “treatment” wetlands designed to reduce nutrients from secondary wastewater (Cooper and Findlater, 1990; Hammer, 1989; Kadlec and Knight, 1996), little is known of the comparative ability of native

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assemblages vs. invasive-dominated vegetation to remove nutrients from through-flowing water. We compared N-retention capabilities of wet prairie vegetation as it converted to dominance by a well-known aggressive plant in experimental systems of known nutrient status.

Elevated nutrient levels accelerate the expansion of *Phalaris arundinacea* L. (reed canary grass), a highly aggressive invader of temperate North American wetlands (Galatowitsch et al., 1999), in experimental settings (Kercher and Zedler, 2004; Maurer and Zedler, 2002). Increased N alone facilitates its suppression of native wetland vegetation (Green and Galatowitsch, 2002). Thus, *Phalaris* is presumed to have high N uptake and to increase retention of N within a wetland. Conchou and Fustec (1988) describe *Phalaris* as a “nutrient pump” that is useful in reducing nutrients released to downstream systems if its aerial biomass is harvested before senescence.

Phalaris has been recommended for use in treatment wetlands, because harvesting its above-ground biomass could remove a high proportion of the N entering a wetland (Dubois, 1994). Hurry and Bellinger (1990) found that harvesting *Phalaris* shoots every 3 months from a treatment wetland receiving continual flow of sewage effluent removed nearly $50 \text{ g N m}^{-2} \text{ year}^{-1}$, which approximated 11% of the site’s annual N loading. Bernard and Lauve (1995) report that *Phalaris* accumulated more biomass and N in its tissues in a constructed wetland receiving nutrient-rich landfill leachate than in an unpolluted control site. N uptake approximated 35 g m^{-2} or about 10% of the annual N input to the polluted site. However, evidence that it is capable of greater accumulation of N in its biomass than other wetland plants is lacking (Kao et al., 2003; McJannet et al., 1995). In experimental wastewater treatment wetlands in Sweden, the amount of N in harvested biomass of *Phalaris* did not differ from other grasses (Geber, 2000).

If *Phalaris* accumulates more N in its biomass than other wetland vegetation, it could affect N accumulation in soils and N leakage in discharged waters. Geber (2000) reported that soil and porewater N associated with *Phalaris* in treatment wetlands were low throughout the growing season and speculated that the risk of N leakage in discharged waters was low. No comparisons were made of soil and porewater N

associated with other species in the wetland (ibid.). Invasive species can alter soil N, but patterns and degrees of change vary among species, for the same species at different sites, and among ecological processes (Ehrenfeld, 2003; Meyerson et al., 2000; Otto et al., 1999; Templer et al., 1998; Windham 2001). Few studies examine changes in the leaching of N from wetlands dominated by invasive species (Ehrenfeld, 2003). Yet, if wetlands are to be restored to reduce N loading locally and downstream (e.g., from the US Midwest to the Gulf of Mexico; Hey, 2002; Mitsch et al., 2001), it will be prudent to encourage growth of species that can remove large amounts of N. Managers will need to know if native species or invasive macrophytes remove more N.

Phalaris commonly invades wetlands in disturbed landscapes impacted by urban development and changes in hydraulic conditions (Galatowitsch et al., 2000; Kercher et al., 2004; Werner and Zedler, 2002). Although this clonal C3 grass is considered a native species to North America, cultivars were extensively introduced from northern Europe for streambank erosion control and pasture forage (Galatowitsch et al., 1999; Merigliano and Lesica, 1998). In the 1950s, Curtis (1959) documented *Phalaris* in wet prairies and sedge meadows in southern Wisconsin. Currently, it dominates (>50% cover) over 40,000 ha of southern Wisconsin wetlands (Bernthal and Willis, 2004). Understanding if there is a tradeoff of higher N retention when *Phalaris* displaces native species becomes critical when deciding to control its invasions or justify its use in treatment wetlands.

We used experimental mesocosms to test the assumption that wet prairie vegetation retains more N after invasion by *Phalaris*. Mesocosms have been used to demonstrate how plant species richness affects phosphorus leakage in water (Engelhardt and Ritchie, 2001). They are a useful tool for comparing N retention, because N inputs and hydrologic loading and retention times can be regulated without the extensive structures that would be required in the field. Controlling hydrologic conditions is important because frequency and duration of flooding affects N removal in wetland systems (Busnardo et al., 1992). We tested the assumption with experimental systems that had well-established wet prairie vegetation and followed responses in the 2nd and 3rd years

after the invader was introduced. We hypothesized that experimental systems with wet prairie vegetation would show:

- (1) Greater accumulation of N in biomass with *Phalaris* invasion.
- (2) Greater total N and inorganic N in soil with *Phalaris* invasion.
- (3) Less release of inorganic N to water flowing through the mesocosms with *Phalaris* invasion.

Materials and methods

Experimental design

A two-factor experiment that varied N addition and vegetation type used 20 mesocosms arranged in a randomized complete block design. The mesocosms were imbedded in a large outdoor experiment that tested the relationship and interactions of disturbances on *Phalaris* invasions (Kercher and Zedler, 2004). In the larger experiment, five blocks, double rows of 16 mesocosms running north to south, differed in shade cast by trees along the eastern edge

of the University of Wisconsin Arboretum facility. We compared N retention capabilities of species-rich wet prairie vegetation with no *Phalaris* (resident treatment) and *Phalaris*-dominated (invasion treatment) vegetation under high- and low-N additions. Each treatment was replicated once per block and was randomly assigned within each block of the larger experiment.

On May 19, 2000, black plastic oval-shaped stock tanks measuring 1.25 m × 0.92 m × 0.65 m deep with approximately 1.1 m² in surface area (Freeland Industries, Portage, Wisconsin, USA) were filled to a depth of 15 cm with locally quarried, screened sandstone (St. Peter's sandstone) and topped with 30 cm of screened, pulverized loamy topsoil from a supplier in Verona, Wisconsin, USA. Twenty-five species were selected to represent a wet prairie assemblage from southern Wisconsin (Curtis, 1959). On July 4, 2000, after 2 months of cold-moist stratification, seeds were sown at a rate of 650 seeds m⁻² in each mesocosm. Four grasses comprised 50% of the total number of seeds and 21 forbs and sedges comprised the remainder. Mesocosms were watered daily and weeded four times in 2000 and

Table 1. Mean percent of intercepts ± 1 S.E. for each species in the 20 mesocosms from the line intercept sampling in June 2001 and June 2002 prior to treatment initiation

Species planted	Percent of intercepts	
	June 2001	June 2002
Graminoids		
<i>Agrostis gigantea</i> Roth ^a	28.5 ± 0.9	27.5 ± 0.8
<i>Andropogon gerardii</i> Vitman	17.2 ± 1.2	17.4 ± 1.3
<i>Glyceria striata</i> (Lam.) A.S. Hitchc.	7.8 ± 1.1	4.3 ± 0.8
<i>Spartina pectinata</i> Bosc ex Link	2.6 ± 0.5	4.2 ± 0.9
<i>Phalaris arundinacea</i> L.	0.0	3.4 ± 0.8
<i>Carex vulpinoidea</i> Michx.	1.5 ± 0.4	2.5 ± 0.4
Forbs		
<i>Desmodium canadense</i> (L.) DC.	10.7 ± 1.8	10.3 ± 1.4
<i>Verbena hastata</i> L.	14.1 ± 1.2	6.9 ± 0.8
<i>Silphium perfoliatum</i> L.	6.5 ± 0.9	6.0 ± 0.9
<i>Symphyotrichum novae-angliae</i> (L.) Nesom	3.0 ± 0.5	4.5 ± 0.8
<i>Helenium autumnale</i> L.	3.2 ± 0.5	4.4 ± 0.6
<i>Pycnanthemum virginianum</i> (L.) T. Dur. & B.D. Jackson ex B.L. Robins & Fern.	1.0 ± 0.5	1.7 ± 0.4
<i>Asclepias incarnata</i> L.	2.6 ± 0.5	1.6 ± 0.3

Species were seeded into the mesocosms in July 2000, except for *Phalaris* which was introduced as small plants and seeds in May and June of 2002. Species with a mean percent of intercepts < 1.0 for both sampling episodes are excluded from this table. Nomenclature follows the USDA, NRCS (2002).

^aThe wet prairie seed mix sown in Summer 2000 was intended to have *Calamagrostis canadensis*, but when the plants flowered in 2001, the grass provided by the seed company was identified as *Agrostis gigantea*, a naturalized species native to Eurasia (Fassett, 1951).

2001. By June 2002, the mesocosms contained a 2-year-old diverse wet prairie assemblage composed of native and one naturalized species (Table 1).

Treatments

Phalaris arundinacea L. seeds (Olds Seed Solutions, Madison, Wisconsin, USA) were sown in flats on March 7, 2002, transplanted to plug trays 4 weeks later and grown in a greenhouse. On May 21, 2002, we transplanted four 10-week-old *Phalaris* plants into each of the 10 mesocosms randomly selected for invasions, placing them 20 cm from the adjacent “corner” walls at a depth of 10 cm, covering the roots. On June 5, 2002, *Phalaris* was seeded in the same mesocosms at a rate of 11 g m^{-2} (twice the supplier’s recommended rate) and the wet prairie species were clipped at the soil level to facilitate *Phalaris* germination (Lindig-Cisneros and Zedler, 2001, 2002) and expansion of the young transplants (Maurer and Zedler, 2002; Morrison and Molofsky, 1998). The remaining 10 mesocosms, which retained the resident vegetation, received equalized soil disturbance but no *Phalaris* introductions. Clipping the resident treatment would have risked loss of native species, thereby jeopardizing the experimental comparison of species-rich vs. *Phalaris*-dominated vegetation.

We applied Forever Green Lawn Builder Turf Food (Eau Claire Crop Oil Company, Eau Claire, Wisconsin, USA), containing 27.0% N (1.2% $\text{NH}_4\text{-N}$; 25.8% urea-N), 3% P_2O_5 , 4% K_2O , 1% S, and 1% Fe, to 10 of the mesocosms, of which 5 were invasion and 5 were resident treatments. The nutrient treatment matched the recommended rate of the fertilizer manufacturer and totaled 14.2 g N , 1.6 g P , and 2.1 g K m^{-2} in 2002. The remaining 10 mesocosms received no nutrient additions. Between June 17 and September 23, 2002 mesocosms were flooded on an intermittent cycle with 2 days flooding followed by 12 days of draw-down during which mesocosms were watered as needed. The flooding regime was based on hydrograph data showing flashy hydroperiods in stormwater basins in southern Wisconsin and northern Illinois (Miller, 2001; Veltman, 2002). The intermittent flooding did not reduce species richness of the wet prairie vegetation (Kercher and Zedler, 2004). *Phalaris* expanded in the invasion treatments during the 2002 growing season.

Because conversion to a *Phalaris* monotype was incomplete in 2002, additional protocols were applied in 2003 to facilitate its dominance in the invasion treatment. Standing dead material was removed from all 20 mesocosms in February 2003 to equalize growing conditions. On April 23, 2003, the invasion treatments were sown with *Phalaris* seeds at a rate of 11 g m^{-2} . On May 28–29, 2003, we clipped the wet prairie species to facilitate the spread of *Phalaris* clones, as in 2002, and we added 8-week-old *Phalaris* transplants that were grown in the greenhouse. Nine *Phalaris* transplants were evenly spaced along three transects within each mesocosm. Clipped vegetation was cut into small pieces and distributed along the outer edge of each mesocosm to retain each system’s N. The resident treatment received equalized soil disturbance but no *Phalaris* introductions. Vegetation in the resident treatment was unclipped in May 2003 to retain native species. Standing dead material was removed from all 20 mesocosms in February 2004 to equalize growing conditions, but no protocols were applied to induce *Phalaris* dominance in 2004.

The fertilizer used in 2002 was replaced with a granular ammonium–nitrate fertilizer (Royster-Clark Inc., Norfolk, Virginia, USA) applied at high ($48 \text{ g N m}^{-2} \text{ year}^{-1}$) and low ($12 \text{ g N m}^{-2} \text{ year}^{-1}$) treatment levels in 2003 and 2004. The high rate induces *Phalaris* dominance and is representative of the nitrate levels common in agricultural landscapes (Green and Galatowitsch, 2002). The N treatment was divided into five applications per year and added on June 2, June 16, June 30, July 14 and July 28, 2003 and on May 31, June 14, June 28, July 12 and July 26, 2004. The high-N treatment was applied to the mesocosms that received nutrients in 2002; the low-N treatment was applied to mesocosms that had no nutrient addition in 2002. During each N application, mesocosms were flooded for 2 days (75 L of water), followed by 12 days during which the mesocosms were drained but watered as needed.

Data collection

Species composition. We used a line intercept method to sample the vegetation within each mesocosm and calculate similarity among treatments. On June 4–7, 2001, June 3–4, 2002, September 18–24, 2002, August 5–7, 2003, and July 29–30, 2004,

two 1-m long dowels marked at 10-cm intervals were placed parallel to the long axis of the mesocosm 30 cm from the sides (32 cm apart) and equidistant from the ends. We recorded the total number of intervals intercepted by each species along each line and calculated the proportion of intervals intercepted by each species within a mesocosm. Similarity was calculated as

$$S = \sum \min(p_{1i}, p_{2i})$$

where p_{1i} is the average proportion of intervals intercepted by species i in treatment 1 and p_{2i} is the average proportion of intervals intercepted by species i in treatment 2 (Whittaker, 1975).

Soil. We collected four soil cores (2.54 cm diameter \times 10 cm deep) from each mesocosm on May 29, August 13 and October 29, 2003 and on June 3, July 29, August 17, and September 30, 2004. Homogenized composite soil samples for each mesocosm were analyzed by the University of Wisconsin Soil and Plant Analysis Lab for concentrations of extractable $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$ in 2003 and 2004 and total N in 2004. Dried and ground samples from 2003 were analyzed for total N using a LECO CNS 2000 Elemental Combustion Analyzer (St. Joseph, Michigan, USA). Soil samples were analyzed for pH using a Barnant 20 Digital pH/mV/ORD meter (Barrington, IL, USA) and soil moisture by weight loss after oven drying for 48 h at 110 °C.

We measured soil redox potential on May 30, 2003, prior to treatment initiation and on August 12 and October 28, 2003 and on June 1, July 27, August 16, and September 29, 2004, when the mesocosms were flooded prior to water sampling. Redox was measured in five blocks, except October 28, 2003 and July 27, 2004 when measurements were limited to two and three blocks, respectively. Redox was measured using four platinum electrodes, a calomel reference electrode and a Barnant 20 Digital pH/mV/ORD meter (Barrington, IL, USA). In each mesocosm, platinum electrodes were placed \sim 30 cm from opposite sides along the two central axes and the calomel reference electrode was placed in the center. Electrodes were inserted into the soil to a depth of 10 cm and allowed to stabilize before a reading was taken. We adjusted the readings by adding the potential of the calomel reference electrode (244 mV).

Water. We collected water samples to test for N leakage on August 12 and 15, 2003 when plants were at peak growth and on October 28, 2003 when plants were senescing. In the second year, we collected water samples on June 1, 2004 during early season growth, on July 27 and August 16, 2004 when plants were at peak growth, and on September 29, 2004 when plants were senescing. Mesocosms were flooded with 75 L of water 24 h prior to sampling. On August 14, 2003, ammonium–nitrate fertilizer was added at the same rates used for the treatment applications (31.0 and 7.75 g of fertilizer in the high and low treatments, respectively). On May 31 and July 26, 2004, ammonium–nitrate fertilizer was added during treatment applications. No fertilizer was applied during flooding for August 12 and October 28, 2003 and August 16 and September 29, 2004 samples. Water samples were collected from outflow valves at the base of each mesocosm and kept on ice until submitted to the UW Soil and Plant Analysis Lab for analysis of $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$ concentrations. Water samples were analyzed for pH using a Barnant 20 Digital pH/mV/ORD meter (Barrington, IL, USA).

Plant tissues. On August 20–21, 2003 and on August 18–19, 2004, above-ground biomass was collected from a random quadrant (0.27 m²) in each mesocosm. Biomass was separated into *Phalaris*, other graminoids, and forbs and chopped into 20-cm segments starting at the base. Canopy segments were homogenized and random samples were separated for N analysis. Biomass was oven dried at 60 °C for 48 h, weighed, and the remainder not used for N analysis was returned to the mesocosms 2 days after clipping to retain N within each system and to reduce the impact of removing vegetation on the soil.

On August 22, 2003 and August 19, 2004, below-ground biomass samples were collected using a 10.2-cm-diameter soil core to a depth of 10 cm. Soil cores were taken from the center of the quadrant used to sample above-ground biomass in 12 of the 20 mesocosms (blocks 1, 3 and 5) in order to limit soil disturbance and compare N levels from disturbed and undisturbed mesocosms in late season. Cores were washed over a 2-mm mesh to separate soil particles and stones from below-ground biomass. Biomass was oven dried at 60 °C for 48 h and weighed. Separate above-ground biomass

samples of *Phalaris*, other graminoids, and forbs and composite below-ground biomass samples were ground and analyzed by the UW Soil and Plant Analysis lab for tissue N concentration.

Data analysis

Two-way ANOVAs with N and vegetation treatments as independent variables were run using R (version 1.7.1; R Development Core Team, 2003). Our response variables were $\text{NH}_4\text{-N}$, $\text{NO}_3\text{-N}$ and total N in soil samples, $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$ in water samples, biomass, and average N concentrations and total N accumulation in plant tissues. Net changes in N concentrations in water samples between August 12 and October 28, 2003 and between June 1 and July 27, 2004 and in soil samples between August 13 and October 29, 2003 and between June 3 and July 29, 2004 were tested for treatment effects and interactions.

Boxcox analyses indicated that log transformations were appropriate to correct for non-normality. We tested the robustness of using one-half the lower detection limit for water samples that had $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$ concentrations below the detection limit. ANOVAs were run with and without extreme data points for $\text{NO}_3\text{-N}$ in water samples from August 2003 and June and July 2004, $\text{NH}_4\text{-N}$ in water samples from July 2004, and $\text{NO}_3\text{-N}$ in soil samples from August and October 2003. Extreme points were up to $25 \times$ greater than the next highest data point from the same sampling date. In water samples from July 2004, two outliers, one from the high-N resident treatment and one from the low-N invasion treatment, had $\text{NO}_3\text{-N}$ concentrations $> 19 \times$ greater than the average of the other mesocosms from the same treatment. We used Tukey's Honest Significant Difference to separate treatment means if an ANOVA was significant. Differences in tissue N concentrations of the forbs, *Phalaris*, and other graminoids were tested using paired *t*-tests and a Bonferonni correction for multiple tests.

Results

Because species composition is the primary treatment factor in the experiment, the vegetation is described first. We expected the vegetation in the

resident and invasion treatments to diverge as *Phalaris* invaded. The similarity index provides an indication of how similar the vegetation was among the four treatments and whether *Phalaris* was dominant in the invasion treatments. Physical conditions are described second, followed by N concentrations in the soil, in the water discharged from the mesocosms, and in plant tissues. Data mentioned in text are means \pm S.E. Significant differences in N are reported as "X% more" N in soil, water or plant tissue [e.g., if treatment A has 100% more soil N than treatment B, then soil N in treatment A = soil N in treatment B + (100% \times soil N in treatment B)].

Species composition

In June 2002, 2 weeks prior to nutrient and flooding treatments and two weeks after adding the first *Phalaris* transplants, the mesocosms averaged 12.7 ± 0.5 species, with 5.6 ± 0.2 graminoids and 7.1 ± 0.3 forbs. Graminoids averaged $61.7 \pm 0.8\%$ of the line intercepts, with *Agrostis gigantea* having the highest percent in all treatments (Table 1). *Phalaris* comprised $6.7 \pm 0.5\%$ of the intercepts in the invasion treatments. As desired, mesocosms were initially similar for the resident and invasion treatments and the high-N and low-N treatments (Table 2).

In September 2002, overall similarity between the resident and invasion treatments was lower, but *Phalaris* was not yet dominant in the invasion treatment. The resident treatment was no more than 0.66 similar to the high-N invasion treatment (Table 2). The percent of *Phalaris* intercepts was $1.5 \times$ greater with high-N treatment ($18.2 \pm 3.1\%$) than with low-N treatment ($11.9 \pm 0.2\%$). At the end of the first-year treatments, mesocosms were similar for the high-N and low-N treatments and between the resident treatment and the low-N invasion treatment, warranting additional protocols in the second year to induce *Phalaris* dominance in the invasion treatment.

In August 2003, *Phalaris* was dominant in the invasion treatment and the overall similarity between the resident and invasion treatments had dropped (Table 2). Graminoids were less common in the resident treatment ($51.4 \pm 2.2\%$ of the line intercepts) but more common in the invasion treatment ($88.1 \pm 2.5\%$ of the line intercepts). *Phalaris* comprised $25.6 \pm 1.0\%$ of

Table 2. Similarity between treatments in June and September 2002, August 2003, and July 2004

Treatment comparisons	June 2002	Sept. 2002	Aug. 2003	July 2004
Invasion, high N vs. resident, high N	0.85	0.66	0.42	0.26
Invasion, high N vs. resident, low N	0.86	0.65	0.46	0.38
Invasion, low N vs. resident, high N	0.86	0.80	0.63	0.43
Invasion, low N vs. resident, low N	0.84	0.82	0.67	0.51
Invasion, high N vs. invasion, low N	0.90	0.80	0.75	0.71
Resident, high N vs. resident, low N	0.88	0.88	0.83	0.75
Invasion vs. resident	0.88	0.75	0.55	0.40
High N vs. low N	0.92	0.86	0.83	0.78

Similarity was calculated using the minimum mean proportion of intercepts by species within a treatment. *Phalaris* was added in the invasion treatments as transplants in May 2002 and May 2003 and as seeds in June 2002 and April 2003.

the intercepts in the low-N and $46.9 \pm 5.6\%$ in the high-N invasion treatments, intercepting 100% of the intervals in each mesocosm.

In July 2004, *Phalaris* remained dominant in the invasion treatments, comprising $28.9 \pm 1.0\%$ of the intercepts in the low-N and $43.6 \pm 4.9\%$ in the high-N invasion treatments and intercepting $>90\%$ of the intervals in each mesocosm. The resident treatment was less similar to the invasion treatment, being no more than 0.38 similar to the high-N invasion treatment and 0.51 similar to the low-N invasion treatment (Table 2). The percent of graminoid intercepts continued to decrease in the resident treatment ($29.8 \pm 2.3\%$), while remaining high in the invasion treatment ($83.5 \pm 2.0\%$).

Physical parameters

Two-way ANOVAs showed occasional treatment effects in the physical parameters of the mesocosms. The pH of discharged water was higher from the high-N than low-N treatment in October 2003 (7.59 ± 0.01 vs. 7.54 ± 0.01 , respectively; $P = 0.003$; Table 3) and from the resident than invasion treatment in July 2004 (7.13 ± 0.03 vs. 7.00 ± 0.03 ; $P = 0.017$). We found vegetation and N-treatment effects on soil pH in May 2003 ($P = 0.0035$ and 0.039 , respectively) and in June 2004 ($P = 0.0003$ and 0.009 , respectively). Soil pH in the invasion treatment was higher than the resident treatment in May 2003 (7.91 ± 0.03 vs. 7.80 ± 0.04 , respectively) but lower than the resident treatment in June 2004 (7.36 ± 0.02 vs. 7.51 ± 0.03 , respectively). The high-N treatment had lower soil pH than

the low-N treatment in May 2003 and June 2004. Soil moisture was 6% greater in the invasion vs. resident treatment in May 2003 ($18.9 \pm 0.2\%$ vs. $17.8 \pm 0.4\%$; $P = 0.017$) and 5% greater in the invasion vs. resident treatment in August 2004 ($20.2 \pm 0.2\%$ vs. $19.2 \pm 0.3\%$; $P = 0.011$), when more soil was visible in the resident treatment. No other treatment effects were detected in the physical parameters. We do not report sporadic block effects for some physical parameters, for total soil N, or for $\text{NH}_4\text{-N}$ concentrations in discharged water, as none were strong or interpretable.

Soil nitrogen

Baseline soil $\text{NH}_4\text{-N}$ concentrations in May 2003, 1-week before N treatments, showed significant treatment effects ($P < 0.05$). The resident treatment had 32% more soil $\text{NH}_4\text{-N}$ than the invasion treatment (12.33 ± 0.71 and 9.35 ± 0.44 mg $\text{NH}_4\text{-N kg}^{-1}$ soil, respectively; Figure 1a). No further differences in soil $\text{NH}_4\text{-N}$ ($P > 0.2$) were detected in the resident and invasion treatments after N treatments began except in August 2004. The invasion treatment had 27% more soil $\text{NH}_4\text{-N}$ than the resident treatment (3.68 ± 0.24 vs. 2.90 ± 0.31 mg $\text{NH}_4\text{-N kg}^{-1}$ soil, respectively; $P = 0.017$) in August 2004, three weeks after the final N application when the vegetation was near peak biomass, but no differences in soil $\text{NH}_4\text{-N}$ were detected in September 2004. The high-N treatment had more soil $\text{NH}_4\text{-N}$ in May, August and October 2003 and June and August 2004 ($P = 0.042$, 0.003 ,

Table 3. Environmental conditions of the four treatments on water and soil sampling dates

	High-N Resident	High-N Invasion	Low-N Resident	Low-N Invasion
Water pH				
Aug. 12, 2003	7.65 ± 0.09	7.57 ± 0.10	7.66 ± 0.10	7.62 ± 0.16
Aug. 15, 2003	7.07 ± 0.03	7.14 ± 0.08	7.04 ± 0.01	7.08 ± 0.04
Oct. 28, 2003	7.60 ± 0.01 ^a	7.59 ± 0.01 ^{a,b}	7.55 ± 0.01 ^{a,b}	7.53 ± 0.02 ^b
June 1, 2004	7.16 ± 0.02	7.18 ± 0.02	7.11 ± 0.03	7.16 ± 0.03
July 27, 2004	7.16 ± 0.05	6.97 ± 0.04	7.11 ± 0.05	7.03 ± 0.05
Aug. 16, 2004	7.17 ± 0.02	7.15 ± 0.02	7.18 ± 0.02	7.09 ± 0.04
Sept. 29, 2004	7.38 ± 0.02	7.31 ± 0.03	7.30 ± 0.03	7.35 ± 0.04
Soil pH				
May 2003	7.79 ± 0.05 ^a	7.85 ± 0.05 ^{a,b}	7.82 ± 0.06 ^a	7.96 ± 0.03 ^b
Aug. 2003	7.78 ± 0.02	7.87 ± 0.08	7.83 ± 0.02	7.80 ± 0.03
Oct. 2003	8.46 ± 0.03	8.41 ± 0.02	8.40 ± 0.01	8.41 ± 0.04
June 2004	7.46 ± 0.04 ^{c,d}	7.32 ± 0.02 ^c	7.56 ± 0.02 ^c	7.40 ± 0.02 ^{d,e}
July 2004	7.37 ± 0.02	7.41 ± 0.03	7.32 ± 0.03	7.36 ± 0.01
Aug. 2004	7.61 ± 0.05	7.65 ± 0.05	7.69 ± 0.06	7.67 ± 0.07
Sept. 2004	7.86 ± 0.04	7.82 ± 0.02	7.79 ± 0.04	7.82 ± 0.05
Soil moisture (%)				
May 2003	17.8 ± 0.5	19.0 ± 0.4	17.8 ± 0.6	18.7 ± 0.2
Aug. 2003	18.9 ± 0.4	18.9 ± 0.3	19.1 ± 0.2	19.5 ± 0.5
Oct. 2003	18.2 ± 0.5	18.3 ± 0.3	18.1 ± 0.4	18.6 ± 0.4
June 2004	19.4 ± 0.2	19.1 ± 0.2	19.7 ± 0.7	19.5 ± 0.4
July 2004	20.0 ± 0.2	19.7 ± 0.3	19.4 ± 0.2	19.6 ± 0.3
Aug. 2004	19.4 ± 0.5	20.0 ± 0.4	19.0 ± 0.3	20.0 ± 0.3
Sept. 2004	19.8 ± 0.2	20.1 ± 0.2	19.7 ± 0.2	20.0 ± 0.3
Soil redox (mV)				
May 2003	529.7 ± 9.8	513.1 ± 8.4	525.5 ± 6.3	499.3 ± 9.5
Aug. 2003	280.8 ± 8.6	288.7 ± 8.7	275.0 ± 7.2	287.6 ± 5.1
Oct. 2003	487.3 ± 5.7	492.8 ± 9.2	501.0 ± 11.3	511.6 ± 11.5
June 2004	319.0 ± 9.3	321.4 ± 7.3	311.5 ± 15.6	305.2 ± 9.3
July 2004	303.9 ± 3.8	311.6 ± 23.7	296.3 ± 8.6	308.3 ± 10.2
Aug. 2004	291.3 ± 12.1	302.6 ± 14.6	299.8 ± 12.3	307.3 ± 19.1
Sept. 2004	350.2 ± 6.0	353.8 ± 6.3	346.0 ± 3.5	347.2 ± 8.4

Data are mean ± 1 S.E. Within dates, treatment means that differed significantly following Tukey's Honest Significant Difference ($P < 0.05$) are indicated by different letters. Water samples were collected 24 h after flooding but no N pulse on August 12 and October 28, 2003 and August 16 and September 29, 2004, and 24 h after flooding with a N pulse on the remaining dates. Mean soil redox was based on 8 mesocosms in 2 blocks on October 2003 and 12 mesocosms in 3 blocks on July 2004.

0.037, 0.0001, and 0.008, respectively). The high-N treatment had 18% more soil $\text{NH}_4\text{-N}$ than low-N treatment (11.74 ± 0.89 vs. 9.93 ± 0.46 mg $\text{NH}_4\text{-N}$ kg^{-1} soil, respectively) in May 2003, increasing to 157% more soil $\text{NH}_4\text{-N}$ (17.28 ± 2.13 vs. 6.73 ± 0.39 mg $\text{NH}_4\text{-N}$ kg^{-1} soil, respectively) in June 2004, and declining to no significant difference in July and September 2004.

No differences in soil $\text{NO}_3\text{-N}$ concentrations ($P > 0.3$; Figure 1b) were detected between the resident and invasion treatments on any of the dates sampled in 2003 and 2004. The high-N

treatment had more soil $\text{NO}_3\text{-N}$ on all dates sampled ($P \leq 0.001$). Baseline $\text{NO}_3\text{-N}$ in May 2003 was 165% greater in the high-N (1.09 ± 0.12 mg $\text{NO}_3\text{-N}$ kg^{-1} soil) than low-N treatment (0.41 ± 0.03 mg $\text{NO}_3\text{-N}$ kg^{-1} soil). In August 2004, after the final N application, $\text{NO}_3\text{-N}$ was 549% greater in the high-N (2.79 ± 0.69 mg $\text{NO}_3\text{-N}$ kg^{-1} soil) than low-N treatment (0.43 ± 0.04 mg $\text{NO}_3\text{-N}$ kg^{-1} soil). A two-way ANOVA showed a N-treatment effect on the net change in soil $\text{NO}_3\text{-N}$ from August to October, 2003 ($P = 0.002$) with soil $\text{NO}_3\text{-N}$ increasing 58%

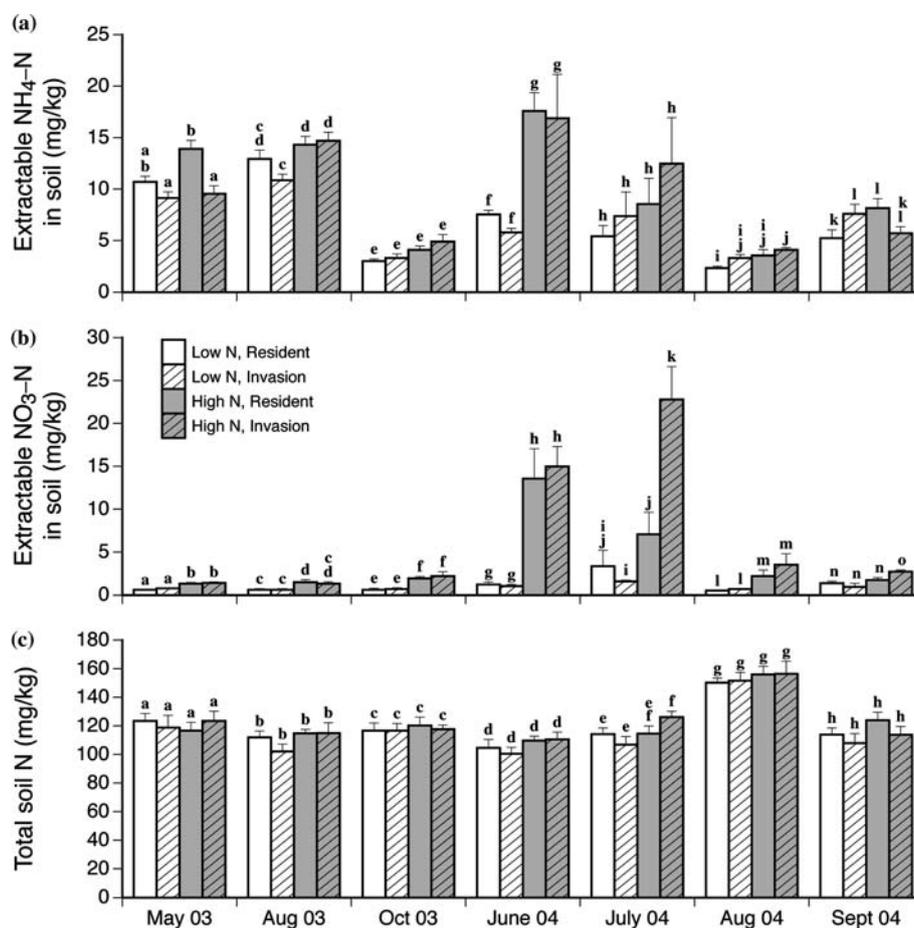


Figure 1. Concentrations of extractable soil NH₄-N (a), extractable soil NO₃-N (b), and total soil N (c) from the four treatments sampled on May 29, August 13 and October 29, 2003 and June 3, July 29, and August 17, and September 30, 2004. Within dates, treatment means that differed significantly following Tukey's Honest Significant Difference ($P < 0.05$) do not share a common letter. Data are mean + 1 S.E. Treatment means and S.E. exclude extreme points that were removed from the two-way ANOVAs.

in the high-N mesocosms and decreasing 12% in the low-N mesocosms.

Two-way ANOVAs of total soil N concentrations showed no treatment differences in 2003 and no differences between the resident and invasion treatments in 2004 ($P > 0.05$; Figure 1c). The high-N treatment had 7% more total soil N than the low-N treatment (110 ± 3 vs. 102 ± 3 mg N kg⁻¹ soil, respectively; $P = 0.003$) in June 2004 and 10% more total soil N (120 ± 3 vs. 109 ± 3 mg N kg⁻¹ soil, respectively; $P = 0.027$) in July 2004, coinciding with differences in soil NO₃-N.

Nitrogen in discharged water

No differences were detected in NH₄-N concentrations in discharged water from the resident and

invasion treatments in 2003 or 2004 ($P > 0.1$; Figure 2a). There were occasional differences in NH₄-N in discharged water from the high-N and low-N treatments. The discharged water from the high-N treatment had 100% more NH₄-N than the low-N treatment (0.18 ± 0.06 vs. 0.09 ± 0.02 mg NH₄-N L⁻¹, respectively; $P = 0.017$) on August 12, 2003, 24 h after flooding without N application, and 628% more NH₄-N (1.82 ± 0.73 vs. 0.25 ± 0.23 mg NH₄-N L⁻¹, respectively; $P = 0.011$) on July 27, 2004, 24 h after flooding and the final N application. NH₄-N concentrations in the discharged water from the high-N and low-N treatments did not differ on the other sampling dates ($P > 0.1$).

No differences were detected in NO₃-N concentrations in water discharged from the resident and

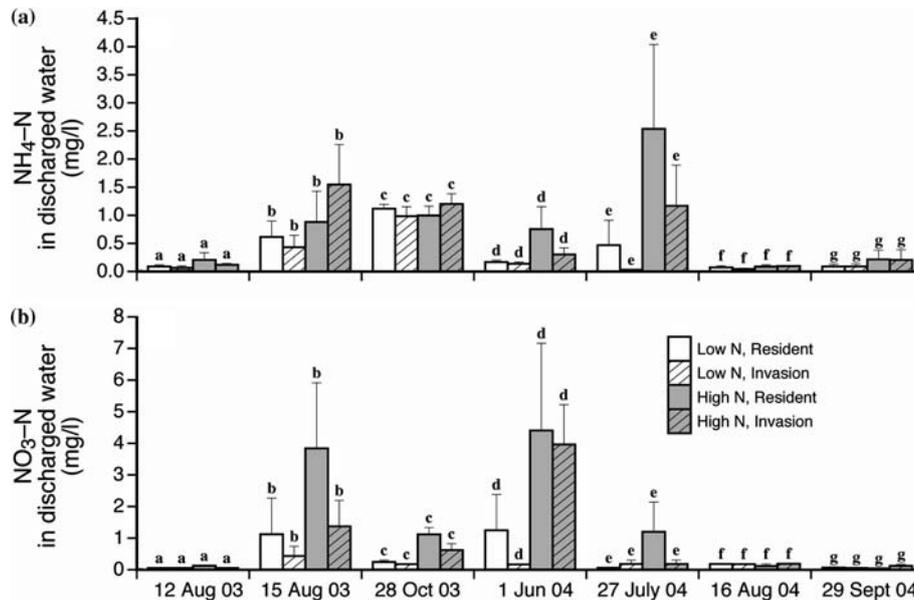


Figure 2. Concentrations of NH₄-N (a) and NO₃-N (b) in the discharged waters from the four treatments sampled 24 h after flooding with no N addition on August 12 and October 28, 2003 and on August 16 and September 29, 2004 and 24 h after flooding with a N addition on August 15, 2003 and on June 1 and July 27, 2004. Within dates, treatment means that differed significantly following Tukey's Honest Significant Difference ($P < 0.05$) do not share a common letter. Data are mean + 1 S.E. We used half the lower detection limit for water samples with concentrations below the detection limit of the analysis. Treatment means and S.E. exclude extreme points that were removed from the two-way ANOVAs.

invasion treatments in 2003 or 2004 ($P > 0.1$; Figure 2b). Differences in NO₃-N in discharged water from the high-N and low-N treatments were not consistent. Discharged water from the high-N treatment had over 100% more NO₃-N than the low-N treatment 24 h after flooding without N application on August 12 and October 28, 2003 ($P = 0.022$ and 0.0002 , respectively) and 480% more NO₃-N 24 h after flooding and a N application on June 1, 2004 ($P = 0.013$). No differences in NO₃-N in discharged water from the high-N and low-N treatments were detected on the other sampling dates ($P > 0.05$). Outliers in NO₃-N concentrations did not always come from the same mesocosm. A two-way ANOVA showed a N-treatment effect on the net change in NO₃-N concentrations from August 12 and October 28, 2003 ($P = 0.0005$), with NO₃-N increasing 1000% in the water from the high-N treatments and 425% in the water from the low-N treatments.

Plant tissue nitrogen

Total above-ground biomass was significantly affected by N treatment in August 2003 and August

2004 ($P < 0.0001$ and $P < 0.0007$, respectively; Figure 3a) and by vegetation treatments in August 2003 and August 2004 ($P = 0.0004$ and 0.022 , respectively). We report above-ground biomass by plot (0.27 m^2), collected from a random quadrant in a mesocosm. The high-N treatment had over 91% more above-ground biomass than the low-N treatment (458.3 ± 35.2 vs. $236.1 \pm 31.9 \text{ g plot}^{-1}$, respectively in August 2003 and 732.5 ± 101.1 vs. $382.5 \pm 40.9 \text{ g plot}^{-1}$, respectively in August 2004). Above-ground biomass was 52% greater in the resident vs. invasion treatment (418.5 ± 43.8 vs. $275.9 \pm 44.1 \text{ g plot}^{-1}$, respectively) in August 2003 and 49.7% greater in the resident vs. invasion treatments (668.4 ± 112.6 vs. $446.5 \pm 57.2 \text{ g plot}^{-1}$, respectively) in August 2004.

The high-N resident treatment had at least 120% more forb biomass than the low-N resident treatment in August 2003 (297.0 ± 68.3 vs. $134.2 \pm 35.9 \text{ g plot}^{-1}$, respectively) and August 2004 (641.5 ± 138.6 vs. $233.9 \pm 39.6 \text{ g plot}^{-1}$, respectively). In contrast, the high-N resident treatment had 27% more graminoid biomass than low-N resident treatment in 2003 (227.0 ± 34.4 vs. $178.7 \pm 41.6 \text{ g plot}^{-1}$, respectively) and

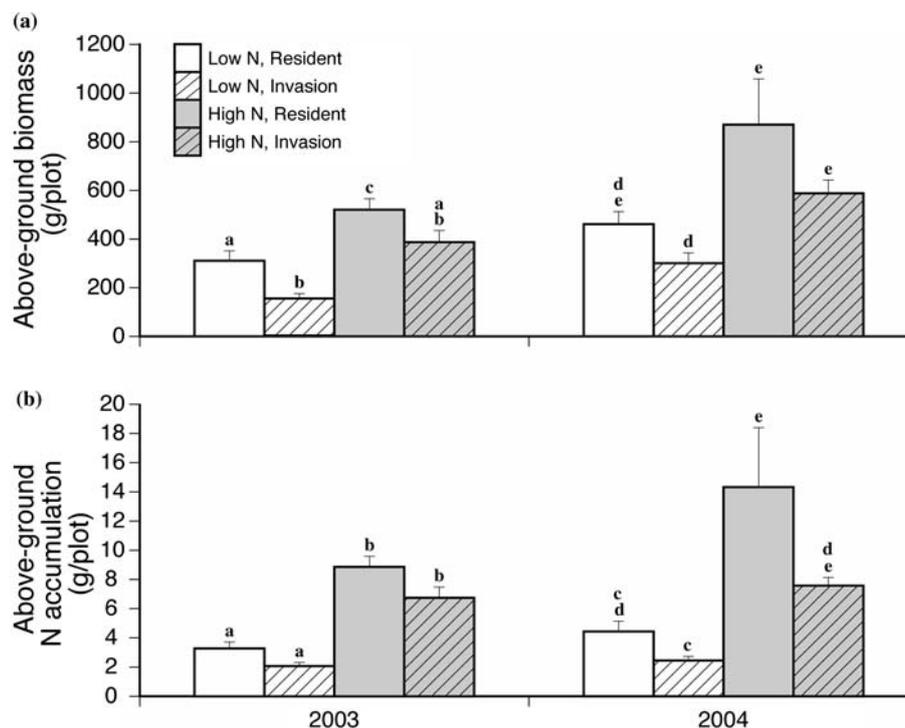


Figure 3. Above-ground biomass (a) and N accumulation in above-ground tissues (b) from the four treatments sampled in August 2003 and August 2004. Within dates, treatment means that differed significantly following Tukey's Honest Significant Difference ($P < 0.05$) do not share a common letter. Data are mean + 1 S.E.

only 2% more in 2004 (233.7 ± 76.7 vs. 227.7 ± 41.5 g plot⁻¹, respectively). Between 2003 and 2004, forbs increased from 55% to 75% of the above-ground biomass in the high-N resident treatment and from 43% to 51% of the above-ground biomass in the low-N resident treatment.

In the invasion treatment, *Phalaris* above-ground biomass was more than 400% greater with the high-N treatment than the low-N treatment in both 2003 and 2004. From August 2003 and August 2004, *Phalaris* biomass increased 56% in the high-N treatment (from 247.2 ± 29.6 to 385.6 ± 49.3 g plot⁻¹) and 58% in the low-N treatment (from 48.4 ± 6.5 to 76.8 ± 21.6 g plot⁻¹). In both years, *Phalaris* comprised 66% of the total above-ground biomass in the high-N treatment. In the low-N treatment, *Phalaris* comprised 30% of the biomass in August 2003 and 25% in August 2004. From August 2003 and August 2004, the biomass of other graminoids increased more in the low-N invasion treatment (81%) than in the high-N invasion treatment (18%). Consequently, the biomass of other graminoids, which was 36% greater in the high-N than low-N

invasion treatment in 2003, was 13% greater in the low-N than high-N invasion treatment in 2004. Forbs produced <5% of the above-ground biomass in the invasion treatment in 2003 and <6% of the above-ground biomass in the high-N and <13% in the low-N invasion treatments in 2004.

Mean above-ground tissue N concentration was 46% greater ($P = 0.0005$) in the high-N ($1.76 \pm 0.12\%$ N) than in the low-N treatment ($1.20 \pm 0.08\%$ N), but did not differ between resident and invasion treatments in August 2003 ($P > 0.1$). Consequently, there was 196% more total N accumulation in above-ground tissues (calculated from biomass and concentration of total N in tissues), with high-N vs. low-N treatments (7.7 ± 0.6 vs. 2.6 ± 0.3 g N plot⁻¹, respectively; $P < 0.0001$; Figure 3b) and 39% more with the resident vs. invasion treatments (6.0 ± 1.0 vs. 4.3 ± 0.9 g N plot⁻¹, respectively; $P = 0.009$) in August 2003. In August 2004, mean above-ground tissue N concentration was 63% greater ($P < 0.0001$) in the high-N ($1.41 \pm 0.09\%$ N) than in the low-N treatment ($0.86 \pm 0.04\%$ N)

and 20% greater ($P = 0.03$) in the resident ($1.24 \pm 0.13\%$ N) than in the invasion treatment ($1.03 \pm 0.08\%$ N). Paired t -tests showed greater tissue N concentration in forbs ($1.46 \pm 0.09\%$ N) than *Phalaris* ($1.07 \pm 0.07\%$ N; $P = 0.002$) or other graminoids ($0.84 \pm 0.04\%$ N; $P < 0.0001$). Accumulation of N in above-ground tissues was 218% greater in the high-N vs. low-N treatment (10.8 ± 2.2 vs. 3.4 ± 0.5 g N plot⁻¹, respectively; $P < 0.0001$; Figure 3b) and 90% greater in the resident vs. invasion treatments (9.3 ± 2.5 vs. 4.9 ± 0.9 g N plot⁻¹, respectively; $P = 0.009$) in August 2004.

Because the data were highly variable, no treatment effects were found for below-ground biomass in August 2003 or August 2004 ($P > 0.3$). The high-N treatment had over 90% greater N concentration in below-ground tissues than low-N treatment ($1.51 \pm 0.11\%$ vs. $0.79 \pm 0.08\%$ N, respectively; $P = 0.004$) in August 2003 and ($1.38 \pm 0.13\%$ vs. $0.70 \pm 0.04\%$ N, respectively; $P = 0.0015$) in August 2004 and 100% more N accumulation in below-ground tissues than the low-N treatment (0.2 ± 0 vs. 0.1 ± 0 g N core⁻¹, respectively; $P = 0.025$) in August 2004. No differences were detected between the resident and invasion treatments.

Discussion

Because elevated N levels accelerate the expansion of *Phalaris*, this aggressive invader is presumed to have high N uptake and to increase retention of N within a wetland. Wetland managers (e.g., the Wetland Team of Wisconsin Department of Natural Resources) often ask if this species retains more N than the native wetland vegetation it displaces when deciding to control its invasions or, alternatively, to allow its use in treatment wetlands. Our comparison of wet prairie vegetation in mesocosms showed that *Phalaris* invasion did not (1) increase N accumulation in wet prairie vegetation, (2) increase N retention in soil of wet prairie vegetation, or (3) decrease N leakage in water discharged from wet prairie vegetation.

Invasion of Phalaris did not increase N accumulation in plant tissues

As expected, above-ground biomass and N accumulation in plant tissues increased with high-N

treatment in both the resident and invasion treatments (Bernard and Lauve, 1995; Figiel et al., 1995; Green and Galatowitsch, 2002; Kline and Boersma, 1983; Wetzel and van der Valk, 1998). We also expected *Phalaris*' suppression of wet prairie vegetation to increase with the high-N treatment, because Green and Galatowitsch (2002) found that the above-ground biomass of *Phalaris* was more than doubled, while the native wetland vegetation was reduced by nearly 50%, as NO₃ additions increased from 12 to 48 g N m⁻² yr⁻¹. In response to our 4-fold increase in N additions, *Phalaris* biomass increased >400%, more than doubling the proportion of *Phalaris* to total biomass. In contrast, the biomass of the other graminoids in the invasion treatment was only 36% greater with high-N treatment in 2003 and dropped to 13% greater with low-N treatment in 2004. In wetland communities with and without *Phalaris* invasions, Green and Galatowitsch (2002) found that native graminoid biomass declined while native forb biomass increased as NO₃ additions increased over 2 years. While we did not find a decrease in graminoid biomass between 2003 and 2004 in any of the treatments, graminoid biomass increased more with low-N than the high-N treatment in the mesocosms with and without *Phalaris* invasions.

In contrast to *Hypothesis 1*, wet prairie vegetation accumulated more N in its plant tissues without *Phalaris* invasions. Because tissue N concentration did not differ between the resident and invasion treatments in 2003, the accumulation of N in plant tissues was greater in the vegetation with no invading *Phalaris* as a result of more above-ground biomass. We expected tissue N concentration to be similar between the resident and invasion treatments, because we have no evidence that *Phalaris* concentrates more N its tissues than other wetland species. In an outdoor experiment using small pots, McJannet et al. (1995) found that the tissue N concentration of *Phalaris* (~0.7% to 1.2% N) was near the middle of the range for 41 wetland species. Further support for the suggestion that *Phalaris* lacks unusually high N uptake ability comes from Kao et al. (2003), who found no differences in tissue N concentration or accumulation of N in biomass between *Phalaris* (~1.5% N and 11.8 g N m⁻²) and the four native species they tested in the field. Our tissue N concentration averaged 1.0%

in the low-N and 1.5% in the high-N treatment over 2 years.

The invasion process continued in 2004, but none of the changes supported *Hypothesis 1*. There was no evidence that our 2002–2003 clipping of natives in the invasion treatments reduced biomass. On the contrary, another experiment (Kercher and Zedler, 2004) showed that reducing the canopy of native competitors released *Phalaris* and increased overall biomass, with a strong positive correlation between light penetration through the canopy and *Phalaris* biomass. The above-ground biomass increased in both the resident and invasion treatments between 2003 and 2004, and the percent difference remained similar (~50% more above-ground biomass in the resident treatment in both years despite clipping in 2003 and no clipping in 2004).

In August 2004, more N accumulated in the above-ground plant tissues in the resident treatment where the vegetation had ~50% more above-ground biomass and 20% greater mean tissue N concentration. The resident treatment had a greater abundance of native forbs, which had considerably more N in their tissues than the graminoid species. If we extrapolate to a wastewater wetland situation, one could harvest species-rich vegetation and remove substantial amounts of N.

Invasion of Phalaris had little effect on soil N

Phalaris invasions had much less effect on soil N concentrations than the N treatments, which increased inorganic soil N on all of the sampling dates. The addition of 14 g N m⁻² in the high-N treatment in 2002 was sufficient to increase soil NH₄-N and NO₃-N in May 2003 prior to N treatments. We expected the high-N treatment to have more soil NH₄-N, especially on the sampling dates following a N application, because NH₄⁺ are readily immobilized through ion exchange onto negatively charged soil particles (Mitsch and Gosselink, 1993) and because, for 2 days preceding soil sampling, the mesocosms were flooded. Anaerobic conditions reduce nitrification (Mitsch and Gosselink, 1993). The high-N treatment had more soil NH₄-N for nearly 2 years; we detected a drop during the 2 days after the last N application in July 2004. Soil

NH₄-N was dynamic in time; however, and in August 2004 it was greater in the high-N treatment but in September 2004 it was not different between the high-N and low-N treatments. Between August and October 2003 during which time the mesocosms were not flooded, soil NH₄-N decreased and soil NO₃-N increased. These changes may have occurred from increases in nitrification and decreases in denitrification during aerobic conditions, and less N uptake by plants late in the growing season (Mitsch and Gosselink, 1993; Richardson and Vepraskas, 2001). Total soil N, which was composed of >80% organic N in 2003, did not differ among the treatments in part because differences in inorganic N were low. The high-N treatment had more total soil N only when soil samples were collected 2 days after a N application.

In contrast to *Hypothesis 2*, *Phalaris* did not increase soil total N or NO₃-N and had little effect on soil NH₄-N during 2003 and 2004. Although the resident treatment had more soil NH₄-N prior to the N treatments in 2003, this difference did not persist after N treatments were applied and *Phalaris* became more dominant in the invasion treatment. Soil NH₄-N was greater in the invasion treatment only on 1 of the 6 sampling dates when *Phalaris* was dominant. Soil NH₄-N is dynamic in these systems. The difference between the invasion and resident treatments in August 2004 was small (<1 mg NH₄-N kg⁻¹ soil) and did not persist in September 2004. Plant uptake may account for lower soil NH₄-N in the resident treatment, which had ~50% more above-ground biomass. Greater accumulation of N in plant tissues does not necessarily coincide with lower soil NH₄-N, however. For example, Otto et al. (1999) found more accumulation of N in the above-ground tissues of invasive *Phragmites australis* than in the native *Typha latifolia* but no differences in soil NH₄-N between the two species.

Plant species can develop positive feedbacks to nutrient cycles within wetlands. For example, fast-growing species in N-rich systems tend to have faster tissue turnover rates, lower nutrient resorption efficiency, and shorter residence times of nutrients (Aerts, 1999; Hobbie, 1992; van der Krift and Berendse, 2001, 2002; Vazquez de Aldana and Berendse, 1997), which can result in increased releases of N into a wetland

and increased nutrient losses from wetland ecosystems (Shaver and Mellilo, 1984). Longer-term N accumulation in plant tissues may be reduced by shorter residence time of N in the plants and faster biomass turnover (Ryser, 1996). Consequently, higher soil N concentrations have been associated with fast-growing, N-demanding species (Tilman and Wedin 1991). Although we harvested vegetation to calculate biomass and N accumulation within the mesocosms, most of the biomass was returned to the mesocosms to retain N within each system. The remaining vegetation was left intact to measure N releases in discharged waters when the plants were senescing. While we found that higher N additions accelerate the expansion of *Phalaris*, we found no consistent evidence that invasions of *Phalaris* increase soil N concentrations within these experimental systems.

Invasion of Phalaris did not decrease N in discharged water

Several results lead us to reject *Hypothesis 3*, that invaded wet prairie vegetation would release less inorganic N in through-flowing water. First, $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$ concentrations in the water discharged from the mesocosms were similar between the resident and invasion treatments on all sampling dates, usually coinciding with similar soil inorganic N concentrations. Secondly, more soil $\text{NH}_4\text{-N}$ with invading *Phalaris* in August 2004 did not result in more $\text{NH}_4\text{-N}$ released to water discharged from the mesocosms. Thirdly, the noise in the data was stronger than the treatment effects; i.e., high variability and outliers did not always come from the same mesocosm. While the high-N treatment generally increased soil $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$, the release of inorganic N to the water discharged from the high-N mesocosms was not consistently greater. $\text{NO}_3\text{-N}$ concentrations in the soil and in the discharged water were higher in October 2003, when the plants were senescing, than in August 2003, when plants were at peak biomass. NO_3^- is mobile in soil and can be quickly depleted through assimilation by plants or microbes, denitrification or leaching (Mitsch and Gosselink, 1993).

General points and suggestions

Although the resident treatment had more above-ground biomass and tissue N accumulation, it did not exceed the *Phalaris* invasion treatment in total soil N, extractable inorganic soil N, or inorganic N released in the discharged water. Furthermore, differences in soil $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$ did not consistently coincide with differences in inorganic N leakage in the water. These findings demonstrate the need to test multiple parameters to determine whether patterns in N retention affect N leakage to downstream systems. High variability, especially in the leakage of N to the discharged water, warrants additional investigation of N retention patterns of native vegetation with and without *Phalaris* invasions at larger spatial scales, where sampling can be more extensive.

Our study tested one wetland type (wet prairie) under selected environmental conditions (low hydrologic disturbance, namely, intermittent flooding), so we do not generalize to other situations. With other disturbance regimes, *Phalaris* may alter N retention. For example, Kercher and Zedler (2004) found that *Phalaris* invades most strongly with increasing disturbance (e.g., prolonged flooding and nutrient additions). Longer flooding episodes, however, resulted in loss of wet prairie species (ibid.) and would not allow comparison of invasions with species-rich wet prairies. Elevated nutrient levels lead to shifts in plant community composition, decreases in plant species diversity and losses of rare or uncommon species in wetlands of western Europe and North America (Bedford et al., 1999). Further investigations are needed to compare the effects of *Phalaris* invasions on N retention in wetlands subjected to alternative disturbance regimes, including harvest cycles typical of treatment wetlands, and to identify native vegetation tolerant of such disturbances.

Despite the limitations of our study, the findings establish doubt that this aggressive invader retains more N than the native species it displaces. Overall there was no evidence that vegetation invaded by *Phalaris* had greater N-removal capacity than the wet prairie it displaced. In the absence of evidence that native species cannot remove sufficient N, we suggest that treatment wetlands employ aggressive native species instead of *Phalaris*. If managers of such wetlands can

indeed sustain native species, their efforts would serve biodiversity conservation without impairing water treatment. At the least, the concept deserves field testing.

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Understanding invasion as a process: the case of *Phalaris arundinacea* in wet prairies

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Abstract Invasive plants that most threaten biodiversity are those that rapidly form a monospecific stand, like the clonal grass, *Phalaris arundinacea*. Understanding complex and potentially interacting factors that are common in urban and agricultural landscapes and underlie rapid invasions requires an experimental, factorial approach. We tested the effects of flooding and nutrient and sediment additions ($3 \times 3 \times 3 = 27$ treatments, plus a control with no additions) on invasion of *Phalaris* into mesocosms containing wet prairie vegetation. We discovered a three-step invasion and degradation process: (1) initially, resident native species declined with prolonged flooding and sediment additions, and (2) prolonged flooding, sedimentation, and nutrients accelerated *Phalaris* aboveground growth; biomass rose to 430 times that of the control within just two growing seasons. The dramatic expansion of *Phalaris* in the second year resulted in the formation of monospecific stands in over one-third of the treatments,

as (3) native species continued their decline in year 2. Disturbances acted alone and in combination to make the resident wetland community more invasible and *Phalaris* more aggressive, leading to monospecific stands. Yet, *Phalaris* did not always “win”: under the least disturbed conditions, the resident plant canopy remained dense and vigorous and *Phalaris* remained small. When anthropogenic disturbances coincide with increases in the gross supply of resources, more tolerant, fast-growing, and morphologically plastic plants like *Phalaris* can invade very rapidly. The fluctuating resource hypothesis should thus be refined to consider the role of interacting disturbances in facilitating invasions.

Keywords Invasive species · *Phalaris arundinacea* · Reed canarygrass · Runoff · Wetlands · Wisconsin

Introduction

The spread of invasive plants into natural habitats is a ubiquitous global problem with negative economic and ecological impacts (Wilcove et al. 1998; Pimentel et al. 2005). While many invaders spread rapidly (Nichols et al. 1990; Lonsdale 1993; Johnson and Carlton 1996; Yeang et al. 1997; Barnes 1999; Rice et al. 2000; Leppäkoski and Olenin 2000; Conklin and Smith 2005), the

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causes of their expansion and reasons why some proceed to form monospecific stands (displacing native species) are not well understood. Although several species-based and ecosystem-based hypotheses have been proposed, there is little exploration of interactions among multiple causes. Species-based hypotheses include superior competitiveness (e.g., due to release from natural enemies, Keane and Crawley 2002; Mitchell and Power 2003; Torchin and Mitchell 2004), allelopathy (Bais et al. 2003; Hierro and Callaway 2003; Vivanco et al. 2004), and the possession of life history traits that promote invasiveness (Thébaud et al. 1996; Kolar and Lodge 2001; Grotkopp et al. 2002; Gerlach and Rice 2003).

Ecosystem-based hypotheses that propose to explain how communities become invulnerable include the availability of unused resources and exposure to disturbances that weaken the native species and allow more tolerant species to invade (reviewed in Inderjit 2005). The “fluctuating resource hypothesis” posits a primary role of increased resource availability in the environment in facilitating invasions (Davis et al. 2000; Davis and Pelsor 2001; Suding et al. 2004). While excess resources can arise through the reduction of resource use by native (resident) species and through an increase in the gross supply of resources, this hypothesis does not explicitly predict interactions that might amplify invasion. Researchers need to pay greater attention to the ways that multiple mechanisms might interact to influence invasions (Blumenthal 2005).

In many parts of the United States, monospecific stands of reed canary grass [*Phalaris arundinacea* L.] form in wetlands and riparian areas in urban and agricultural contexts (Galatowitsch et al. 2000; Lavergne and Molofsky 2004; Lavoie and Dufresne 2005). *Phalaris arundinacea* is a cool-season, long-lived perennial grass found in the temperate zones of the Northern Hemisphere. It is capable of reproducing vegetatively via rhizomes and tillers or sexually by seeds. Although native to North America, it is believed to have become more aggressive following repeated introductions of agronomically-important cultivars for forage and soil stabilization in the 1960’s (Galatowitsch et al. 2000; Lavergne and Molofsky 2004). In southern Wisconsin alone, over 40,000 ha of wetlands are

now dominated by this species (Bernthal and Willis 2004). Once invaded by *Phalaris*, wet meadows retain few species (Fig. 1; Kercher et al. 2004).

Because we and others have demonstrated links between stormwater runoff and dominance by *Phalaris* in the landscape (Galatowitsch et al. 2000; Kercher et al. 2004), we proceeded to ask how components of urban and agricultural runoff interact to cause invasion, comparing the separate and combined effects of excess water, nutrients, and sediments. We introduced *Phalaris* seedlings to wet prairie vegetation in 140 replicate 1.1-m² mesocosms and determined (a) how resident species respond to individual and multiple disturbances, and (b) which combinations of disturbances cause monospecific stands of *Phalaris* to develop. By the end of the first growing season (year 1), we found that multiple interacting disturbances sometimes amplified invasion rates (reported in Kercher and Zedler 2004a), but invasion was incomplete and monospecific stands were reached in only three of the 28 treatments. We expected results in year 2, which we present in this paper, to follow patterns similar to those in

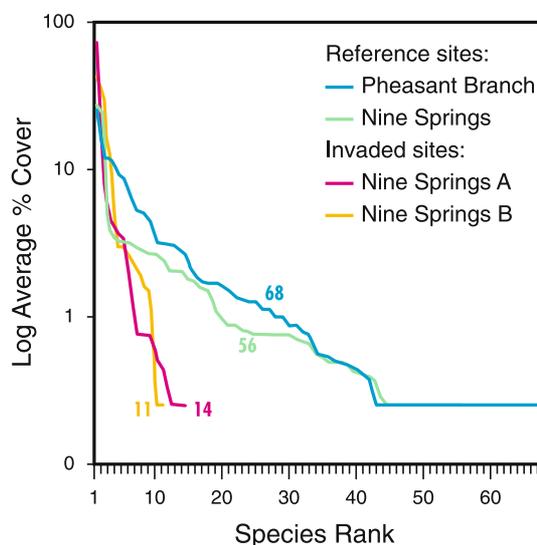


Fig. 1 Dominance-diversity curves (species in descending order of mean cover) from four wet meadows near Madison, WI (data from Kercher et al. 2004). The reference sites have greater evenness of cover and more species than those invaded by *Phalaris arundinacea*. Each curve represents $n = 30$ 1-m² plots within a 0.45-ha area

year 1, but with greater levels of invasion and more treatments attaining monospecific stands.

Materials and methods

We varied nutrient levels, sediment types, and flood regime (3 levels each) in 140 1.1-m² mesocosms arranged in a full-factorial, randomized complete block design (1 replicate per block) within a fenced outdoor research facility at the University of Wisconsin-Madison Arboretum (43° 3' N, 89° 24' W; elevation, 264 m). Mesocosms were seeded with a mix of herbaceous plant species typical of a wet prairie community in southern Wisconsin. After allowing the native species to establish for 2 years, we introduced four 3-month-old *Phalaris* plants to each mesocosm and initiated treatments in June of 2002.

Initial starting conditions were: 14.0 species per 1.1-m² mesocosm (1 SE = 0.09, $n = 140$), *Phalaris* biomass = 1.4 g/0.27 m² (1 SE = 0.08, $n = 30$), and resident (native species) biomass = 128.0 g/0.27 m² (1 SE = 2.6, $n = 5$). Resident species that were present at the start of the experiment in frequencies $\geq 0.05\%$ were the grasses *Andropogon gerardii*, *Agrostis gigantea*, *Glyceria striata*, and *Spartina pectinata*; the sedge *Carex vulpinoidea*; and the forbs *Asclepias incarnata*, *Cicuta maculata*, *Desmodium canadense*, *Helenium autumnale*, *Lobelia siphilitica*, *Pycnanthemum virginianum*, *Silphium perfoliatum*, *Symphotrichum novae-angliae*, *Thalictrum dasycarpum*, *Tradescantia occidentalis*, and *Verbena hastata*.

In both years of the invasion experiment, nutrients were added at three levels (none, low, and high) in the form of lawn fertilizer (Forever Green Lawn Builder Turf Food, Eau Claire Coop Oil Company, Eau Claire, Wisconsin, USA), containing 27% nitrogen (1.2% ammonical N; 25.8% urea N), 3% available phosphate (P₂O₅), 4% soluble potash (K₂O), 1% sulfur, and 1% iron. Nutrients were added to mesocosms once every 4 weeks, on June 17, July 15, and August 12, 2002 and May 27, June 24, and July 22, 2003. The high nutrient treatment matched the rate recommended by the fertilizer manufacturer, and the low nutrient treatment was one-fourth that amount. Total amount of nutrients added per

year (g/m²/yr) was 14.21 g N, 1.58 g P, and 2.10 g K in the high treatment, and 3.55 g N, 0.395 g P, and 0.525 g K in the low treatment.

Sediments were added once in June of 2002. We varied sediment type (none, fine mason sand, or topsoil) in an attempt to separate the effects of sediment as a physical disturbance (fine mason sand) from the effects of sediment as disturbance plus nutrient addition (loamy topsoil). Approximately 53 l (corresponding to a layer of sediment ~5 cm deep) were added to mesocosms by sprinkling sediments over the top as evenly as possible from buckets, then spraying with water to distribute the sediment evenly across the soil surface, mimicking a sediment plume. This technique caused minimal stem and leaf breakage.

We subjected the mesocosms to one of three flood regimes (constant, early season, and intermittent), superimposed on the natural rainfall regime. Constant flood treatments were flooded a total of 14 weeks during the growing season, from June 17–September 23, 2002 and May 27–September 2, 2003. Early season flood treatments were flooded a total of 4 weeks during the growing season, from June 17–July 15, 2002 and May 27–June 24, 2003. Every 2 weeks we drained the standing water in flooded mesocosms to the soil surface and then reflooded them immediately. Intermittent flood treatments were flooded during the first 2 days of every 14-day cycle for 7 cycles, beginning June 17–19, 2002 and May 27–29, 2003. When flooded, mesocosms contained standing water 12–15 cm above the soil or sediment surface. Five additional mesocosms were designated the “no-treatment controls” and received no nutrients, sediments, or floods.

Phalaris inflorescences were counted and collected throughout the second growing season. At the end of the second growing season, we documented the species present and we collected aboveground biomass of *Phalaris* and resident species from a random quadrant of each mesocosm (area = 0.27 m²). All biomass (including inflorescences) was dried in a 60°C oven, and the mass was recorded after it stabilized.

Data were analyzed with three-way analyses of variance (ANOVAs) using flood regime, nutrient addition level, and sediment type as the indepen-

Table 1 ANOVA table for *Phalaris* biomass and resident species richness in the second year of the experiment. Richness is based on the number of resident species that were seeded during the pre-invasion phase in 2000 and were present in line transect intervals sampled in September of 2003. Significant *P*-values are highlighted in bold. Signifi-

cant LSD tests ($\alpha = 0.05$) for main effects are designated using “>” and no significant difference is designated using “=”. Treatments are H = high, L = low, O = no for nutrient addition (nutr); T = topsoil, S = sand, O = no for sediment type (sed); and C = constant, E = early season, and I = intermittent for flood regime (flood)

Source	DF	<i>Phalaris</i> biomass		<i>Resident Species Richness</i>	
		<i>P</i> -value	LSD	<i>P</i> -value	LSD
block	4	0.0003		<0.0001	
nutr	2	<0.0001	H > L > O	0.2859	
sed	2	<0.0001	T = S > O	0.0154	O = S > T
flood	2	<0.0001	C > E > I	<0.0001	I > E > C
nutr × sed	4	0.2756		0.4373	
nutr × flood	4	0.0268		<0.0001	
sed × flood	4	0.0004		0.0651	
nutr × sed × flood	8	0.1058		0.3227	

dent variables and *Phalaris* biomass, number of *Phalaris* inflorescences per mesocosm, resident species richness, and resident species biomass as the dependent variables. For ANOVAs that were significant, Fisher’s Least Significant Difference test was used to separate means for main effects, and Tukey’s Honest Significant Difference test was used to compare all pairs of means for interactions. Paired *t*-tests were used to compare *Phalaris* biomass in the no-treatment controls between 2002 and 2003 and the ratio of *Phalaris* biomass to resident species biomass across years. Alpha = 0.05 for all statistical tests. Data that did not meet assumptions of normality were log-transformed.

Results

In year 2, species richness was lower in the treatments subjected to prolonged flood events compared to the intermittently flooded treatment ($p < 0.0001$; Table 1), and declines of 1–3 resident species per mesocosm were detected in year 2 for 7 of the 9 treatments with constant flooding. There was a significant interaction between nutrient level and flood regime on resident species richness ($p < 0.0001$; Fig. 2). Resident species richness was >20% higher under intermittent flooding and high nutrient additions compared to no nutrient additions. Addition of topsoil sediments resulted in significantly fewer resident species than sand and no sediment

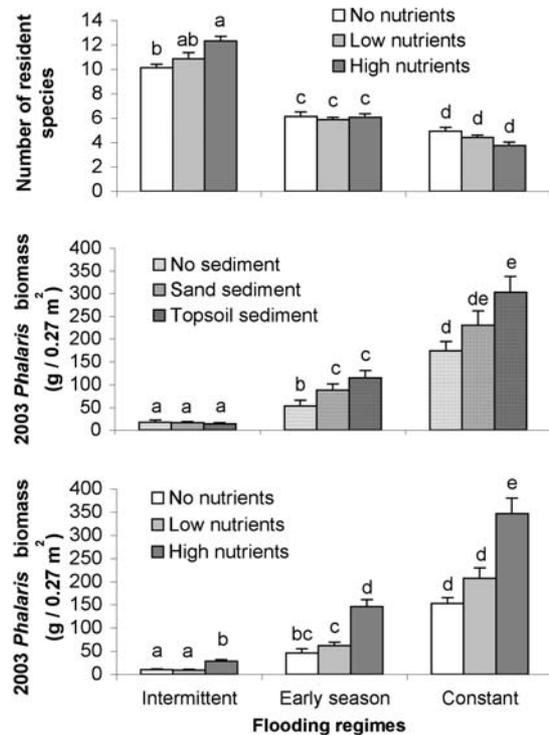


Fig. 2 Significant interactions between (a) flood regime and nutrient level on resident species richness, and significant interactions between (b) flood regime and sediment type and (c) flood regime and nutrient level on *Phalaris* aboveground biomass in year 2 of the invasion experiment. Treatment means that differed significantly following Tukey’s Honest Significant Difference test ($p < 0.05$) do not share a common letter. Data are mean + 1 SE

treatments in year 2 ($p = 0.0154$, Table 1), even though sediments were only added in year 1 (Kercher and Zedler 2004a). A block effect on species richness was also observed (Table 1), with more species in blocks that received more shade.

Phalaris aboveground biomass ranged from as low as 1 g/plant in the no-treatment control to as high as 432 g/plant in the treatment with high levels of nutrients, topsoil sediment, and constant flooding (Figs. 3 and 4). Monospecific stands resulted in 11 treatments (HTC, HSC, HOC, LTC, LSC, LOC, OTC, OSC, OOC, HTE, and OTE; H = high nutrients, L = low nutrients, O in the first position = no nutrients; T = topsoil sediment, S = sand sediment, O in the central position = no sediment; E = early-season flooding and C = constant flooding). Monospecific stands did not form with intermittent flooding. The ratio of *Phalaris* to resident species biomass increased significantly from an overall mean of 0.49 ± 0.08 in year 1 to 1.64 ± 0.16 in year 2 ($p = 0.0002$), indicating further expansion of *Phalaris* at the expense of the residents in the second year. *Phalaris* declined significantly only in the no-treatment control, where biomass in year 2 was only 1.0 ± 0.6 g/0.27 m², compared to 3.5 ± 1.4 g/0.27 m² in year 1 ($p = 0.005$).

All main effects on *Phalaris* biomass were highly significant in year 2 ($p < 0.0001$; Table 1). Nutrient additions and prolonged floods increased *Phalaris* biomass, and both topsoil and sand addition increased *Phalaris* biomass relative to no sediment addition (Table 1). A block effect was also observed (Table 1), with greater biomass of *Phalaris* in the blocks that received more sunlight. There were significant interactions between sediment type and flood regime ($p = 0.0004$) and between nutrient level and flood regime ($p = 0.0268$) on *Phalaris* biomass (Table 1, Fig. 2). While adding sediments to intermittently-flooded mesocosms had little or no effect on *Phalaris* biomass, combining sand or topsoil sediments with prolonged floods lasting 4 weeks or 14 weeks increased *Phalaris* biomass, in some cases doubling it (Fig. 2). Similarly, intermittently-flooded mesocosms that received low levels of nutrient inputs showed no increase in *Phalaris* biomass, but *Phalaris* biomass increased by ~35% when low levels of nutrients coincided with

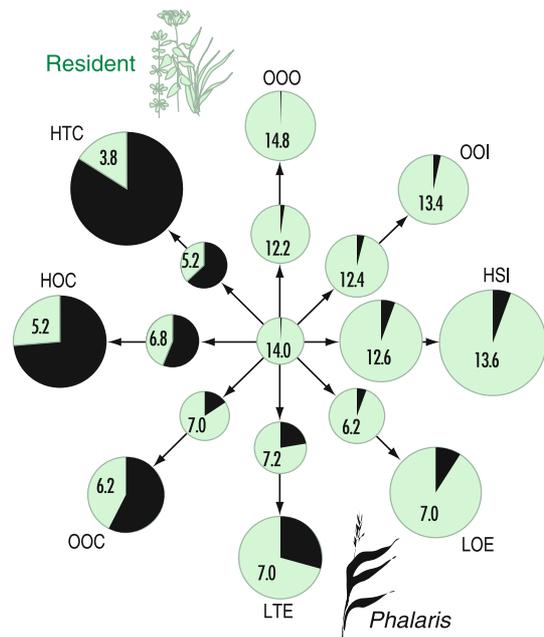


Fig. 3 Responses of vegetation to treatments, arranged in order of increasing ratio of *Phalaris* biomass to resident species biomass in year 2, starting at 12:00 and moving clockwise. The center pie shows starting conditions (see Materials and Methods). The inner ring of pies shows conditions at the end of year 1; and the outer ring of pies shows conditions at the end of year 2 for 8 representative treatments, chosen systematically to represent the progression from least (OOO) to most (HTC) invaded in year 2 of the experiment. The numbers on the pies are mean species richness of resident species, excluding *Phalaris*. Pie size represents mean total biomass, separated into residents (green) and invading *Phalaris* (black). Letters are the treatment codes; first letter O = no nutrients, L = low or H = high nutrients; second letter O = no sediment, S = sand, or T = topsoil; and third letter I = intermittent flood, E = early season flood, C = constant flood; OOO = no-treatment control. Treatment rankings of *Phalaris*:resident biomass ratios in year 2, from lowest to highest, are as follows (bold type indicates a treatment depicted here): **OOO**, LOI, LSI, **OOI**, LTI, HTI, OTI, **HSI**, OSI, HOI, OOE, **LOE**, OSE, HOE, LSE, **LTE**, OTE, HSE, HTE, **OOE**, LOC, OSC, OTC, **HOC**, LSC, HSC, LTC, **HTC**

prolonged floods (Fig. 2). Although high levels of nutrient addition nearly tripled *Phalaris* biomass under intermittent flooding, the absolute increases in *Phalaris* biomass were five and 12 times greater when floods lasted 4 weeks and 14 weeks, respectively (Fig. 2).

The flowering responses of *Phalaris* became apparent in year 2 of the experiment (only one



Fig. 4 Photos of mesocosms showing two contrasting conditions at the end of year 2: (A) low level of *Phalaris arundinacea* invasion and high resident plant diversity in the no nutrients/sand sediment/intermittent flood, or OSI, treatment, and (B) monospecific stand of *Phalaris* in the high nutrients/topsoil sediment/constant flood, or HTC, treatment

Phalaris plant flowered in the first year in the HTC treatment): 363 out of 560 (65%) *Phalaris* plants flowered in year 2. Overall, the mean number of inflorescences was 32.4 ± 3.2 per mesocosm ($n = 140$), the median number was 17, and the range was 0–196; i.e., inflorescence counts were highly skewed. Most inflorescences appeared on plants subjected to both high nutrients and constant flooding (mean = 110.6 ± 8.9 inflorescences/mesocosm; $n = 15$). There was a very strong correlation between inflorescence counts and *Phalaris* biomass in year 2 ($r^2 = 0.89$), indicating that larger clones produced more inflorescences. ANOVA results for inflorescence counts showed the same main effects and interactions as for *Phalaris* biomass (Table 1).

Discussion

Our experiment recreated the invasion of species-rich wet prairie vegetation by a clonal grass species, *Phalaris arundinacea*. We tested the effects of three components of runoff on native and invasive wetland species in 140 replicate 1.1-m² mesocosms and identified a three-step wetland invasion and degradation process: (1) rapid initial loss of resident native species due to early season and constant flooding (floods lasting 4 weeks and 14 weeks, respectively) and sedimentation events

in year 1 (Kercher and Zedler 2004a), (2) sustained rapid growth of *Phalaris* as prolonged flooding, nutrients and sediment inputs interacted to increase the biomass (both years) and reproduction (year 2) of the more tolerant and opportunistic *Phalaris*, and (3) additional, albeit more gradual, losses of resident species in year 2 in the most heavily-disturbed and heavily-invaded treatments.

The most abrupt declines in resident species richness occurred in the first six weeks of the experiment, with up to 50% of species lost due to prolonged flooding and addition of sediments (Kercher and Zedler 2004a). As resident species died, light availability and subsequent invasion levels increased [$\ln(\text{Phalaris biomass}) = 2.74 * (\text{July 2002 light transmission}) + 1.94$; $R = 0.55$, $p < 0.0001$, Kercher and Zedler 2004a]. Biomass of *Phalaris* increased from 6 g/mesocosm [1.1-m² area] at the start of the experiment in year 1 to as high as 256 g/mesocosm (in the high nutrients/constant flood treatment) only 4 months later (Kercher and Zedler 2004a). While we found that prolonged flooding, which killed several resident species, was more important than the other factors, it facilitated invasion most in combination with either nutrients or sediments. The correlation between plant death from flooding and *Phalaris* invasion is likely due to the release of above- and/or below-ground resources when residents died. Light availability probably played a key role, as nutrient additions alone had relatively small effects, and moreover we found a fairly strong positive, linear relationship between light transmission through the plant canopy and aboveground biomass of *Phalaris* at the end of the first year of the experiment (as noted above). It is also possible that, in the absence of prolonged flooding (i.e. under the intermittent flood regime), added nutrients were taken up by resident plants, leading to little increase in nutrient availability for *Phalaris* (and hence comparatively little invasion) in that treatment. Another mesocosm experiment demonstrated that the same resident species did in fact increase both their productivity and nitrogen retention when ammonium-nitrate was added under an intermittent flood regime (Herr-Turoff and Zedler 2005).

There is a growing recognition that interacting factors can determine whether invasions occur

and how rapidly they occur, as has been suggested for predators and resources (Blumenthal 2005), resource availability and the diversity of the resident community (Romanuk and Kolasa 2005), and habitat fragmentation and grazing disturbances (Hobbs 2001). We suggest augmenting the fluctuating resource hypothesis (Davis et al. 2000) to include interactions between resource uptake by resident species and resource additions. The interactions clearly enhanced the ability of the clonal grass *Phalaris arundinacea* to invade a wet prairie system. In particular, resource additions that occur when resident species are unable to immobilize them (in this study, due to their death) leave more resources available for invaders and allow greater levels of invasion. Similar results were reported for studies where both disturbance level and fertilizer addition were varied (e.g., Hobbs and Atkins 1988; Burke and Grime 1996).

This study is unique in documenting a broad spectrum of invasion outcomes after two years: with the least amount of disturbance, *Phalaris* remained a minor component of the plant community, whereas invasion was overwhelming when multiple disturbances were combined (Figs. 3 and 4). *Phalaris* invasion following the decline of resident species was likely tied to its very high growth rate relative to native wetland species under high nutrient conditions (e.g., elevated nitrate-N, Green and Galatowitsch 2001; Perry et al. 2004). We speculate that the positive interaction between nutrients and flooding occurred when light became plentiful and nutrients then became the limiting resource. In addition, *Phalaris* possesses other key traits that likely confer invasiveness under the combinations of reduced competition and increased runoff – e.g., tolerance of anoxia (e.g., by producing aerenchyma and adventitious roots, Kercher and Zedler 2004b), morphological plasticity, which allows it to rapidly capitalize on invasion opportunities (Zedler and Kercher 2004, Lavergne and Molofsky 2004), and ability to shift its growth form to tussocks under chronically flooded conditions and sward forms in more aerated soils (Herr-Turoff 2005).

Phalaris is a symptom of anthropogenic disturbances, perhaps even a “human symbiont”

(Larson 2005). Therefore, multiple causes of invasion must be abated. Stormwater runoff from urban areas and agricultural fields can be reduced in quantity and improved in quality if management takes a watershed approach using depressions, swales, and other measures to enhance infiltration into the ground. Due to complex interactions among disturbance factors, simple reductions in fertilizer use, flooding, or sedimentation alone will not likely suffice to protect wetlands from this tolerant, fast-growing, and morphologically plastic invader.

Phalaris propagules are very common in North American temperate agricultural landscapes due to widespread planting since the 1930’s for cattle forage and soil stabilization, thus locations where it can be most easily controlled will depend on the site’s context and condition. Control of large monospecific stands of *Phalaris* will need to be coordinated among landowners, because this invader would rapidly return to a restoration site, either vegetatively or by swamping the seed bank (Wilcox 2004). Restoring the original community will likely prove difficult, requiring removal of *Phalaris* plants and seeds (using herbicide and/or removal of sod), cessation of disturbances (Herr-Turoff 2005), replanting of native species, long-term surveillance, spot-treating of re-invading clones, and a long-term commitment to biodiversity restoration.

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Multiple disturbances accelerate invasion of reed canary grass (*Phalaris arundinacea* L.) in a mesocosm study

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Abstract Disturbances that intensify with agriculture and/or urban development are thought to promote the spread of invasive plants, such as the clonal perennial reed canary grass (*Phalaris arundinacea* L.). To test this relationship and interactions among disturbances, we subjected wet prairie assemblages within 1.1 m² mesocosms to invasion by *Phalaris* and addition of nutrients, sediments, and flooding. Species richness decreased with the application of sediments and/or flooding of 4 consecutive weeks or longer. Losses of up to six dominant and subdominant species in these treatments increased light transmission through the plant canopy by as much as 400% over the control. Light availability in July and September was a strong predictor of end-of-season aboveground biomass of *Phalaris*. *Phalaris* was also 35% and 195% more productive when nutrients were added at low and high levels, respectively. Multiple factors in combination were usually additive in their effects on invasion, but sediments and nutrients interacted with flood regime to synergistically increase invasion in some cases. A separate experiment likewise revealed a synergistic interaction between added nutrients and simulated grazing. We suggest that multiple factors be mitigated simultaneously to reduce invasion of *Phalaris*.

Keywords Eutrophication · Flooding · Fluctuating resource hypothesis · Invasibility · Invasive species

Introduction

Agricultural activities and urban development can accelerate eutrophication and exacerbate physical disturbances such as sedimentation, flooding, and grazing within wetlands (e.g., Watson et al. 1981; Ewing 1996). The conversion of diverse wetlands to near-monotypes of invasive species can follow (Galatowitsch et al. 2000; Werner and Zedler 2002), although it is unclear how this conversion occurs. The role of disturbance in facilitating plant invasions was recognized early on by Elton (1958). Empirical support for the disturbance hypothesis comes from several studies (Crawley 1987; Hobbs and Atkins 1988; Rejmánek 1989; Burke and Grime 1996), although Larson et al. (2001) failed to relate the distributions of five of six common alien invaders to anthropogenic disturbances in a mixed-grass prairie. Eutrophication has likewise been proposed to increase invasibility, and several studies of grassland and herbaceous wetland communities support the nutrient hypothesis (Vermeer and Berendse 1983; Hobbs and Atkins 1988; Huenneke et al. 1990; Burke and Grime 1996; De Kroon and Bobbink 1997; Woo and Zedler 2002).

The hypothesis of fluctuating resource availability synthesizes many of the above findings. As articulated by Davis et al. (2000), plant communities are rarely at equilibrium with their resources, and when resource supply exceeds uptake by the resident vegetation, either through an increase in gross supply or a decrease in resource uptake by the resident vegetation, the community becomes vulnerable to invasion; this can happen whether communities are species rich or species poor (Davis et al. 2000). This hypothesis also predicts the most invulnerable condition occurs when increases in the gross supply of resources coincide with decreases in the uptake of resources by the resident plant community.

Phalaris arundinacea, a clonal C3 grass that has been bred and widely planted for forage and erosion control, has spread into many wetlands in temperate North America and Canada, where it often forms dense monotypic stands (Galatowitsch et al. 1999). *Phalaris*

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has occurred with high frequency in southern Wisconsin wetlands since at least the 1950s (Curtis 1959). Currently over 40,000 ha of wetlands in Wisconsin are dominated by *Phalaris* (T. Bernthal, Wisconsin DNR, unpublished data from satellite imagery).

We followed the invasion of *Phalaris* within experimental mesocosms designed to mimic a temperate North American wet prairie community. We allowed native species to establish for 2 years prior to introducing 3-month-old plants of *Phalaris* and introducing disturbances: eutrophication, sedimentation, flooding, and grazing. Our specific questions were:

1. How do single and multiple disturbances in combination affect an assemblage of resident plant species (~15 native and 1 naturalized species)?
2. Will the invasibility of an established assemblage increase as a result of single disturbances, and will multiple disturbances in combination have additive or interactive effects on invasion by *Phalaris*?
3. What physical and biotic conditions produce the slowest and most rapid invasion by *Phalaris*?

Table 1 List of species and plant families seeded into the mesocosms and their relative frequency ($n=150$ mesocosms) as of June 2001, a year before the experiment began, and as of June 2002, immediately prior to initiation of treatments. Species sampled with a

Materials and methods

Experimental design

Two separate and simultaneous experiments used a total of 150 mesocosms in a randomized complete block design. A "block" consisted of 15 side-by-side pairs of mesocosms arranged in a line running north to south within an outdoor mesocosm facility. All treatments were replicated once within each of five blocks and were assigned randomly within blocks. The first (hereafter called the Main Experiment) was a 3×3×3 fully-crossed experiment designed to test the effects of nutrient level, sediment type, and flood regime on the invasibility of a wet prairie assemblage by *Phalaris*. Each of the 135 mesocosms in the Main Experiment were labeled with a 3-letter code designating the: (1) nutrient level (0, Low, or High), (2) sediment type (0, Sand, or Topsoil), and (3) flood regime (Intermittent, Early season, or Constant).

A second experiment (hereafter called the Grazing Experiment) tested the effects of nutrient level and artificial grazing on invasibility. A total of 10 mesocosms (2 per block) were artificially "grazed" by clipping all resident vegetation to the soil surface, and nutrients were either withheld or added at the same high level used in the Main Experiment. The 10 grazed mesocosms were subjected to intermittent flooding and were compared to their ungrazed counterparts (00I and H0I) in the Main Experiment to yield a 2×2 factorial design.

Five additional mesocosms (one per block) represented the "control" treatment and were labeled "000." These mesocosms received plants of *Phalaris* but had no nutrient/sediment inputs and were never flooded.

frequency <0.5% for both sampling episodes are excluded from this table. *Phalaris arundinacea* plants were added to mesocosms in May 2002. Scientific names and families are per the USDA, NRCS (2002)

Species planted	Family	June 2001 (%)	June 2002 (%)
Grasses			
<i>Andropogon gerardii</i> Vitman ^a	Poaceae	18.6	18.3
<i>Agrostis gigantea</i> Roth ^{b, d}	Poaceae	25.7	23.5
<i>Glyceria striata</i> (Lam.) A.S. Hitchc ^b	Poaceae	8.0	6.1
<i>Spartina pectinata</i> Bosc ex Link ^a	Poaceae	2.8	4.5
<i>Phalaris arundinacea</i> L. ^b	Poaceae	–	7.2
Forbs/Sedge			
<i>Asclepias incarnata</i> L.	Asclepiadaceae	3.6	1.8
<i>Carex vulpinoidea</i> Michx. ^b	Cyperaceae	1.8	2.7
<i>Cicuta maculata</i> L.	Apiaceae	0.4	0.5
<i>Desmodium canadense</i> (L.) DC. ^c	Fabaceae	10.5	9.6
<i>Helenium autumnale</i> L.	Asteraceae	3.3	3.9
<i>Lobelia siphilitica</i> L.	Campanulaceae	0.3	0.5
<i>Pycnanthemum virginianum</i> (L.) T. Dur. & B.D. Jackson ex B.L. Robins. & Fern.	Lamiaceae	0.6	0.8
<i>Silphium perfoliatum</i> L.	Asteraceae	6.4	5.8
<i>Symphyotrichum novae-angliae</i> (L.) Nesom	Asteraceae	3.5	4.9
<i>Thalictrum dasycarpum</i> Fisch. & Avé-Lall.	Ranunculaceae	0.5	0.6
<i>Tradescantia occidentalis</i> (Britt.) Smyth	Commelinaceae	0.4	0.5
<i>Verbena hastata</i> L.	Verbenaceae	13.3	6.4

^a C4 species

^b C3 species

^c Nitrogen-fixing species

^d In year 2 (2001) the "*Calamagrostis canadensis*" plants flowered and were identified as *Agrostis gigantea*, a naturalized species native to Eurasia (Fassett 1951)

Experimental setup

On 19 May 2000, 150 oval-shaped black plastic stock tanks (Freeland Industries, Portage, Wis., USA) measuring 1.25 m × 0.92 m × 0.65 m deep, or approximately 1.1 m² in area, were arranged into 5 blocks of 30 tanks each within a fenced outdoor research facility at the University of Wisconsin Arboretum, Madison, Wis., USA. Each tank was filled to a depth of 15 cm with locally quarried, screened sand (St. Peter's sandstone) and topped with 30 cm of screened, pulverized loamy topsoil from a supplier in Verona, Wis., USA.

Twenty-five herbaceous plant species were chosen to simulate a wet prairie assemblage in southern Wisconsin (Curtis 1959) and to represent a range of plant families and phenological guilds (Table 1). On 4 July 2000, following 2 months of cold-moist stratification, seeds were planted into the mesocosms at a rate of 650 seeds per m², which is typical for tallgrass prairie restorations (Diboll 1996). Four grasses comprised 50% of the total number of seeds planted into each mesocosm and 21 forbs and sedges comprised the rest (Table 1).

Mesocosms were watered daily during the growing season and weeded twice a year in 2000 and 2001. In spring 2002 (year 3), we planted *Phalaris* seedlings into the mesocosms. We chose to add seedlings instead of seed to reduce interannual variation in the number of *Phalaris* propagules. On 7 March 2002, seeds of *Phalaris arundinacea* (Olds Seed Solutions, Madison, Wis., USA) were started in flats. Four weeks later the seedlings were transplanted into plug trays and grown in a greenhouse until May 21–23, when we transplanted 4 (~10-week-old) *Phalaris* plants into each mesocosm. Each plant was situated 20 cm from the two adjacent corner walls and was planted to a depth of 10 cm. At this time, 30 extra *Phalaris* plants were clipped at soil level, oven dried, and weighed to estimate initial aboveground biomass.

Nutrient additions

Forever Green Lawn Builder Turf Food (Eau Claire Crop Oil, Eau Claire, Wis., USA), containing 27% nitrogen (1.2% ammonical N; 25.8% urea N), 3% available phosphate (P₂O₅), 4% soluble potash (K₂O), 1% sulfur, and 1% iron, was added to mesocosms once every 4 weeks, on 17 June, 15 July, and 12 August 2002. The high nutrient treatment (H) matched the rate recommended by the fertilizer manufacturer and totaled 18.73 g of fertilizer per mesocosm for each application. The low nutrient treatment (L) was 1/4 the recommended rate, or 4.68 g per mesocosm. The total amount of nutrients added to mesocosms over the three application episodes in 2002 (g m⁻² year⁻¹) was 14.21 g N, 1.58 g P, and 2.10 g K in the high treatment, and 3.55 g N, 0.395 g P, and 0.526 g K in the low treatment. This corresponded to an N: P ratio of 4:1 on an atomic basis, which is high in P relative to the Redfield ratio of 16:1. Our high nutrient treatment approximated the lowest level of nutrients applied by Woo and Zedler (2002) to wetland field plots over the course of one season, which significantly increased invasive *Typha × glauca* biomass over control plots. We sprinkled the granular fertilizer as uniformly as possible in the mesocosms during drawdown periods, and then immediately reflooded or watered the mesocosms.

Sediment additions

Sediments were added once in year 3 (2002). We varied sediment type in an attempt to separate the effects of sediment as a physical disturbance (fine mason sand) from the effects of sediment as disturbance plus nutrient addition (loamy topsoil). Topsoil sediment (T) came from a commercial source in Verona, Wis., USA, and was added to 45 mesocosms from June 12 to 13. Approximately 53 l (corresponding to a layer of sediment ~5 cm deep) were added to each mesocosm as follows: the fine, crumbly screened topsoil was sprinkled over the top as evenly as possible from buckets, then the

topsoil was further evened out using a squirt hose with a sprinkler nozzle attachment. This technique caused minimal stem/leaf breakage.

Fine mason sand sediment (S) from a commercial source in Madison, Wisconsin, USA was added to another 45 mesocosms from June 13–14 in the same manner as topsoil. Mean total nitrogen, phosphorus, and potassium levels were 801, 34, and 78 ppm in the topsoil sediment (based on 4 subsamples), respectively, versus 108, 5, and 13 ppm in the sand (based on 1 subsample), corresponding to an N: P ratio of 10.6:1 and 9.8:1 on an atomic basis, respectively.

Flood regimes

We subjected mesocosms to one of three flood regimes, superimposed on the natural rainfall regime. When flooded, mesocosms contained standing water 12–15 cm above the soil/sediment surface. Constant flood (C) treatments were flooded a total of 14 weeks, from 17 June to 23 September 2002. Every 2 weeks we drained the standing water in these mesocosms to the soil surface and then reflooded them immediately. Early season flood (E) treatments were flooded a total of 4 weeks, from 17 June to 15 July 2002. On 1 July, the standing water in these mesocosms was drained to the soil surface and they were immediately reflooded. For the remainder of the season, these mesocosms were watered as needed. Intermittent flood (I) treatments were flooded during the first 2 days of every 14-day cycle for 7 cycles. During the drawdown phase of each cycle, these mesocosms were watered as needed. Intermittent flooding episodes occurred during 17–19 June, 1–3 July, 15–17 July, 29–31 July, 12–14 August, 26–28 August, and 9–11 September 2002.

Data collection

Light and soil redox potential

Photosynthetically active radiation (PAR) was measured in all mesocosms on 28–31 May, 23 July to 1 August, and 19–22 September 2002 at 9 points per mesocosm on a regular 3 × 3 grid. Light levels (nm m⁻² s⁻²) were measured above the plant canopy and at the soil level at each point between 5:30 and 8:30 a.m. using a photometer with a spherical sensor (Model IL1400A, International Light, Newburyport, Mass., USA). We calculated the ratio of light transmitted through the canopy at each sampling point by dividing the light level at the soil surface by the light level above the plant canopy.

Soil redox potential was measured in a subset of the mesocosms from the Main Experiment using platinum electrodes, a calomel reference electrode, and a Barnant 20 Digital pH/mV/ORD meter (Barrington, Ill.; Patrick et al. 1996). Sixteen mesocosms per block were chosen to test the effects of (1) nutrient and flood regime (using data from all mesocosms in the Main Experiment except those receiving sand and topsoil sediments—i.e., using 00I, L0I, H0I, 00E, L0E, H0E, 00C, L0C, and H0C) and (2) sediment type and flood regime (using data from all mesocosms except those receiving nutrients—i.e., using 00I, 00E, 00C, 0SI, 0SE, 0SC, 0TI, 0TE, and 0TC) on redox potential. Redox measurements occurred on 2–3 July 2002, when all treatments were flooded, and on 6–7 August 2002, when only mesocosms receiving the constant flood (C) treatment were flooded. Two electrodes were placed ~30 cm from opposite ends of a mesocosm, and sunk into the soil to a depth of 10 cm. For mesocosms that received sediments, the electrodes penetrated the top 5 cm-layer of sediment plus 5 cm of the original topsoil below. Readings were adjusted by adding 244 mV prior to statistical analysis based on the standard hydrogen electrode. Redox values from a single data collection episode were used since a quality control study found no significant variation in redox potential over the course of 1 day.

Species composition and abundance

All live species present and the height of the tallest stem for each species were recorded three times for each mesocosm, from 28 to 31 May, 15 to 19 July, and 11 to 18 September 2002. Vegetation was also sampled three times using a line intercept method: two 1-m long wooden dowels, each divided into ten 0.1 m intervals, were situated parallel to the long axis of each tank 30 cm from the sides of the tank (and 40 cm apart) and equidistant from the ends of the tank. Then the total number of intervals intercepted by each species along each line was recorded. Line intercept sampling occurred from 3 to 7 June, 22 to 24 July, and 18 to 24 September 2002.

Biomass collection

A random quadrant in each mesocosm (area =0.27 m²) was sampled for aboveground biomass of *Phalaris* and resident species by clipping all standing plants at soil level. Sampling of the *Phalaris* occurred from 30 September to 4 October 2002. Sampling of resident species occurred from 7 to 11 October 2002. Litter (defined as any fallen, dried plant parts) was also collected in the same quadrant at this time. Plants and litter were oven dried for 2 days at 60°C and weighed.

Data analysis

Three-way ANOVAs with nutrient level, sediment type, and flood regime as independent variables (for the Main Experiment) and two-way ANOVAs with nutrient level and grazing status as independent variables (for the Grazing Experiment) were conducted using SAS (SAS 1999). Our response variables were: light transmission, species richness, biomass of the resident species (g 0.27 m⁻²), *Phalaris* frequency (the number of 0.1 m sampling intervals crossed by *Phalaris* out of 20 possible per mesocosm), and *Phalaris* biomass (g 0.27 m⁻²). Invasibility of the wet prairie assemblage was quantified using both the *Phalaris* frequency and *Phalaris* biomass data.

The nine light transmission values per mesocosm were analyzed as subsamples in the three-way ANOVAs, but a single (average) light transmission value was calculated for each mesocosm to use in regressions on end-of-season *Phalaris* biomass values. The redox potential data from both the July and August measurement episodes were subjected to two-way ANOVAs to test separately for (1) effects of nutrients and flood regime, and (2) effects of sediments and flood regime (see above) within the Main Experiment. The two readings per mesocosm were analyzed as subsamples in the ANOVAs. Alpha =0.05 for all statistical tests. If ANOVAs were significant, means were separated using either the LSD method (for main effects) or Tukey’s method for comparing all pairs of means (for interactions).

To examine vegetation patterns related to the treatments, vegetation data were subjected to Canonical Correspondence Analysis (CCA) in PC-Ord (McCune and Mefford 1997; McCune and Grace 2002). The main matrix consisted of the number of “hits” of each species sampled in a mesocosm, summed across the two transect lines (data range =0–20 per species per mesocosm) in June, July, and September 2002. The second matrix listed the nutrient level, sediment type, and flood regime corresponding to each mesocosm. Three ordination axes were scaled using Hill’s method, and WA scores were used to graph the ordinations. Monte-Carlo tests with *n* =100 randomizations were used to test *H*₀: no relationship between the main and second matrix.

Results

Physical variables

July 2002 light transmission measurements revealed strong evidence for a flooding main effect (*P* <0.0001; Table 2). The highest light levels occurred in the constant flood treatment (mean±SE, 47.4±1.7%), followed by the early season flood (24.9±1.5%) and then the intermittent flood treatment (10.7±0.8%). Note that the early season flood treatment had ~2 weeks to recover from flooding

Table 2 *P*-values from 3-way ANOVAs of 12 response variables measured in the Main Experiment in 2002. Significant *P*-values (α=0.05) are highlighted in bold. (*nutr* nutrient level, *sed* sediment type, *flood* flood regime)

Source	Df	Light transmission			Phalaris frequency		
		May	July	Sept	June	July	Sept
Block	4	0.2751	0.0005	0.3168	0.3196	0.8011	0.4534
Nutr	2	0.0810	0.6345	<0.0001	0.3738	0.1871	<0.0001
Sed	2	0.0639	<0.0001	<0.0001	0.9531	0.1978	<0.0001
Flood	2	0.0151	<0.0001	<0.0001	0.3392	<0.0001	<0.0001
nutr × sed	4	0.6534	0.4450	0.9157	0.1354	0.1642	0.3365
nutr × flood	4	0.4058	0.1010	0.0321	0.8120	0.8972	0.0591
sed × flood	4	0.6340	<0.0001	<0.0001	0.5809	0.0614	<0.0001
nutr × sed × flood	8	0.5676	0.7031	0.1437	0.0116	0.9966	0.0373

Source	Df	Species richness			Aboveground biomass		
		May	July	Sept	Phalaris	Residents	Litter
Block	4	<0.0001	0.4394	0.0374	0.0004	0.1066	0.0298
Nutr	2	0.5628	0.1894	0.1845	<0.0001	<0.0001	0.6494
Sed	2	0.2955	<0.0001	0.0002	<0.0001	0.0006	0.0005
Flood	2	0.7751	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
nutr × sed	4	0.9582	0.6364	0.4179	0.4511	0.1721	0.1851
nutr × flood	4	0.2277	0.1008	0.5112	<0.0001	<0.0001	0.6468
sed × flood	4	0.6256	0.0541	0.0008	<0.0001	0.0001	0.0083
nutr × sed × flood	8	0.4510	0.5696	0.4592	<0.0001	0.1284	0.2050

prior to measurement. A block effect ($P=0.0005$) and sediment main effect ($P<0.0001$) also appeared in July along with a sediment \times flooding interaction ($P<0.0001$; Table 2). Both topsoil and sand additions resulted in greater light transmission through the plant canopies ($32.3 \pm 3.0\%$ and $30.6 \pm 2.6\%$, respectively) than no sediment addition ($20.2 \pm 1.9\%$). In September the block effect disappeared, but the sediment and flooding main effects and sediment \times flooding interactions were still present, and a strong nutrient effect had developed ($P<0.0001$ for all; Table 2). The highest light levels occurred in mesocosms with no nutrient addition ($30.3 \pm 2.2\%$), followed by those that received low nutrient levels ($27.5 \pm 2.5\%$), and the least amount of light was transmitted through plant canopies in the high nutrient treatment ($23.1 \pm 2.5\%$). Plants receiving high levels of nutrients appeared to be denser and to stay green longer than those in the no/low nutrient treatments (personal observation).

The May 2002 light transmission levels were not related to the final biomass of *Phalaris* (Pearson's $\rho=0.047$, $F_{(1,133)}=0.30$, $P=0.58$); however, final *Phalaris* biomass was positively related to light transmission levels in July ($\rho=0.55$, $F_{(1,133)}=57.0$, $P<0.0001$; Fig. 1) and September ($\rho=0.31$, $F_{(1,133)}=13.67$, $P=0.0003$). Resident plant biomass was likewise unrelated to light transmission values in May 2002 but was significantly negatively related in July and September ($\rho=-0.80$ and -0.72 , respectively; $P<0.0001$ for both).

Soil redox potentials showed significant flooding ($P<0.0001$) and sediment ($P<0.02$) main effects in both July and August. Redox potentials ranged from a low of -51 mV for the treatment with no nutrients, sand addition, and constant flooding (OSC) to a high of 496.5 mV for the control (000) treatment in July. During the July measurement episode, all treatments except the controls (000) were flooded, but intermittently flooded mesocosms had only been flooded for 1–2 days versus 2 weeks for early season

and constant floods. In July, the intermittent flood treatment had significantly higher redox potentials (222.1 ± 11.2 mV) than both the early season and constant flood treatments (-74.6 ± 12.1 mV, and 46.3 ± 16.5 mV, respectively). In August, when only the constant flood treatment was flooded and the early season flood treatment had been drained for about 3 weeks, redox values ranged from 34.1 mV for the OSC treatment to 527.7 mV for the HOI treatment, with the control treatment (000) measuring 436.2 mV on average. Both intermittent and early season flood treatments had higher redox values (489.0 ± 7.1 mV, and 479.8 ± 8.4 mV, respectively) than the constant flood treatment (47.3 ± 5.2 mV). A sediment effect was also noticeable in both July and August, with sand addition resulting in lower redox values than no sediment addition in July (57.2 ± 27.4 mV vs 136.2 ± 16.1 mV) and with sand addition having lower redox values than topsoil addition in August (321.7 ± 38.9 mV vs 361.9 ± 41.6 mV).

Biotic variables

Species richness

Prior to the application of treatments, mesocosms contained 14–21 species (mean 16.7 ± 0.1 species). By the end of the experiment, species richness declined to a nadir of 6–7 species in the HSC (H=high nutrients, S=sand, C=constant flood), HTC (T=topsoil), LSC (L=low nutrients), and OSC (0=no nutrients) treatments. The May 2002 census showed no preexisting differences in species richness among designated treatments (Table 2); however, blocks declined in species from east to west, likely an artifact of shading in the eastern blocks. In July 2002 there were significant sediment and flooding main effects ($P<0.0001$ for both; Table 2), with lower numbers of species occurring in topsoil/sand sediment and early/constant flood treatments compared to the no sediment and intermittent flood treatments, respectively. The September 2002 census again showed a block effect on species richness ($P=0.037$) and strong evidence for sediment and flooding main effects and a sediment \times flooding interaction ($P<0.0008$ for all; Figs. 2, 3); this interaction arose in large part because the combination of topsoil sediment and early season flooding resulted in the recruitment of weedy annuals from the topsoil seed bank following drawdown of the flood water.

Mesocosms assigned to the nutrient and grazing treatments had similar numbers of species prior to treatment. Fewer species were found in the grazed treatment as of July ($P=0.006$), but this effect was no longer detected in September ($P=0.81$).

Assemblage responses

Abrupt declines in species richness in the Main Experiment occurred with flooding and, to a lesser extent, sediment addition (Fig. 2). Ten species declined with 4 or

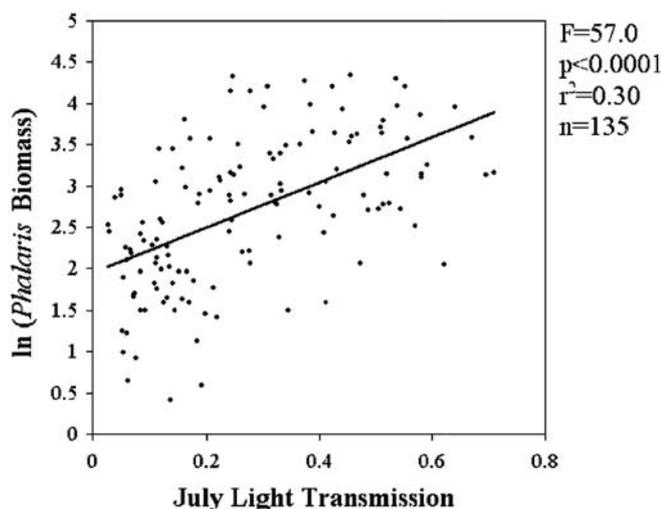


Fig. 1 Linear regression showing the relationship between percent light transmission through the plant canopy as of July 2002 and ln-transformed aboveground *Phalaris* biomass (g) for one randomly chosen plant per mesocosm in the Main Experiment ($n=135$)

Fig. 2 Main effects on species richness (September 2002 data), aboveground biomass of *Phalaris*, and aboveground biomass of resident species (+ SE bars) in the Main Experiment. Within graphs, treatments that differed significantly following LSD tests do not share a common letter. (*Inter*: intermittent flood, *Early* early season flood)

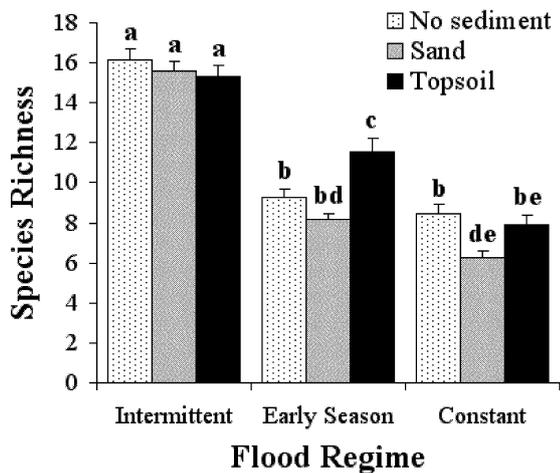
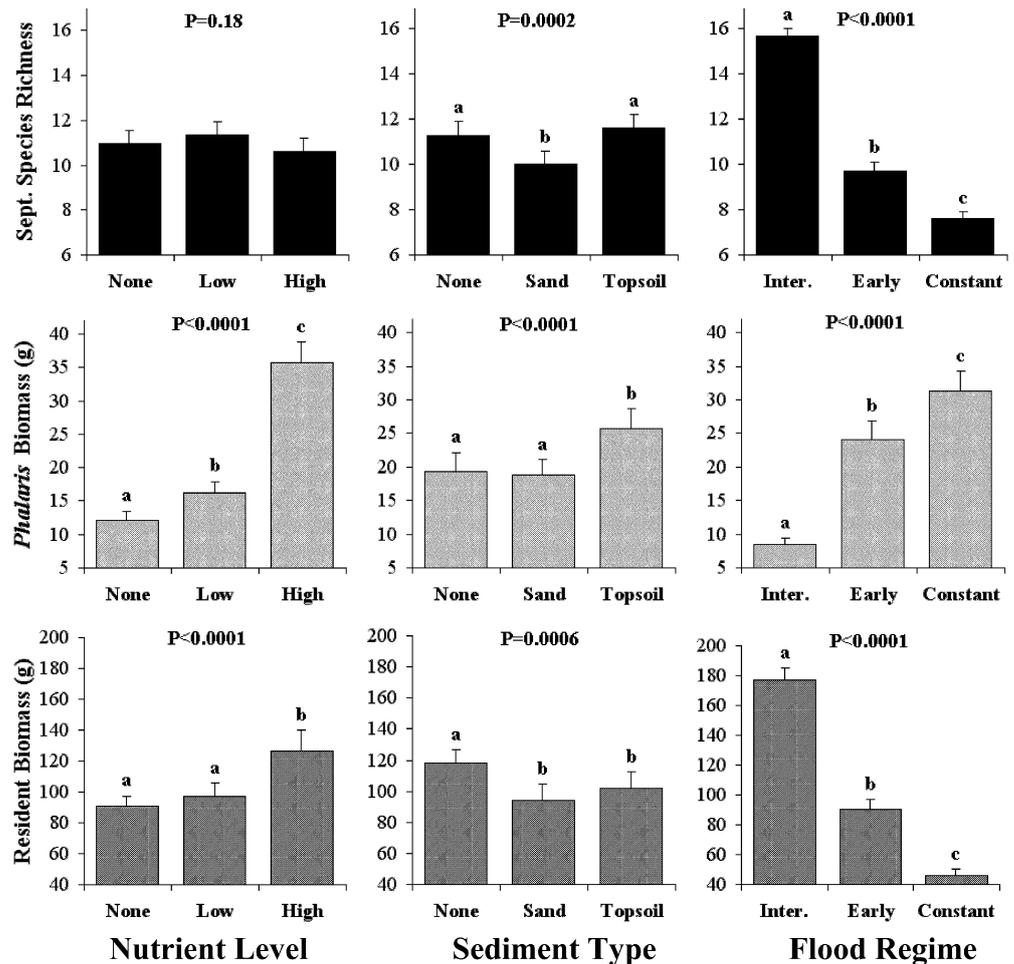


Fig. 3 Effects of two interacting factors, sediment type and flood regime, on species richness. Standard error bars are shown, and means that differed significantly do not share a common letter

more weeks of constant inundation. Dominant taxa that declined were the C3 grass *Agrostis gigantea* Roth, the C4 grass *Andropogon gerardii* Vitman, the legume *Desmodium canadense* (L.) DC., and the widespread forbs *Silphium perfoliatum* L., and *Verbena hastata* L. (Table 3). Taxa

that were short (<15 cm tall, generally due to immature status) and rare in the mesocosms also declined in the sediment addition and early season/constant flood treatments, e.g. *Anemone canadensis* L., *Cicuta maculata* L., *Thalictrum dasycarpum* Fisch. & Avé-Lall., and *Zizia aurea* (L.) W.D.J. Koch.

Three CCA ordination axes explained 1.4, 17.2, and 17.7% of the variance of the vegetation data in June (pre-treatment), July, and September, respectively (Table 4). Monte-Carlo tests were not significant for the three ordination axes based on the June data ($P > 0.34$ for all) but were significant for both July and September ($P < 0.02$ for all). Sediment type was moderately correlated with Axis 2, and nutrient level was weakly positively correlated with Axis 3, but flood regime had a high correlation with Axis 1 both in July and September and explained the most variance in the species data (Table 4). Dramatic changes in species composition and abundance attributable to flood regime were already apparent by July, when the mesocosms separated into two clusters in the ordination graph, a small cluster that contained mesocosms subjected to intermittent or no flooding and a larger cluster that contained early season/constant flooded mesocosms (Fig. 4). There was a clearer separation of the early season and constant flooded mesocosms along Axis 1 in September (Fig. 4).

Table 3 Species that increased or decreased in frequency in three of the treatments in the Main Experiment, based on the number the times the species crossed line transects sampled in September 2002. "Changes" in frequency are relative to the least manipulated level of the factor. Uncommon species were excluded from this analysis

Treatment	Species that increased (% increase)	Species that decreased (% decrease)
High nutrients	<i>Asclepias incarnata</i> (+88) <i>Phalaris arundinacea</i> (+47) <i>Spartina pectinata</i> (+23)	<i>Andropogon gerardii</i> (-13)
Topsoil sediment	<i>Phalaris arundinacea</i> (+30) <i>Spartina pectinata</i> (+25)	<i>Carex vulpinoidea</i> (-49) <i>Andropogon gerardii</i> (-32)
Constant flooding	<i>Asclepias incarnata</i> (+483) <i>Spartina pectinata</i> (+105) <i>Phalaris arundinacea</i> (+103)	<i>Desmodium canadense</i> (-100) <i>Symphyotrichum novae-angliae</i> (-99) <i>Agrostis gigantea</i> (-92) <i>Verbena hastata</i> (-87) <i>Glyceria striata</i> (-85) <i>Andropogon gerardii</i> (-83)

Response of *Phalaris*

During the 2002 growing season, 1 *Phalaris* plant died out of the 600 planted; this occurred in a topsoil sediment treatment and was probably due to accidental burial. Two *Phalaris* plants flowered, both in high nutrient treatments. Initial aboveground biomass of *Phalaris* at the time of planting was 1.4 ± 0.08 g per plant; after 4 months the mean biomass across all 150 mesocosms was 21.2 ± 1.5 g per plant (0.27 m^{-2}) and ranged from a low of 3.5 ± 0.6 g in the 000 (control) treatment to a high of 64.0 ± 5.0 g in the H0C (H=high nutrients, 0=no sediment, C=constant flood) treatment. The proportion of *Phalaris* to total aboveground biomass ranged from a low of 0.027 ± 0.003 for the 000 treatment to a high of 0.677 ± 0.08 for the HTC treatment.

End-of-season aboveground biomass of *Phalaris* was affected by block ($P = 0.0004$), nutrient level, sediment type, and flood regime ($P < 0.0001$ for all; Table 2, Fig. 2). Addition of low and high nutrients, topsoil sediment, early season flooding, and constant flooding all increased *Phalaris* biomass relative to the least manipulated level (Fig. 2). There were also significant sediment \times flooding, sediment \times nutrient, and three-factor interactions ($P < 0.0001$ for all; Fig. 5). Topsoil and sand sediment addition combined with early season flooding increased the biomass of *Phalaris* ~90–120% above expected (additive) levels, but sand sediment combined with constant flooding appeared to have antagonistic effects, causing a ~40% reduction in *Phalaris* biomass (Fig. 5). Nutrient addition combined with early season flooding accelerated invasion 30–50% over expected levels (Fig. 5).

Phalaris frequencies showed only a flooding main effect as of July ($P < 0.0001$, Table 2), with constant (7.0 ± 0.3 intervals) and early season (6.7 ± 0.3 intervals) flood treatments having a higher frequency of *Phalaris* than the intermittent flood treatment (4.6 ± 0.2 intervals), along with a significant sediment \times flooding ($P < 0.0001$) and three-factor ($P = 0.037$) interaction. Treatment effects on *Phalaris* frequencies in September were identical to those for biomass (Figs. 2, 5), except that (1) both topsoil and sand sediment treatments increased frequencies of *Phalaris* compared to no sediment, and (2) *Phalaris* frequencies increased significantly at high levels of nutrient addition but not at low levels. The sediment \times flooding interaction was attributable to a 53–63% increase in *Phalaris* frequencies over expected levels when sand or topsoil sediments were combined with early season flooding and a 22% increase over expected levels when topsoil sediment was combined with constant flooding.

In the Grazing Experiment, the two-way ANOVA on *Phalaris* biomass showed strong evidence for both nutrient and grazing main effects ($P = 0.0007$ and 0.0018 , respectively) and a nutrient \times grazing interaction ($P = 0.0291$). Mesocosms that were grazed had significantly greater biomass of *Phalaris* (27.8 ± 6.4 g 0.27 m^{-2}) than those that were not grazed (10.5 ± 1.9 g); likewise, fertilization increased biomass of *Phalaris* (28.9 ± 6.1 g vs 9.4 ± 1.5 g for no nutrients). The combination of nutrient addition and grazing resulted in an approximate 200% increase in *Phalaris* biomass over expected levels (Fig. 5).

Grazed mesocosms had significantly lower initial frequency of *Phalaris* ($P = 0.027$), but by July, this pattern

Table 4 Canonical Correspondence Analysis (CCA) results of July and September vegetation data from the Main Experiment. Shown for each of the three primary ordination axes are correlations

Canonical coefficients	July			September		
	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3
Nutrient level	0.148	-0.053	0.271	0.224	-0.096	0.306
Sediment type	0.164	-0.346	-0.065	0.250	-0.376	-0.117
Flood regime	0.661	0.036	-0.014	0.764	0.106	-0.029
% of variance explained	14.7	1.9	0.7	14.9	2.1	0.7
Pearson correlation, Spp-Envt	0.685	0.556	0.411	0.788	0.539	0.455

(canonical coefficients, standardized) with nutrient level, sediment type, and flood regime, percent of total variance explained by the axis, and Pearson's (species-environment) correlations

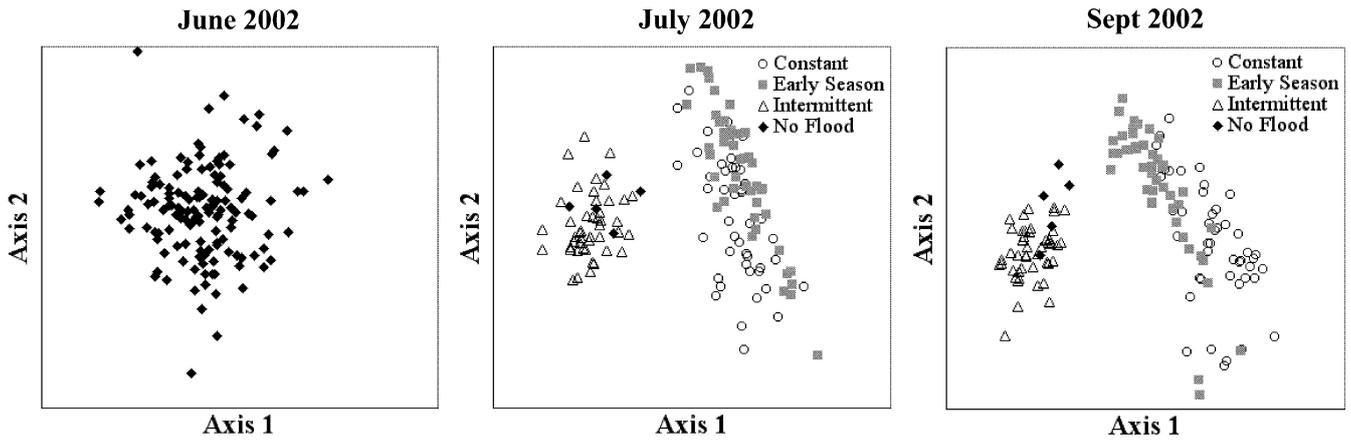


Fig. 4 Graphs of the CCA ordinations of vegetation data from the 135 mesocosms used in the Main Experiment, as of June (prior to the start of the experiment), July, and September 2002. Mesocosms are coded by flooding treatment

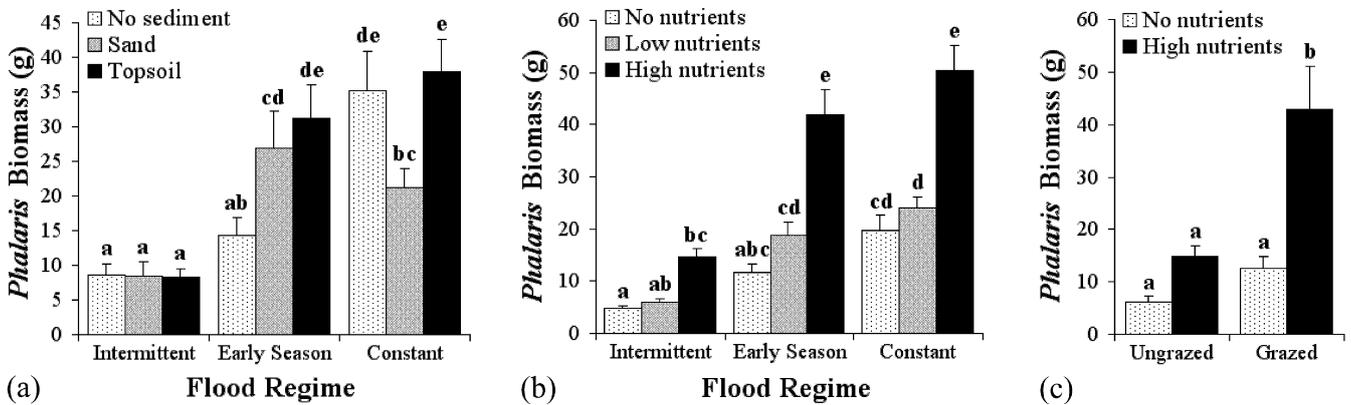


Fig. 5 Effects of interacting factors on *Phalaris* biomass: (a) sediment type and flood regime, (b) nutrient level and flood regime, and (c) nutrient level and grazing status. Standard error bars are

shown, and within each graph, means that differed significantly do not share a common letter

was reversed by a strong grazing effect: grazed mesocosms had a higher frequency of *Phalaris* (7.9 ± 0.5 intervals) than ungrazed mesocosms (5.2 ± 0.4 ; $P = 0.0006$). In September, this strong grazing effect held (10.8 ± 1.4 vs 6.2 ± 1.0 ; $P = 0.006$). In September there was also a nutrient effect, with a higher frequency of *Phalaris* (10.4 ± 1.6) under high levels of nutrients than no nutrients (6.6 ± 0.7 ; $P = 0.018$).

Resident species biomass

Final resident species biomass ($\text{g } 0.27 \text{ m}^{-2}$) averaged $104.5 \pm 5.4 \text{ g}$ overall, and ranged from $32.7 \pm 11.7 \text{ g}$ in the HTC treatment to $247.8 \pm 5.5 \text{ g}$ in the HSI (I=intermittent flood) treatment. Resident biomass showed significant nutrient, sediment, and flooding main effects (Fig. 2) as well as a sediment \times flooding and nutrient \times flooding interactions ($P < 0.0006$ for all; Fig. 6). Early season flooding, constant flooding, sand sediment, and topsoil sediment all decreased resident biomass relative to the intermittent flood and no sediment treatments, respectively (Fig. 2). Only high nutrient addition increased resident biomass relative to no nutrient addition (Fig. 2).

The nutrient \times flooding interaction occurred because resident species drastically increased biomass production when high levels of nutrients were combined with intermittent flooding but not when high nutrients were combined with early season or constant flooding (Fig. 6). The sediment \times flooding interaction was attributable to abrupt declines in resident biomass that occurred when sediment additions were combined with early season or constant flooding (Fig. 6), a pattern which mirrors that of *Phalaris* biomass (Fig. 5).

In the Grazing Experiment, there was strong evidence for nutrient and grazing main effects ($P < 0.0001$ for both). High nutrients resulted in higher resident biomass ($165.2 \pm 17.3 \text{ g}$) than no nutrients ($100.4 \pm 15.8 \text{ g}$), and grazed mesocosms had approximately half the resident biomass of ungrazed mesocosms ($92.4 \pm 15.3 \text{ g}$ and $173.2 \pm 13.6 \text{ g}$, respectively).

Discussion

We imposed a constant propagule pressure of *Phalaris arundinacea*, known to invade temperate wetlands in North America (Galatowitsch et al. 1999), and assessed

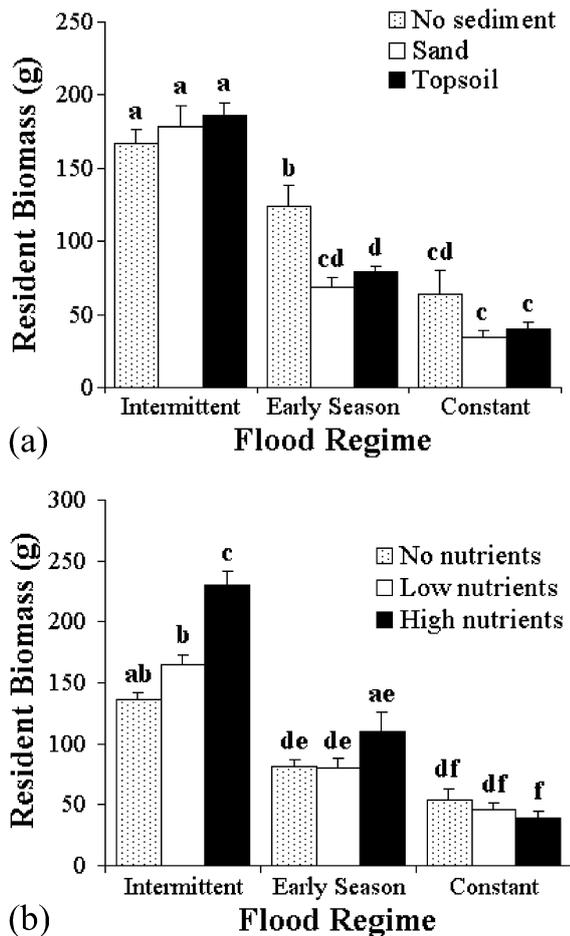


Fig. 6 Effects of interacting factors on resident biomass: (a) sediment type and flood regime, and (b) nutrient level and flood regime. Standard error bars are shown, and within each graph, means that differed significantly do not share a common letter

invasibility of a wet prairie assemblage as a function of single or multiple manipulations. In two separate experiments we varied: (1) nutrient level, sediment type, and flood regime, and (2) nutrient level and grazing status. Prior to treatments, our planted assemblages resembled southern Wisconsin wet prairies in the dominant and subdominant species present (Curtis 1959). The major exception was that a widespread naturalized species, *Agrostis gigantea*, contaminated the native seed mix and became one of the three dominant species. Initial species richness exceeded that reported by Cottam and Wilson (1966) for 1 m² plots sampled in wet-mesic (12.6 species m⁻²) and mesic (9.4 species m⁻²) portions of a 30-year-old restored prairie in southern Wisconsin. Aboveground biomass in the least manipulated treatments (unfertilized, no sediment addition, and either no flooding or intermittent flooding) was similar to values reported for a natural wet prairie (Van der Valk 2000) and herbaceous wetland communities sampled by Day et al. (1998).

Prolonged flooding caused the largest changes in the biotic and physical variables we measured. Flooding for 4 weeks was sufficient to cause about 2/3 of the resident taxa to decrease in abundance or die out, resulting in large

increases in light availability. Floods lasting 14 weeks further decreased species richness and increased light levels in the mesocosms. Redox potentials responded primarily to flooding, with prolonged floods reducing the oxygen available to plants at a depth of 10 cm. Sediment additions had similar, but less intensive, effects than flooding. Nutrient additions had no effect on species richness but did significantly increase *Phalaris* frequency, *Phalaris* biomass, and resident species biomass.

The results from this study support both the nutrient hypothesis of invasibility, since fertilization increased both the biomass and frequency of *Phalaris*, and the disturbance hypothesis of invasibility, since floods of increasing intensity/duration and addition of sediments increased the biomass and frequency of *Phalaris*. With disturbance, we saw both a reduction in resident species biomass and a concomitant increase in light and space, which allowed the more tolerant *Phalaris* to expand. Our results highlighting the importance of increased nutrients (an increase in gross resource supply) and increased light availability (a decrease in the uptake of a resource by resident species) in facilitating invasion are consistent with Davis et al.'s (2000) fluctuating resource hypothesis and corroborate other studies of *Phalaris*.

In another mesocosm study, Green and Galatowitsch (2002) found that *Phalaris* suppressed the shoot biomass of native species at all the levels of NO₃-N they added, but *Phalaris* showed increased suppression of the natives at the highest (48 g m⁻²) dose level. Maurer and Zedler (2002) reported increased vegetative spread of *Phalaris* into shady environments when parent plants were fertilized, but invasion was most rapid when both nutrient and light levels were highest. Negative relationships between canopy cover and *Phalaris* have also been shown for the spread of transplants into natural plant communities by Morrison and Molofsky (1998) and by Lindig-Cisneros and Zedler (2002a, 2002b) for establishment of *Phalaris* from seed. According to the latter, species-rich canopies reduced light penetration and resulted in lower germination within microcosms, mesocosms, and field plots.

Earlier (Maurer et al. 2003) we hypothesized an interaction whereby hydrologic disturbances simultaneously make sites more invasible and *Phalaris* more aggressive. Our experiment demonstrates that invasibility of a wet prairie assemblage by *Phalaris* almost always increased when multiple disturbances or disturbances plus nutrients were combined. Although combined factors were often additive in their effects on invasibility, there were three notable synergies. In the first case, sediments combined with early season flooding doubled the expected biomass of *Phalaris* and simultaneously reduced the biomass of resident species to half the expected level. Second, nutrient addition combined with early season flooding accelerated invasion over expected levels by ~30–50%. Third, the combination of nutrient addition and grazing resulted in a doubling of *Phalaris* biomass over expected levels. Ours may be the first explicit test of interactive effects on invasibility and the first demonstra-

tion of both additive effects and interactions. Interactions, particularly those that involve synergisms, have important implications for our ability to predict the rates and magnitude of invasions. In nature, the most realistic scenario is that multiple abiotic and biotic factors act simultaneously. Outcomes will likely differ from predictions based on factors acting in isolation or multiple factors acting with solely additive effects.

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Flood tolerance in wetland angiosperms: a comparison of invasive and noninvasive species

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Abstract

We assessed the biomass production, biomass allocation patterns, height growth, and root airspace of seventeen wetland plant taxa, including two potentially invasive species, grown under high nutrient conditions and subjected to four hydrologic regimes: constant drawdown, cyclic flooding and drawdown, cyclic flooding and drought, and constant flooding for the duration of the experiment (~10 weeks). We found that: (1) the potentially invasive reed canary grass (*Phalaris arundinacea*) and broadleaf cattail (*Typha latifolia*) responded to treatments similarly; both outgrew the other perennial species in all four hydrologic regimes; (2) *Phalaris* had the highest levels of root airspace of all the taxa; (3) the grasses and graminoids nearly always tolerated flooding better than the broadleaf forbs, perhaps in part due to greater quantities of root airspace; and (4) the species that were most sensitive to flooding are typically found in drier, groundwater-fed, and more nutrient-poor environments. We hypothesize that *Phalaris* and *Typha*, which are both tall and productive, should be competitive dominants under a variety of hydrologic conditions, at least where nutrients are abundant, as in urban and agricultural landscapes. Eight of the noninvasive taxa tolerated flooding but produced less biomass and/or were shorter or shorter-lived than *Phalaris* and *Typha*. Among the five taxa that were most sensitive to flooding were slow-growing habitat specialists; such species will likely experience declines in areas that become impounded or experience greater volumes of runoff. © 2004 Elsevier B.V. All rights reserved.

Keywords: Invasive species; *Phalaris arundinacea*; *Typha latifolia*; Urban runoff; Wetland plants

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1. Introduction

Hydrologic conditions, especially flooding regimes, are known to be a strong if not primary influence on wetland plant community composition and processes (Mitsch and Gosselink, 1993; Keddy, 2000). When affected by urban development, natural hydrologic regimes typically have increased frequency and severity of flooding (Watson et al., 1981; Pitt, 1996; Detenbeck et al., 1999), lowered water tables and reduced groundwater recharge (Brinson, 1993) compared to previous, more natural conditions. Associated shifts in the vegetation of temperate freshwater wetlands include a loss of biodiversity, decreased floristic quality and an expansion of invasive plant species (Galatowitsch et al., 2000; Brinson and Malvarez, 2002; Choi and Bury, 2003; Kercher et al., 2004).

“Invasive plants” are species or strains that rapidly increase their spatial distribution by expanding into existing plant communities. Based on a survey of the literature, Richardson et al. (2000) define invasive plants as plants “that produce reproductive offspring, often in very large numbers, at considerable distances from parent plants (approximate scales: >100 m, <50 years for taxa spreading by seeds and other propagules; >6 m/3 years for taxa spreading by roots, rhizomes, stolons, or creeping stems), and thus have the potential to spread over a considerable area” (p. 98). Although invasive plants are often exotic, they are sometimes native (e.g., *Typha domingensis* in the Florida Everglades; Wu et al., 1997) or hybrids between native and exotic strains (e.g., *Typha* × *glauca*; Galatowitsch et al., 1999). In North America, two plant species that are invasive by this definition are reed canary grass (*Phalaris arundinacea*), an erect, cool season perennial grass that occurs in 43 of the United States plus Canada, and broadleaf cattail (*Typha latifolia*), an erect perennial semi-aquatic graminoid that is ubiquitous throughout North America and occurs in all 50 of the United States plus Canada and Mexico (Wisconsin State Herbarium, 2003; USDA and NRCS, 2003). Although both are native to North America, *Phalaris* and *Typha* are capable of spreading large distances via seed and rhizome fragments and, once established in a wetland, can undergo rapid clonal spread and form dense monotypic stands with few coexisting species (Grace and Wetzel, 1981; Barnes, 1999; Veltman, 2002; Kercher et al., 2004).

Although the process of conversion to a monotype has not been well-studied, greater tolerance of flooding may be one factor that favors invasive plants like *Phalaris* and *Typha* in stormwater-impacted wetlands (Zedler and Kercher, 2004). Several researchers have experimentally investigated the flooding responses of herbaceous hydrophytes (e.g., Lieffers and Shay, 1981; Rubio et al., 1995; Ewing, 1996; Lentz and Dunson, 1998; Hunter et al., 2000; Clarke and Baldwin, 2002; Bonilla-Warford and Zedler, 2002), but fewer studies have compared the flooding responses of invasive and noninvasive wetland species (Newman et al., 1996; Lempe et al., 2001; Vandersande et al., 2001; Miller and Zedler, 2003). We grew seventeen wetland plant taxa, including the two invasive species *P. arundinacea* and *T. latifolia*, and subjected them to four hydrologic regimes within experimental pots. Our goals were: (1) to assess the flood tolerance (defined here as the ability to produce biomass under flooded conditions relative to unflooded conditions) of the noninvasive and invasive taxa; (2) to rank taxa in each experimental environment relative to other taxa on the basis of biomass production and height growth, two variables that affect a

taxon's ability to dominate (Grime, 1979); and (3) to assess whether the differential flood tolerance of taxa relates to root airspace, growth rates, and/or biomass allocation patterns.

2. Methods

2.1. Experimental setup

We conducted the experiment within a fenced outdoor research facility at the University of Wisconsin-Madison Arboretum (Dane County, Wisconsin, USA; latitude 43.7°, longitude 89.20°) during the summer of 2000. We employed a completely randomized design and varied two factors, taxon and hydrologic treatment. We grew 16 species (Table 1) and two source populations of *Spartina pectinata* under four hydrologic regimes. The 17 taxa were selected from a pool of 29 on the basis of high seed germinability and production of ample seedlings. There were five replicates of each taxon-treatment combination for a total of 340 experimental units. Each unit consisted of a 19-l white plastic bucket with a 3.8-l plastic nursery pot inside. Pots received the following treatments (Fig. 1): (1) watered constantly from the bottom with ~5 cm of standing water but never flooded, or constant drawdown (hereafter called the “Low” treatment); (2) flooded with 15 cm of water above the soil surface for 4 days and then watered from the bottom for 4 days (“4 High/4 Low”); (3) flooded 15 cm for 4 days and then not watered for 4 days (“4 High/4 Dry”); or (4) constantly flooded with 15 cm of water (“High”).

Seeds of the grass, sedge, and forb taxa were collected from wild populations (*P. arundinacea*, *Solidago gigantea*, *S. pectinata*, and *T. latifolia*) in Wisconsin or purchased from native plant nurseries. After a month of cold-moist stratification, seeds were sown in flats in a greenhouse at the University of Wisconsin on April 26–27, 2000. Seedlings were

Table 1

Sixteen species chosen for experimentation. Data are scientific name, plant family, and common name (USDA and NRCS, 2003)

Species	Family	Common name
<i>S. pectinata</i> Bosc ex Link	Poaceae	Prairie cordgrass
<i>P. arundinacea</i> L.	Poaceae	Reed canary grass
<i>T. latifolia</i> L.	Typhaceae	Broadleaf cattail
<i>Asclepias incarnata</i> L.	Apocynaceae	Swamp milkweed
<i>B. ciliatus</i> L.	Poaceae	Fringed brome
<i>C. canadensis</i> (Michx.) Beauv.	Poaceae	Bluejoint grass
<i>C. granularis</i> Muhl. ex Willd.	Cyperaceae	Limestone meadow sedge
<i>C. stricta</i> Lam.	Cyperaceae	Upright sedge
<i>E. maculatum</i> L.	Asteraceae	Spotted joe-pye weed
<i>Glyceria striata</i> (Lam.) A. S. Hitchc.	Poaceae	Fowl mannagrass
<i>O. riddellii</i> (Frank ex Riddell) Rydb.	Asteraceae	Riddell's goldenrod
<i>Symphotrichum puniceum</i> (L.) A. & D. Löve	Asteraceae	Purplestem aster
<i>Eupatorium perfoliatum</i> L.	Asteraceae	Common boneset
<i>H. grosseserratus</i> Martens	Asteraceae	Sawtooth sunflower
<i>S. gigantea</i> Ait.	Asteraceae	Giant goldenrod
<i>B. cernua</i> L.	Asteraceae	Nodding beggartick

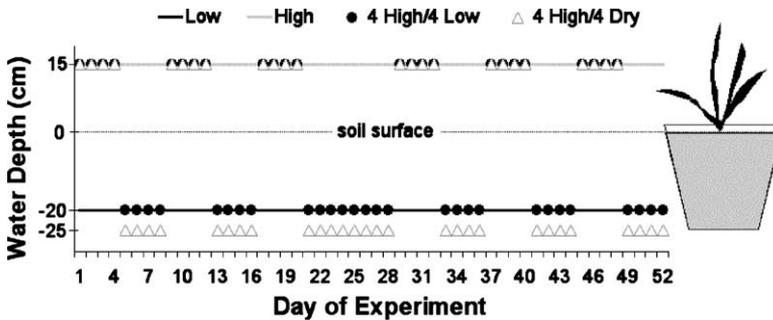


Fig. 1. Depiction of the four experimental hydrologic regimes over time (days). Water depths are relative to the soil surface in the pots.

transplanted to plug trays containing Metro Mix[®] 360 approximately 2 weeks after germination, kept in a greenhouse with natural light and temperatures that ranged from 24 to 33 °C, and watered daily. On June 28, we filled nursery pots with locally-quarried, screened sand and transferred one plant to each pot. Two Osmocote[®] Plus controlled release fertilizer tablets (Scotts Europe b.v., Waardenburg, The Netherlands) were added to opposite sides of each pot, halfway between the plant and the side of the pot. Each pot was then placed within its own bucket and watered daily until the experiment began.

On July 9 (day 1), treatments were initiated by filling the white buckets from the bottom with a garden hose until the proper water level was attained. Floods were administered a total of six times: on July 9, July 17 (day 9), July 25 (day 17), August 6 (day 29), August 14 (day 37), and August 22 (day 45). Nearly 10 cm of rain fell in a series of thunderstorms that occurred during the third dry/drawdown period (July 30 through August 5). As a result, this dry/drawdown period was extended until four consecutive days had no rainfall. At the end of every flood cycle, all 340 buckets were emptied, scrubbed to remove algae, and filled with fresh water. Throughout this experiment, the soil in the pots was consistently within 1–2 °C of ambient temperature.

We monitored plants regularly for flowering/fruitlet status, presence of adventitious roots, and mortality (defined here as no living tissue above the soil surface). Height of the tallest stem, including the inflorescence when present, was measured initially on July 9 and subsequently on September 8. On August 30 (day 53), the last day of the final eight-day cycle, all pots from the 4 High/4 Low and 4 High/4 Dry treatments were subjected to drawdown conditions (i.e., watered from the bottom with ~5 cm of standing water) until plants were harvested beginning on September 18, 2000 (day 72). High treatment buckets remained flooded until biomass was harvested.

2.2. Biomass collection

Shoot biomass was harvested by cutting plant stems at the soil surface. Root biomass, including rhizomes when present, was washed of sand and debris over a wire mesh screen. At this time, three segments of lateral root measuring <10 cm long were collected from different regions of the same plant and stored in a refrigerator until they were used to

estimate root airspace (see below). Root segments could not be collected from some plants due to a near-complete mortality of roots (e.g., *Carex granularis* in the High treatment). Shoot and root biomass was oven dried for 48 h at 60 °C and weighed to the nearest 0.1 g. The root subsamples were excluded from the root biomass measurements since they weighed less than 0.1 g combined.

2.3. Root airspace

Aerenchyma, or root airspace, was estimated for each plant as the percentage weight increase of root samples following vacuum extraction of air and its replacement by water—i.e., $100 \times [(final\ weight\ of\ the\ root\ subsample - initial\ weight)/(initial\ weight)]$. This was similar to the methods used by [Byott \(1976\)](#) and [Johnston \(1977\)](#) to measure leaf mesophyll airspace. Immediately prior to vacuum extraction, each root was patted dry with a tissue and weighed to the nearest 0.001 g. To distinguish among the three root subsamples following vacuum extraction, root tips were color marked with a permanent marker.

The vacuum apparatus employed a 250-mL flask connected to a vacuum pump, which was powered by an AC motor. Approximately 200 mL of water was added to the flask, and the three pieces of root from a single plant were placed in the flask and weighted with a paper clip to keep them submerged. The flask was stoppered and the vacuum applied for exactly two minutes. Thereafter, the roots were again patted dry with a clean tissue and promptly reweighed.

2.4. Statistical analyses

Two-way ANOVAs with taxon and treatment as independent variables were performed in [SAS Institute Inc. \(1999\)](#) using a general linear modeling procedure and the following response variables: shoot, root, and whole-plant biomass, shoot:root biomass ratios, and final plant height. A mixed modeling procedure was used to assess the effects of taxon and treatment on percent root airspace. Following significant *F*-tests, the LSD procedure was used to separate overall treatment and taxon means, and the ‘slice’ command was used to test for simple effects—i.e., differences among taxa within each treatment and differences among treatments within each taxon. For pairwise comparisons of taxa within treatments, we used a Bonferroni-corrected alpha of 0.0004; and for comparisons of treatments within taxa, we used alpha = 0.0005.

A “flood sensitivity value” was calculated for each taxon as $[1 - (\text{mean whole-plant biomass produced in the three flooded treatments})/(\text{mean whole-plant biomass produced in the Low treatment})]$. We use the terms “sensitive” and “tolerant” throughout this paper to denote opposite responses to flooding—sensitive taxa had the lowest biomass production in the flooded treatments relative to the Low treatment, while tolerant taxa had the highest production in the flooded treatments relative to the Low treatment.

Relationships among response variables were assessed using simple linear regressions in S-plus 2000 ([Mathsoft Inc., 1988–1999](#)). Alpha = 0.05 for all statistical tests, except as noted above.

3. Results

Of the 340 plants, 38 (11%) died during the experiment (Table 2). No plants died in the Low treatment, while 13, 12, and 13 plants died in the 4 High/4 Low, 4 High/4 Dry, and High treatments, respectively. A total of 140 of the 340, or 41%, of the plants flowered before they were harvested; 73% of the plants in the Low treatment flowered, and all taxa except *Calamagrostis canadensis*, *Carex stricta*, and *T. latifolia* yielded at least one flowering individual during the experiment (Table 3). For most taxa, flooding resulted in higher shoot:root ratios but less biomass accumulation, shorter plants, and a lower percentage of flowering individuals (Tables 2 and 3).

The two-way ANOVAs for shoot biomass, root biomass, whole-plant biomass, shoot:root ratios, and final plant height were significant for taxon and treatment ($P < 0.0001$ for all; Table 4). Taxon \times treatment interactions were also highly significant ($P < 0.0001$) in all cases. Taxa that produced the most biomass in the Low treatment were *Bidens cernua*, *T. latifolia*, *P. arundinacea*, and *C. stricta* in decreasing order (Table 5 and Fig. 2). Taxa that produced the least biomass in the Low treatment were *Bromus ciliatus*, *Eupatorium maculatum*, *S. gigantea*, and *Oligoneuron riddellii* in increasing order (Table 5 and Fig. 2). Overall, taxa produced significantly more biomass in the Low treatment than in the flooded treatments. The tallest taxa were *T. latifolia* and *S. pectinata*, which grew to 1.3 m in under 5 months, while the shortest taxa were *B. ciliatus*, *E. maculatum*, and *O. riddellii*, none of which exceeded 0.5 m in height (Tables 3 and 5).

The increased shoot:root biomass ratios for all taxa in the flooded treatments were due to (1) reduced root biomass in the flooded treatments relative to the Low treatment, which was

Table 2

Mortality of 17 taxa subjected to three flooding regimes (presented as the number of plants that died out of five possible) and taxon sensitivities to flooding^a

Taxon	4 High/4 Low	4 High/4 Dry	High	Sensitivity ^a
<i>B. ciliatus</i>	5	3	5	0.98
<i>H. grosseserratus</i>	4	4	2	0.95
<i>E. maculatum</i>	3	1	0	0.88
<i>O. riddellii</i>	0	1	5	0.81
<i>C. granularis</i>	0	0	0	0.66
<i>S. gigantea</i>	0	0	0	0.61
<i>E. perfoliatum</i>	0	0	0	0.56
<i>A. incarnata</i>	0	0	0	0.55
<i>S. puniceum</i>	0	0	0	0.48
<i>B. cernua</i>	0	3	0	0.40
<i>G. striata</i>	0	0	0	0.38
<i>S. pectinata</i> -Koshkonong	1	0	0	0.38
<i>C. canadensis</i>	0	0	1	0.33
<i>C. stricta</i>	0	0	0	0.23
<i>P. arundinacea</i>	0	0	0	0.19
<i>T. latifolia</i>	0	0	0	0.15
<i>S. pectinata</i> -Sumner	0	0	0	0.09

Taxa are listed from most to least sensitive to flooding.

^a Sensitivity = $1 - [(\text{mean whole-plant biomass in the three flooded treatments}) / (\text{mean whole-plant biomass in the Low treatment})]$.

Table 3

Summary data for 17 taxa: total number of plants to flower in the Low treatment ($n = 5$) and flooded treatments ($n = 15$), number with adventitious roots in the High treatment ($n = 5$), shoot:root biomass ratios in the Low treatment (+S.E.) and flooded treatments, final plant height in the Low treatment and flooded treatments, and root airspace in the Low and flooded treatments

Taxon	Flowering plants; low	Flowering plants; flooded	Advent. roots; high	Shoot:root; low	Shoot:root; flooded	Final height (cm); low	Final height (cm); flooded	Root airspace; low	Root airspace; flooded
<i>B. ciliatus</i>	1	0	0	3.8 ± 1.2	6.5 ± 3.5	20 ± 5	12 ± 1	0.22 ± 0.16	NA
<i>H. grosseserratus</i>	5	1	3	4.7 ± 2.6	16.3 ± 10.5	151 ± 11	44 ± 10	0.23 ± 0.07	NA
<i>E. maculatum</i>	5	7	4	1.8 ± 0.7	9.5 ± 2.6	44 ± 2	27 ± 4	0.05 ± 0.02	0.35 ± 0.08
<i>O. riddellii</i>	0	1	0	1.7 ± 0.1	7.0 ± 2.1	47 ± 2	29 ± 3	0.34 ± 0.12	0.15 ± 0.07
<i>C. granularis</i>	3	0	0	1.9 ± 0.4	4.7 ± 1.0	66 ± 7	36 ± 6	0.82 ± 0.24	0.62 ± 0.18
<i>S. gigantea</i>	2	2	5	2.3 ± 0.3	13.4 ± 3.9	56 ± 7	43 ± 5	0.14 ± 0.04	0.17 ± 0.06
<i>E. perfoliatum</i>	10	10	5	0.5 ± 0.1	1.1 ± 0.3	52 ± 3	41 ± 1	0.29 ± 0.08	0.23 ± 0.03
<i>A. incarnata</i>	5	3	5	1.4 ± 0.3	1.6 ± 0.1	109 ± 4	83 ± 2	0.19 ± 0.03	0.18 ± 0.01
<i>S. puniceum</i>	10	10	5	2.2 ± 0.4	2.9 ± 0.5	87 ± 6	80 ± 4	0.31 ± 0.02	0.38 ± 0.04
<i>B. cernua</i>	5	12	5	1.7 ± 0.2	5.7 ± 0.7	78 ± 9	82 ± 5	0.37 ± 0.11	0.27 ± 0.05
<i>G. striata</i>	5	14	3	1.0 ± 0.1	1.5 ± 0.2	71 ± 5	56 ± 5	0.19 ± 0.06	0.21 ± 0.04
<i>S. pectinata-K</i>	5	12	0	0.7 ± 0.1	1.2 ± 0.1	129 ± 3	123 ± 9	0.27 ± 0.13	0.62 ± 0.23
<i>C. canadensis</i>	0	0	4	2.1 ± 0.2	3.0 ± 0.5	70 ± 3	75 ± 2	0.24 ± 0.03	0.32 ± 0.05
<i>C. stricta</i>	0	0	2	0.8 ± 0.0	1.0 ± 0.1	94 ± 3	83 ± 3	0.20 ± 0.10	0.47 ± 0.06
<i>P. arundinacea</i>	1	0	5	0.9 ± 0.1	1.2 ± 0.1	81 ± 7	82 ± 4	0.95 ± 0.26	1.11 ± 0.29
<i>T. latifolia</i>	0	0	5	0.6 ± 0.0	0.7 ± 0.0	135 ± 5	120 ± 6	0.62 ± 0.14	0.53 ± 0.07
<i>S. pectinata-S</i>	5	6	0	1.0 ± 0.1	1.4 ± 0.1	131 ± 20	131 ± 10	0.20 ± 0.08	0.31 ± 0.07

Taxa are listed (by their abbreviations) from most to least sensitive to flooding (see Table 2). NA: data not available.

Table 4

Contributions to sums of squares (given as percentages of total) from general linear models of five response variables

Source	Shoot biomass	Root biomass	Whole-plant biomass	Shoot:root ratio	Final plant height
Taxon	61.6	67.8	65.8	25.7	59.1
Flood Trt	6.2	11.2	9.1	13.9	4.9
Interaction	21.5	11.3	15.0	36.9	15.3
Error	10.7	9.7	10.1	23.5	20.7

All main effects and interactions were significant at $P < 0.0001$. Degrees of freedom: taxon = 16, flood regime = 3, interaction = 48, and total = 339.

significant for all taxa except *B. ciliatus*, *S. pectinata*-Sumner, and *T. latifolia*; and (2) the development of adventitious roots off the stems of 51 out of 85 High treatment plants (60%) encompassing all taxa except *B. ciliatus*, *O. riddellii*, *C. granularis*, and both populations of *Spartina* (Table 3).

Both taxon and treatment effects were significant for percent root airspace ($P < 0.0001$ and $P = 0.0003$, respectively), and there was also a significant taxon \times treatment interaction ($P < 0.0001$). Percent root airspace (estimated as the increase in root weight when air was replaced with water) was highly variable within and among taxa, ranging from 5% for *E. maculatum* to 95% for *P. arundinacea* in the Low treatment and from 15% for *O. riddellii* to 111% for *Phalaris* in the flooded treatments (Table 3), but overall, the High treatment had significantly greater root airspace than all other treatments, and *Phalaris* had significantly higher levels of root airspace than the other taxa tested. When grouped by growth form, grasses and graminoids (*C. granularis*, *C. stricta*, and *T. latifolia* in our study) had a higher percent root airspace than broadleaf forbs in the Low treatment and also in the flooded treatments (overall, airspace = $50 \pm 5\%$ for grasses and graminoids versus $30 \pm 3\%$ for forbs; d.f. = 263, $P = 0.001$).

Taxon flood sensitivity values ranged from a low of 0.09 for *S. pectinata*-Sumner to a high of 0.98 for *B. ciliatus* (Table 2). Shoot, root, and whole-plant biomass production in the Low treatment were significantly and inversely related to flood sensitivity ($r^2 = 0.29$, 0.48, and 0.46, respectively; d.f. = 16, and $P < 0.03$ for all), while shoot:root ratios were significantly positively related to flood sensitivity ($r^2 = 0.53$, d.f. = 16, $P = 0.0009$). Neither height nor root airspace correlated with flood sensitivity.

4. Discussion

We hypothesized that invasive potential of wetland angiosperms would be a function of overall sensitivity to flooding [expressed as: $1 - (\text{mean whole-plant biomass produced in the three flooded treatments})/(\text{mean whole-plant biomass produced in the Low treatment})$], and our results indicate that the invasive reed canary grass (*P. arundinacea*) and broadleaf cattail (*T. latifolia*) were among the three most flood-tolerant taxa. Furthermore, both species produced more shoot, root, and whole-plant biomass than nearly all other perennial taxa in the three flooded as well as in the unflooded treatment (Table 5), suggesting that rapid early growth contributes to their flood tolerance and thus allows them to dominate

Table 5

Taxon ranks from highest (1) to lowest (17) for shoot biomass, root biomass, whole-plant biomass, and final plant height

Taxon	Shoot biomass					Taxon	Whole-plant biomass				
	Low	4H/4L	4H/4D	High	Mean rank		Low	4H/4L	4H/4D	High	Mean rank
<i>B. cernua</i>	1	1	13	1	4.0	<i>B. cernua</i>	1	1	13	1	4.0
<i>P. arundinacea</i> ^a	2	2	1	2	1.8	<i>T. latifolia</i> ^a	2	2	3	2	2.3
<i>C. granularis</i>	3	9	4	15	7.8	<i>P. arundinacea</i> ^a	3	3	1	3	2.5
<i>T. latifolia</i> ^a	4	3	6	3	4.0	<i>C. stricta</i>	4	4	2	4	3.5
<i>C. stricta</i>	5	4	2	4	3.8	<i>E. perfoliatum</i>	5	11	8	6	7.5
<i>S. puniceum</i>	6	10	8	8	8.0	<i>S. pectinata</i> -K	6	5	4	7	5.5
<i>C. canadensis</i>	7	6	3	9	6.3	<i>C. granularis</i>	7	10	6	15	9.5
<i>S. pectinata</i> -K	8	7	5	7	6.8	<i>S. puniceum</i>	8	9	10	8	8.8
<i>G. striata</i>	9	5	7	10	7.8	<i>G. striata</i>	9	6	7	11	8.3
<i>E. perfoliatum</i>	10	12	12	6	10.0	<i>C. canadensis</i>	10	8	5	9	8.0
<i>A. incarnata</i>	11	11	10	12	11.0	<i>S. pectinata</i> -S	11	7	9	5	8.0
<i>S. pectinata</i> -S	12	8	9	5	8.5	<i>A. incarnata</i>	12	12	11	10	11.3
<i>H. grosseserratus</i>	13	16	17	13	14.8	<i>H. grosseserratus</i>	13	16	17	13	14.8
<i>O. riddellii</i>	14	13	14	16	14.3	<i>O. riddellii</i>	14	13	14	16	14.3
<i>S. gigantea</i>	15	14	11	11	12.8	<i>S. gigantea</i>	15	14	12	12	13.3
<i>E. maculatum</i>	16	15	15	14	15.0	<i>E. maculatum</i>	16	15	15	14	15.0
<i>B. ciliatus</i>	17	17	16	17	16.8	<i>B. ciliatus</i>	17	17	16	17	16.8

	Root biomass						Height				
	Low	4H/4L	4H/4D	High	Mean rank		Low	4H/4L	4H/4D	High	Mean rank
<i>T. latifolia</i> ^a	1	1	2	1	1.3	<i>H. grosseserratus</i>	1	16	17	13	11.8
<i>P. arundinacea</i> ^a	2	2	3	2	2.3	<i>T. latifolia</i> ^a	2	2	3	2	2.3
<i>B. cernua</i>	3	4	14	5	6.5	<i>S. pectinata</i> -S	3	1	2	1	1.8
<i>E. perfoliatum</i>	4	8	5	6	5.8	<i>S. pectinata</i> -K	4	3	1	3	2.8
<i>C. stricta</i>	5	3	1	3	3.0	<i>A. incarnata</i>	5	4	5	7	5.3
<i>S. pectinata</i> -K	6	5	4	7	5.5	<i>C. stricta</i>	6	5	6	6	5.8
<i>G. striata</i>	7	6	7	10	7.5	<i>S. puniceum</i>	7	9	4	8	7.0
<i>C. granularis</i>	8	11	10	14	10.8	<i>P. arundinacea</i> ^a	8	6	8	5	6.8
<i>S. pectinata</i> -S	9	7	6	4	6.5	<i>B. cernua</i>	9	7	14	4	8.5
<i>S. puniceum</i>	10	9	9	9	9.3	<i>G. striata</i>	10	10	9	11	10.0
<i>A. incarnata</i>	11	12	11	8	10.5	<i>C. canadensis</i>	11	8	7	9	8.8
<i>C. canadensis</i>	12	10	8	11	10.3	<i>C. granularis</i>	12	11	11	15	12.3
<i>H. grosseserratus</i>	13	16	17	15	15.3	<i>S. gigantea</i>	13	14	10	10	11.8
<i>O. riddellii</i>	14	13	12	16	13.8	<i>E. perfoliatum</i>	14	12	12	12	12.5
<i>E. maculatum</i>	15	15	15	13	14.5	<i>O. riddellii</i>	15	13	13	16	14.3
<i>S. gigantea</i>	16	14	13	12	13.8	<i>E. maculatum</i>	16	15	15	14	15.0
<i>B. ciliatus</i>	17	17	16	17	16.8	<i>B. ciliatus</i>	17	17	16	17	16.8

Rankings (1: highest 17: lowest). Taxa are ranked for each of the four treatments and overall ("mean rank"). 4H/4L = 4 High/4 Low; 4H/4D = 4 High/4 Dry.

^a Taxon is known to be potentially invasive in wetlands.

under a range of hydrologic conditions, at least when nutrients are not limiting. Even when their growth was severely curtailed under the dual stresses of flooding and drought (4 High/4 Dry treatment), *Phalaris* and *Typha* still produced more biomass than all taxa except for the native tussock sedge *C. stricta*. Results for plant height were less straightforward:

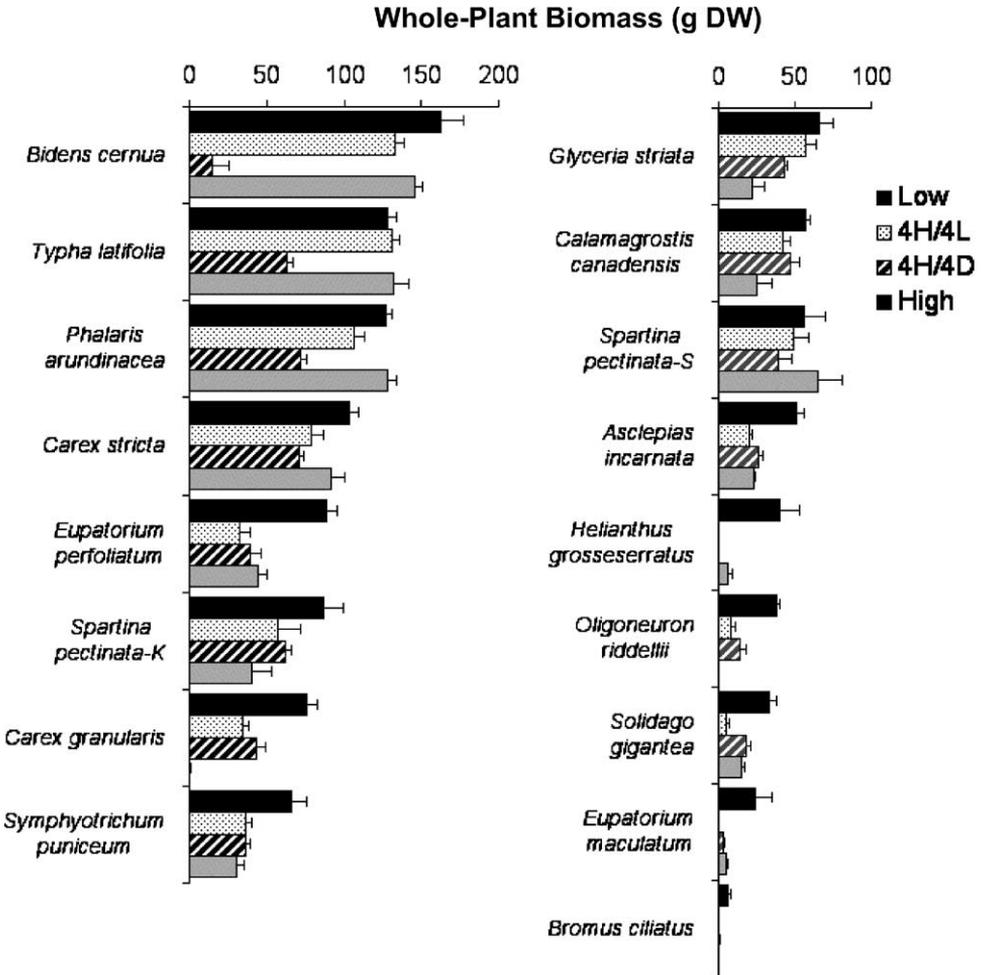


Fig. 2. Summary of whole-plant biomass production for 17 taxa and 4 hydrologic regimes (+S.E. bars, $n = 5$ for each taxon \times treatment combination), presented in order of highest to lowest biomass production in the Low treatment.

Typha was the second tallest of the seventeen taxa, but *Phalaris* was only the sixth tallest (Table 5). Nevertheless, height is only one aspect of canopy architecture and dominance; other important characteristics include canopy layering and cover (e.g., Keer and Zedler, 2002), which we did not measure in this study.

In addition to being the two most productive perennial species, *Typha* and *Phalaris* had similar biomass responses to the experimental treatments (Fig. 2). These two species also have similar distributions and ecological strategies. Both are widely distributed in North America, especially in areas characterized by seasonal or permanent surface water (Goslee et al., 1997), and belong to the same functional group: Boutin and Keddy (1993) classified

both species as “Matrix Clonal Dominants” based on a cluster analysis of 27 morphological and life history traits. *Phalaris* and other *Typha* species (e.g., *Typha angustifolia* and *Typha* × *glauca*) are known to form monotypes in wetlands (Galatowitsch and van der Valk, 1995; Galatowitsch et al., 1999), and their occurrence has been linked to stormwater runoff in a landscape-scale study of Minnesota prairie pothole wetlands (Galatowitsch et al., 2000). Our study suggests that the tall invasive competitors *Phalaris* and *Typha* will likely dominate under a wide range of hydrologic conditions, at least if nutrients are abundant, which is a realistic scenario in urban and agricultural landscapes.

In contrast to the invasive taxa, the widespread, noninvasive taxa characteristic of diverse sedge meadows (Curtis, 1959; Kercher et al., 2004) were moderately tolerant of flooding and attained moderate biomass and height, with the exception of the very tall and sometimes very flood-tolerant *S. pectinata*. The only obligate annual in our study, *B. cernua*, was the most productive species in all but the 4 High/4 Dry treatment, a result that helps explain its rapid colonization and dominance of moist, open, nutrient-rich mudflats. Although it was the superior producer of biomass in three out of four treatments, its short life impairs its ability to persist and compete with perennial invasive species.

Using young plants, we found that rapid accumulation of shoot, root, and whole-plant biomass was associated with greater flood tolerance. Rapid growth rates could allow establishing plants to escape submersion and/or afford them greater morphological plasticity in response to flooding (e.g., adventitious root development to escape anoxic conditions in the root zone, as we saw in 12 of the 17 taxa in the High treatment). The taxa that were most sensitive to flooding—including *B. ciliatus*, *C. granularis*, *E. maculatum*, *Helianthus grosseserratus*, and *O. riddellii*—are commonly found in wetlands with lower water tables and/or groundwater-fed, nutrient-poor wetlands (Curtis, 1959; Gleason and Cronquist, 1963; Goslee et al., 1997). These habitat specialists were short and/or poor producers of biomass in the Low treatment, and most failed to produce adventitious roots in the High treatment. Therefore, these taxa will likely experience the most rapid declines in areas that become impounded or experience greater volumes of runoff.

Based on the literature, we predicted a greater amount of root airspace in flood-tolerant plants and increased root airspace for individual taxa in response to flooding (e.g., Kawase and Whitmoyer, 1980; Hook, 1984; Jackson and Drew, 1984; Justin and Armstrong, 1987; Burdick, 1989; Seliskar, 1990). Although we detected no significant relationship between the flood sensitivity index and root airspace, and no significant increase in root airspace due to flooding for individual taxa, grasses and graminoids nearly always tolerated flooding better than the broadleaf forbs, and we found greater levels of root airspace in the former. Of all the taxa we tested, the invasive wetland grass *P. arundinacea* had the highest amount of root airspace, a trait that could allow *Phalaris* to survive, spread, and form monotypic stands in chronically anoxic soils unfavorable for most native wet meadow species.

We predicted shifts in biomass allocation from roots to shoots in response to flooding based on other studies (e.g., Rubio et al., 1995). We found significant increases in shoot:root ratios for all taxa, as predicted, but we also found a strong direct relationship between flood sensitivity and net change in shoot:root ratio—i.e., the flood-tolerant taxa showed very small increases in shoot:root ratios due to flooding, while sensitive taxa showed sometimes dramatic increases in shoot:root ratios due to flooding, primarily from the death of roots. The more consistent allocation patterns in the flood-tolerant taxa,

including the invasives *Phalaris* and *Typha*, may be related to the presence of aerenchyma in these taxa.

The invasive species in this experiment grew better and were more tolerant of hydrologic stresses than nearly all of the noninvasive taxa in the four hydrologic treatments. In another experimental study of the invasive cattail *T. domingensis* and the noninvasive Everglades species *Cladium jamaicense* and *Eleocharis interstincta*, only *Typha* responded positively to increased water depth (15, 30, and 60 cm) by increasing biomass as much as 60% (Newman et al., 1996). However, not all experimental comparisons of invasive and noninvasive species agree with these findings. Miller and Zedler (2003) report equivalent biomass responses of the invasive grass *P. arundinacea* and the noninvasive grass *S. pectinata* propagated from rhizomes and subjected to four hydroperiods and two water depths within experimental pots, with one exception: *Phalaris* grew best and produced more biomass than *Spartina* when flooding alternated weekly with drawdown. However, resources were limiting in this experiment (Miller and Zedler, 2003). Lempe et al. (2001) found no evidence that the invasive *Lythrum salicaria* was more flood-tolerant than five other noninvasive members of the family Lythraceae. Vandersande et al. (2001) report that the invasive *Tamarix ramosissima* was less tolerant of flooding but was more tolerant of elevated salinity levels than four noninvasive native riparian species. Horton and Clark (2001) found that water level declines and drought, conditions that often occur downstream from dams and diversions, favored seedlings of the exotic desert riparian species *Tamarix chinensis* over the native *Salix gooddingii*. Lorenzen et al. (2001) contrasted the growth of a noninvasive (*C. jamaicense*) and invasive (*T. domingensis*) species of the Florida Everglades and found little effect of anoxia on the growth, biomass allocation, and nutrient use efficiency in either species (but see Newman et al., 1996). Clearly, there are few studies comparing the responses of invasive and noninvasive species to stresses, and even fewer that compare different populations of a single species—and our two populations of *Spartina* differed somewhat in flood tolerance. Hence, it is difficult to generalize. More tests comparing the relative responses of invasive and noninvasive taxa to stresses are needed, and the stresses should match levels—including extremes—found in nature.

While tolerance of flashy or chronically-flooded conditions may be one factor that helps explain the invasiveness of *Phalaris* and *Typha*, their superior growth compared to other perennial species under unflooded conditions (and the inferior growth of the habitat specialists across all treatments; Table 5) hints at the importance of other factors—e.g., nutrients—in enabling some plants to become invasive (e.g., Lorenzen et al., 2001; Kercher and Zedler, 2004). Further experimental tests of invasive versus noninvasive wetland taxa under a range of hydrologic regimes should be combined with a range of nutrient levels to elucidate the independent and interacting roles of flooding and nutrients, as well as to determine the thresholds at which noninvasive species are favored over the invasives.

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Effects of sampling teams and estimation methods on the assessment of plant cover

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Abstract. We evaluated variability in cover estimation data obtained by (1) two sampling teams who double sampled plots and (2) one team that used two methods (line intercepts and visual estimation of cover classes) to characterize vegetation of herbaceous wetlands. Species richness and cover estimates were similar among teams and among methods, but one sampling team scored cover higher than the other. The line intercept technique yielded higher cover estimates but lower species richness estimates than the cover class method. Cluster analyses of plots revealed that 36% and 11% of plots sampled consecutively by two teams or using two methods, respectively, were similar enough in species composition and abundance to be paired together in the resulting clustering tree. Simplifying cover estimate data to presence/absence increased the similarity among both teams and methods at the plot scale. Teams were very similar in their overall characterization of sites when cover estimation data were used, as assessed by cluster analysis, but methods agreed best on their overall characterization of sites when only presence/absence data were considered. Differences in abundance estimates as well as pseudoturnover contribute to variability. For double sampled plots, pseudoturnover was 19.1%, but 57.7% of pseudoturnover cases involved taxa with $\leq 0.5\%$ cover while only 3.4% involved taxa with $> 8\%$ cover. We suggest that vegetation scientists incorporate quality control, calibrate observers and publish their results.

Keywords: Cover class; Line intercept; Observer bias; Observer error; Pseudoturnover; Quality control; Sampling error; Wisconsin.

Introduction

Scientists are increasingly held to high standards for the quality of their data by both reviewers and funding agencies (Anon. 1998). The goal of quality control is to quantify and understand variation and ensure that data meet defined standards of quality, not to eliminate error or variation in the data (Anon. 1996). Despite increasing requests for scientists to quantify and control error in their data, few examples of quality control have appeared in vegetation science literature. Quality control in vegetation sampling requires that sources of variation and the contribution of those sources to the overall variation of the vegetation sample are identified. Of the two general components of variation in data, the accuracy of the sample is of obvious importance but is very difficult to assess, particularly in large-scale field surveys under typical constraints of labour and time shortages. The precision of the sample involves the degree of similarity among measured values without regard to accuracy (Gotfryd & Hansell 1985).

Vegetation sampling precision may be influenced by different observers and type of sampling method used (e.g. cover class vs line intercept). The effect of different observers is generally believed to be an important contributor to variability in the data set (Smith 1944; Lamacraft 1978; Sykes et al. 1983; Gotfryd & Hansell 1985; Nilsson & Nilsson 1985; Kirby et al. 1986; West & Hatton 1990; Lepš & Hadincová 1992; Rich & Woodruff 1992; Rich & Smith 1996; Klimeš et al. 2001), though Oredsson (2000) reported negligible observer error compared to other errors. Likewise, there may be variability attributable to the sampling method(s) chosen by researchers (e.g. Kirby et al. 1986; Rich & Woodruff 1992). Some scientists find reasons to doubt the efficacy of particular methods (e.g. Smith 1944; Guo & Rundel 1997; Oredsson 2000). For example, in a newsletter of the International Association of Vegetation Scientists, Wilson (unpubl.) equated estimating cover by eye to 'guessing cover' and expressed doubt

that even a line intercept method could assess cover accurately in a stand of mixed herbaceous species. He concluded that presence/absence data are the only acceptable alternative. Others argue that even subjective measures, such as cover, are valuable because they add extra information (e.g. Sykes et al. 1983).

The need for quality control of vegetation surveys has been recognized since at least the 1940s (Hope-Simpson 1940; Smith 1944). Considering the temporal limitations, shortages of labour and differences in observer expertise and experience in most large-scale field surveys, the challenge for plant ecologists is to find vegetation sampling methods that are robust (repeatable) across observers and yet efficient in the effort required to characterize the vegetation adequately. We present results from two field research projects in Wisconsin, USA. Each was designed to characterize the species composition and cover within temperate wetland communities dominated by herbaceous grasses, sedges and forbs. We asked:

1. How do sampling teams affect the reporting of species composition and cover? Are biases detectable and, if so, are they attributable to the growth form of the plants?
2. How well does a cover class estimation method match a line intercept sampling method? Are broad cover classes more repeatable than fine classes?

Methods

Two data sets from two separate studies were used. We compared two sampling teams in the first project (southern Wisconsin wet meadows) and two sampling methods in the second project (Lake Michigan wetlands).

Data set 1: Sampling team variability

Twelve wet meadows in Dane County, Wisconsin were sampled by two teams from 10.07-20.07.2000. A sampling team consisted of two trained field botanists. All four botanists were graduate students in Botany or Environmental Studies, and all four had completed an intensive three week summer field course in wetland plant identification in southern Wisconsin.

Ten 1 m × 1 m plots were sampled consecutively ('double sampled') by the two teams (hereafter called Team A and Team B) on each site, for a total of 120 double sampled plots across the 12 sites. Every 9 m along a 90 m transect line, a team would walk a random distance of 1 - 25 m away from and perpendicular to the transect line and place a three sided square PVC frame on the ground. After being sampled by the first team, the corners of the plots were marked so that the second team could locate them.

Within a plot, species were assigned to one of nine cover classes in the log₂ system (Gauch 1982):

1 = ≤ 0.5%; 2 = 0.5-1%; 3 = 1-2%; 4 = 2-4%; 5 = 4-8%;
6 = 8-16%; 7 = 16-32%; 8 = 32-64%; 9 = 64-100%.

Small PVC frames representing the different cover classes were available for use as needed to 'calibrate' the sampling teams. Unknown taxa were collected, pressed, dried and identified by a professional taxonomist (T. Cochrane) at the University of Wisconsin-Madison Herbarium.

Data set 2: Comparison of two vegetation sampling methods

Two methods for estimating plant abundance were compared as part of the Great Lakes Environmental Indicators project. This data set was collected from eight coastal wetlands on the coast of Green Bay and nearby Lake Michigan, Wisconsin, USA. A total of 270 plots were sampled across the eight wetlands; the number of plots sampled on each site was proportional to the area of the wetland.

In each wetland 1 m × 1 m plots were placed in a stratified random design along randomly placed transects that ran nominally perpendicular to the water gradient. Each plot was randomly located within every 20-m interval of the transect, with the exception of a non-random plot that was placed at the wet end of the transect. Plots were situated directly adjacent to the transect line. Within plots, the abundance of each plant species was estimated using a cover class method and a line intercept method. The cover class system was a modified Braun-Blanquet method using six cover categories:

1 = <1%; 2 = 1-5%; 3 = 5-25%; 4 = 25-50%; 5 = 50-75%;
6 = 75-100%.

For the line intercept method, two 1-m sticks were placed within the plot 25 cm and 75 cm from one side and perpendicular to the transect. Each stick was divided into 10 cm intervals and the number of intervals each plant species intercepted was recorded.

Prior to analysis of data set 2, cover class and line intercept data were transformed into percentages. This was done by taking the midpoint of each cover class and the percent of line intervals crossed by a species, respectively.

Data analyses

For data set 1, we compared the species richness values and sums of cover classes reported by the two teams for the double sampled plots using paired *t*-tests and correlation coefficients (*r*). To compare the teams' reporting of the species composition and abundances within plots, the ten double sampled plots from each of

the 12 sites were subjected to a divisive hierarchical cluster analysis using non-standardized Euclidean distances in S-plus 2000 (Anon. 2000). Prior to all cluster analyses, cover class data were transformed into percentages by taking the midpoint of each cover class. Plots were first clustered using the \log_2 system. The analysis was repeated three times, once with cover classes reduced to six categories:

1 = < 4%; 2 = 4-8%; 3 = 8-16%; 4 = 16-32%; 5 = 32-64%; 6 = 64-100%;

then with three cover categories:

1 = < 8%; 2 = 8-32%; 3 = 32-100%;

and finally with presence/absence categories only.

For data set 2, paired *t*-tests and correlation coefficients were calculated to compare the species richness and species abundance estimates for (1) one vs two lines, (2) one line vs cover class and (3) two lines vs cover class. Divisive hierarchical cluster analyses were also used to compare vegetation sampling methods, again considering each of the eight sites separately. In both cluster analyses, the plots that were sampled twice by different teams or by different methods were considered to be 'paired correctly' in the clustering tree if they occupied the same ultimate branch.

Jaccard's and Horn's indices (Brower et al. 1990) were used to assess the similarity of results reported by two sampling teams (using data set 1) and sampling methods (using data set 2) at three different analytical scales. To assess overall similarity, we calculated the mean percent cover of all species sampled by each team across all 12 sites. To compare methods we calculated mean percent cover and frequency values for each species sampled across all eight sites. On the scale of sites, we calculated the similarity among teams or methods by tabulating the mean percent cover values for all species reported from each team or method on a site, and then allowed the differences within each of the 12 or eight sites, respectively, to contribute additively to the final coefficient. On the scale of individual plots, differences among teams or methods within each of the 120 or 270 plots, respectively, contributed additively to the final coefficient.

Results

Sampling team variability (data set 1)

The number of species recorded by the two teams was highly correlated ($r = 0.95$) and 44 out of 120 (36.7%) of the double sampled plots were on the line of no difference (Fig. 1). A paired *t*-test showed no difference between the two teams in species counts in the 120 plots (mean \pm s.e., Team A 9.8 ± 0.5 , Team B 10.0 ± 0.5 ; $t = -1.1$; $df = 119$; $P = 0.27$). Team records for number of taxa in a plot differed by 1.2, on average. Thirty-nine plots differed in the presence of one taxon, 20 plots differed by two taxa, 10 plots by three taxa, four plots by four taxa, two plots by five taxa and one plot by six taxa.

Sums of cover classes per plot were highly correlated for the two teams ($r = 0.92$), but only 16 plots (13.3%) were on the line of no difference (Fig. 1). The sum of cover classes per plot was slightly, but significantly, greater for Team B (31.7 ± 1.2) than Team A (29 ± 1.1 ; $t = -5.37$; $df = 119$; $P < 0.0001$). For sum of cover classes, 22 plots differed by one cover class unit, 9 plots by two units, 11 by three and four, 7 by five and six, 16 by 7, 6 by 8, 3 by 9, 4 by 10, 3 by 11 and one by 12, 13, 14, 15 and 27. There were no large differences among teams in their estimation of the cover of major growth forms (grasses/graminoids, forbs and mosses) that would indicate cover was more difficult to judge in one or more of these three general groups of plants, although Team B scored cover for forbs slightly higher than Team A (Table 1). There was a significant negative relationship between the number of occurrences of a taxon and the percentage of times cover classes differed among teams for that taxon ($r = -0.47$; $F = 37.4$; $df = 132$; $P < 0.0001$).

Pseudoturnover is defined as

$$(A + B)/(S_A + S_B) \times 100, \quad (1)$$

where *A* and *B* are the number of exclusive species found by Team A and Team B, respectively, and S_A and S_B are the total number of species found by Team A and Team B, respectively (Nilsson & Nilsson 1985). The

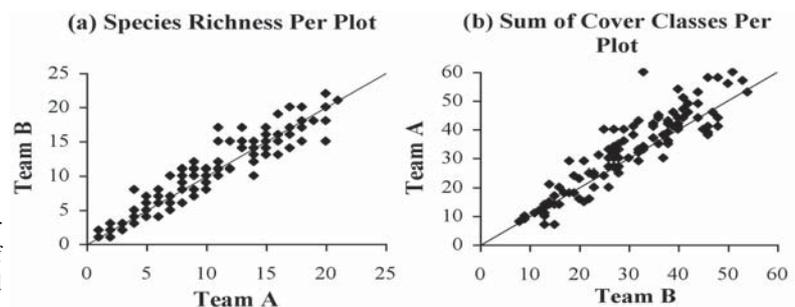


Fig. 1. Comparison of two sampling teams for (a) species richness per 1 m² plot and (b) sum of cover classes per plot. *N* = 120 double sampled plots. The line shown is the line of no difference.

Table 1. Summary of the number of occurrences (N), mean cover class (\pm s.e.) for forbs, grasses/graminoids and mosses as reported separately by two sampling teams in $n = 120$ double sampled plots.

Team	Forbs	Grasses/graminoids	Mosses
Team A	$N = 791$ Mean cover class $2.50 (\pm 0.06)$	$N = 367$ Mean cover class $3.99 (\pm 0.14)$	$N = 22$ Mean cover class $1.55 (\pm 0.17)$
Team B	$N = 792$ Mean cover class $2.82 (\pm 0.06)$	$N = 379$ Mean cover class $3.96 (\pm 0.12)$	$N = 30$ Mean cover class $2.13 (\pm 0.22)$

overall mean pseudoturnover for double sampled plots was $19.1 \pm 1.2\%$ ($n = 120$). Separated by site, pseudoturnover ranged from $9.3 \pm 6.5\%$ ($n = 10$) at Nine Springs Meadow to a high of $30.5 \pm 2.5\%$ ($n = 10$) at Cherokee Ditch (Table 2). A large portion (57.7%) of pseudoturnover was attributable to taxa given the lowest cover class ($< 0.5\%$ cover). Only 3.4% of pseudoturnover was caused by taxa with cover classes six to nine (i.e. $> 8\%$ cover).

The total number of exclusive species found by each team (A + B in the pseudoturnover calculation above) was significantly, positively related to plot species richness ($r = 0.81$; $F = 229.3$; $df = 119$; $P < 0.0001$). Total plot richness also showed significant positive relationships with (a) total number of cases per plot in which the teams did not match exactly on their reporting of cover classes ($r = 0.83$; $F = 261.8$; $df = 119$; $P < 0.0001$) and (b) the total sum of cover class differences per plot ($r = 0.65$; $F = 86.0$; $df = 119$; $P < 0.0001$).

A minority of the double sampled plots (43 out of 120, 36%) was paired correctly in the 12 clustering trees (Table 3). No sites had more than six out of ten double sampled plots paired together when the nine class \log_2

Table 2. Mean pseudoturnover and standard error (s.e.) for the 12 sites sampled (listed alphabetically), $n = 10$ double sampled plots per site and the mean number of species sampled per 1 m^2 plot, based on the 30 unique plots sampled per site. Mean pseudoturnover and mean species richness m^{-2} were highly correlated ($r = 0.81$).

Site	% Pseudoturnover	s.e.	Mean no. spec. m^{-2}
Arboretum Pond	27.5	1.9	13.4
Cherokee Ditch	30.5	2.5	15.5
Cherokee Fen	24.5	2.5	17.7
Cherokee Marsh	15.1	3.1	7.5
Nine Springs Ditch	13.7	6.0	2.3
Nine Springs Fen	19.1	2.0	12.7
Nine Springs Meadow	9.3	6.5	2.2
Pheasant Branch Fen	28.1	4.6	14.3
Pheasant Branch Pond	20.4	2.8	10.3
Southeast Marsh	17.8	2.9	7.0
Syene Road Meadow	12.5	3.8	12.1
Wingra Marsh	11.1	2.9	5.8

Table 3. Number of double-sampled plots that were correctly paired (out of ten possible per site) in a divisive hierarchical cluster analysis using different cover class systems: (1) nine cover classes (\log_2 ; Gauch 1982); (2) six classes (see Methods); (3) three classes (see Methods) and (4) presence/absence information only. The results of a one-way ANOVA were highly significant ($P < 0.0001$), with more plots paired using presence/absence data than cover estimation data.

Site	9 Classes	6 Classes	3 Classes	Pres/Abs
Arboretum Pond	4	7	7	10
Cherokee Ditch	5	4	5	5
Cherokee Fen	1	2	2	5
Cherokee Marsh	0	0	1	9
Nine Springs Ditch	2	2	2	5
Nine Springs Fen	4	4	3	9
Nine Springs Meadow	6	6	7	8
Pheasant Branch Fen	5	5	10	9
Pheasant Branch Pond	2	2	3	6
Southeast Marsh	3	3	1	9
Syene Road Meadow	6	3	5	7
Wingra Marsh	5	5	3	8
Total plots paired	43	43	49	90

system was used. When we pooled cover classes to obtain six or three classes, there was no significant change in the number of correctly paired double sampled plots. However, when presence/absence data were used, the number of correctly paired plots increased significantly to 90 out of 120, or 75% (Table 3; $F = 9.1$; $df = 47$; $P < 0.0001$).

When the ten double sampled plots sampled on a site by a single team were combined to create a single composite vegetation for that site/team and the sites were subjected to cluster analysis, the 12 sites as sampled by Team A were correctly paired with their respective sites as sampled by Team B in the resulting tree, both when cover data and when presence/absence data were used.

Across the three analytical scales (overall, site and plot), the similarity of sampling results reported by two sampling teams using presence/absence data (Jaccard's coefficient) was 0.797, 0.693 and 0.642, respectively. The similarity of quantitative vegetation sampling results (Horn's index) for the teams was 0.894, 0.832 and 0.855 at the overall, site and plot scales, respectively.

Comparison of two sampling methods (data set 2)

The correlation between number of species per plot using the cover class method and the line intercept method was high for one line ($r = 0.84$) and both lines combined ($r = 0.92$). However, when the results for the line intercepts were plotted against the results for the cover class method, species richness values fell below the line of no difference while abundance values fell above the line of no difference (Fig. 2). The line inter-

cept method detected significantly fewer species per plot than the cover class method, both when one line was considered (7.3 ± 0.3 for the cover class method vs 4.2 ± 0.1 for one line intercept; $t = 16.4$; $df = 267$; $P < 0.0001$) as well as when the two lines were considered together (5.4 ± 0.2 for two line intercepts; $t = 14.4$; $df = 267$; $P < 0.0001$; Fig. 2).

Correlation between the two methods for species cover estimates was high ($r = 0.79$ when one line intercept was considered and $r = 0.80$ for two lines), but again paired t -tests showed that species cover differed significantly for the two methods ($t = -35.5$; $df = 2347$; $P \ll 0.0001$), with lower mean percent cover estimates resulting for the cover class method (17.9 ± 0.6 for the cover class method vs 36 ± 0.8 for one line and 36.4 ± 0.8 for two lines; Fig. 2). When species were separated by growth form (grasses/graminoids, forbs, aquatic plants and woody plants), t -tests showed significant differences ($P < 0.005$) for all except woody vegetation at the overall and site scales ($P = 0.15$ and 0.058 , respectively) and aquatic vegetation at the overall and site scales ($P = 0.33$ and 0.31 , respectively).

Thirty out of the 270 plots sampled using cover classes were paired correctly in the clustering trees with those sampled using line intercepts. This number decreased to 25 when both lines were considered and increased to 36 when the line intercept segments were doubled in length to 20 cm each, but neither change was statistically significant ($P = 0.095$ and 0.17 , respectively). However, when presence/absence data were used, the number of correct pairs increased significantly to 136, or 50% ($P = 0.005$). When the cluster analysis was carried out to evaluate sites, four of the eight sites paired correctly when cover data were used, but all eight sites paired correctly when presence/absence data.

Across the three analytical scales (overall, site and plot), the similarity of sampling results for the two sampling methods using presence/absence data (Jaccard's coefficient) was 0.752, 0.656 and 0.630, respectively. Similarity of quantitative vegetation sampling results (Horn's index) for the two methods was 0.931, 0.921 and 0.868 at the overall, site and plot scales, respectively.

Discussion

In vegetation surveys, we need to know the degree to which we can rely on differences among plots and sites as being real or due to sampling error. Although reports of quality control are quite rare in the literature of vegetation surveys we, and others, find differences attributable to sampling team and sampling method that underscore the need to adopt quality control methods.

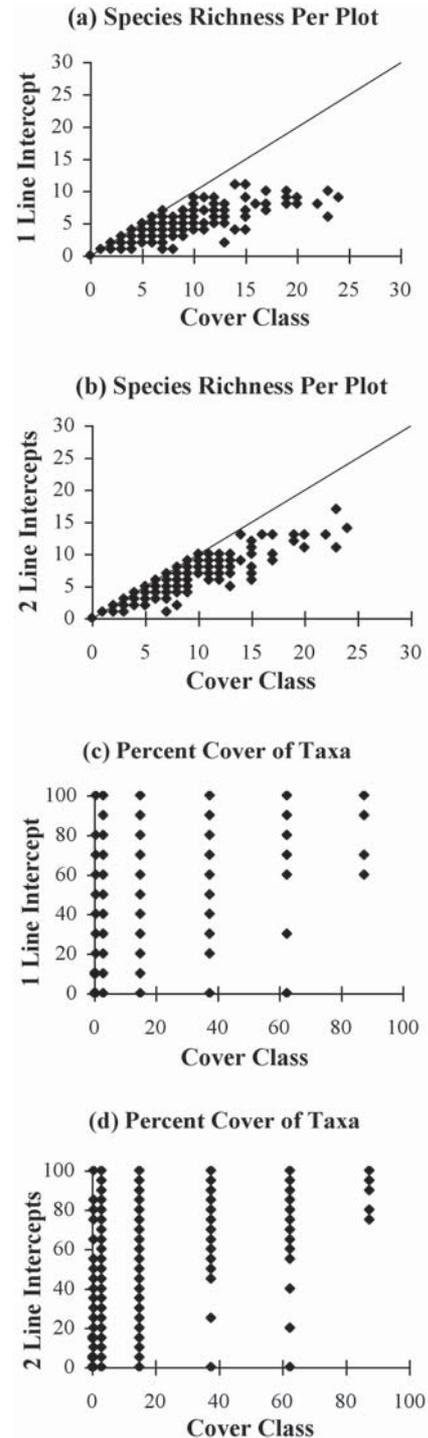


Fig. 2. Comparison of cover class and line intercept sampling methods for species richness (a, b), and percent cover of taxa present (c, d) in $N = 270$ plots. Results for the line intercept method are presented using data from one line only (a, c) or two lines (b, d) per plot. Cover class and line intercept data were transformed into percentages by taking the midpoint of each cover class and the percent of line intervals crossed by a species, respectively. The line shown is the line of no difference.

Quality control allows us to improve vegetation sampling designs by ranking/quantifying sources of variation and identifying errors and biases attributable to the specific sampling approaches used.

Sampling teams increased variability

Two well-trained, skilled sampling teams produced highly correlated results for (1) number of species per plot and (2) sum of all cover classes recorded per plot, two general descriptors of difference that are readily obtained. Few of the records were identical for species richness, but there was no apparent bias between teams for recording numbers of species. Thus, teams agreed on composite measures at the whole survey scale. At the scale of sites and individual plots, however, most plots (100 out of 120 cases) showed some pseudoturnover, and the mean overall pseudoturnover was 19.1% per plot, nearly twice that reported by Nilsson & Nilsson (1985) for two teams sampling vascular plants on 41 islands in southern Sweden (11.4%). It was also much higher than the 13% found by Lepš & Hadincová (1992) comparing two observers who sampled 25-m² plots in oligotrophic meadows, but similar to the 24% reported by Scott & Hallam (2003) within 0.16-m² plots across a range of habitat types. Since a majority of errors in our study involved taxa with the lowest cover classes, our high pseudoturnover rate could be attributable to a prevalence of rare, sterile or immature plants that were easily overlooked or misidentified (Klimeš et al. 2001). In addition, plot placement could have contributed to the high pseudoturnover since plot frames were not kept in place, but the corners of the plot were marked with flags by the first team for the second team to place their frame and sample the plot independently. Thus, slightly different boundaries could have led to the inclusion or exclusion of taxa along the 4 m of edge. If the first team leaves its sampling frame in place until the second team has sampled the plot the accuracy of pseudoturnover estimates would probably increase, but teams sampling sites independently would be more likely to produce greater differences in species lists.

A second source of variability in our study was an apparent team bias in the reporting of cover classes in the log₂ system: Team B tended to score cover higher than Team A. In contrast, Lepš & Hadincová (1992) found no evidence for observer bias in the reporting of cover classes using the Braun-Blanquet method in meadows with herbaceous vegetation types similar to those in our study. There was no obvious tendency for some taxa to show greater variability in cover estimates than others, and there were no large differences among teams in their estimation of the cover within the broad categories forbs, grasses/graminoids and mosses that would indicate any of these growth forms was more difficult to

estimate than the others. In contrast, Sykes et al. (1983) found that observer error was highest for taxa with thin leaves and lowest for taxa with broad leaves, although this error was not consistent within or among observers.

Many of the disagreements were for lower cover classes, which may reflect the preponderance of low cover classes in the log₂ system, but disagreements also occurred for moderately abundant species, with deviations of two or more classes. Overall, there is reason to doubt that teams can agree exactly on cover class estimation. In this study, cover class estimates were made under similar conditions – teams were in the field together, sampling the same transect at the same time, under the same weather conditions and with similar degrees of fatigue. They did not consult on individual plots, but they were able to cross check intermittently. Differences would probably have been greater if these commonalities were lacking.

Variability among teams in cover estimates, as well as pseudoturnover, increased with increasing numbers of species in a plot; this demonstrates an additive effect of observer variability that can probably be ameliorated only through increasing awareness of the phenomenon by sampling crews and perhaps allocating more time and energy to species-rich plots. There was no detectable improvement in team precision over time. We attempted to relate both pseudoturnover and the number of cases in which cover classes disagreed between the two teams with the order in which sites were sampled, but we found a strong pattern in the residual plot, probably indicating site species richness was confounding the result.

The number of correctly paired double sampled plots increased from 43 to 90 out of 120, or from 36% to 75%, when we replaced cover classes with presence/absence data. This result lends some support to Wilson's (unpubl.) assertion that presence/absence data are best, but once again highlights the dual problems of (1) cover class discrepancies and (2) pseudoturnover among the sampling teams, since substitution of cover class data by presence/absence categories did not resolve all discrepancies. Reporting of cover classes can probably be improved only marginally. The subjectivity of cover classes was suggested as early as the 1940s (reviewed in Lepš & Hadincová 1992). Reduction of cover class categories from nine to six to three revealed no improvement in the number of correctly-paired plots, but this reduction was done *a posteriori* and results may have differed if teams had tested different cover class systems in the field. Team biases in cover estimation might be resolved with frequent, formal visual recalibration episodes before sampling each site, although we did not test this approach.

A majority of double sampled plots were not paired in the cluster analyses when cover data were used, but these many plot scale discrepancies had little bearing at

the scale of whole sites. The whole site cluster analysis showed that all 12 sites paired correctly, even though the sites often represented very similar habitat types with many of the same dominant species. Thus the information on species abundance that would be lost in abandoning cover estimation methods may not be justified, particularly for vegetation studies that focus on differences among sites rather than individual plots and that employ multivariate analysis techniques. Lepš & Hadincová (1992) also found robust results using both numerical ordination and classification analyses, suggesting an insensitivity of multivariate methods to sampling errors (but see Gotfryd & Hansell 1985).

Pseudoturnover can be reduced in some cases. Klimeš et al. (2001) report substantial observer variation in the identification of small, rare, sterile plants but warn that efforts to train individuals to identify plants at all ontogenetic stages are counter productive and will not improve the error rate. Instead, they recommend that at least three observers work together and discuss all problems in the field. We found that pseudoturnover due to sampling team occasionally involved dominant or subdominant taxa as well as rare taxa. Some of the errors involving higher cover class categories were identifiable (probable field recording errors and/or misidentifications) and some were not, which makes it difficult for us to recommend a single course of action. However, in a study that spanned numerous habitat types, Scott & Hallam (2003) estimated that 5.9% of specimens were misidentified at species level and 1.9% at genus level.

Our findings highlight the difficulties of identifying some very common taxa, especially sterile specimens e.g. *Aster* spp., *Typha* spp. and *Carex* spp. Clearly, a consensus should be reached among sampling teams on the level of identification required of difficult taxa before sampling begins, based on both the available literature and the advice of expert taxonomists. This would probably entail a reconnaissance survey of the sites to generate initial species lists before intensive quantitative sampling begins. Alternatively, agreements can be reached after sampling but before data are analysed.

Sampling methods produced different results

Two different sampling methods produced highly correlated results for species richness and cover, although there were two biases: cover classes resulted in higher species counts than line intercepts, and line intercepts produced higher estimates of cover. The use of two line intercepts instead of one barely (in the case of cover estimates) or modestly (in the case of species richness) improved the correlation between the two sampling methods. The similarity between the two methods also increased with the scale of analysis.

The high correlations between the sampling methods for general measures of composition and abundance suggest that the two sampling methods capture the same overall information about the vegetation. However, multivariate cluster analyses revealed that the cover class and line intercept methods for assessing species composition and abundance in wetlands produced different results at the plot scale most of the time. Doubling the number of transect lines did not increase the similarity with the cover class method and because abundance as measured by the line intercept was divided into more classes (ten) than the cover class method (six), we repeated the cluster analysis after combining line intercept classes to halve the number, but again this did not improve similarity of the two methods. Only reduction of cover data to presence/absence significantly increased the number of both plots and sites that were paired correctly in the cluster analyses, results which support skepticism of the use of cover estimation techniques in vegetation analyses.

When species were divided by growth form, only submerged aquatic plants and woody plants showed no significant difference in cover between the two methods. In the case of submerged aquatics, this may be because these plants occurred in few plots and when they did occur they covered large contiguous areas. Similarity between the two sampling methods is improved in this case because such widespread species are rarely missed by the line intercept method. Woody plants also occurred in few plots, but at low abundances. This would lead to greater similarity between methods because woody species missed by the line intercept method (scored as zero) would still be similar to a cover class of one.

Conclusions

We conclude that sampling team and sampling method contributed substantially to the overall variability of vegetation sampling. We recommend that all vegetation surveys incorporate quality control studies and that all members of a vegetation survey crew be trained together in field identification and sampling techniques. Multi-year studies will benefit from annual workshops to review taxa and recalibrate sampling techniques. We suggest initial site visits to generate species lists and consultation with professional taxonomists about taxa that are difficult to identify in order to reduce misidentification. When multiple observers conduct the sampling, we advise double sampling of plots and calculation of pseudoturnover as part of the quality control analysis. Plot frames should be left in place for re-sampling. We suggest the use of cluster analysis for

comparing both sampling teams and sampling methods at the scale of plots and sites. Finally, we strongly recommend that researchers include quality control results in their publications, so that others can benefit from the knowledge gained.

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RESEARCH ARTICLE

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Interrelationships
of Hydrologic
Disturbance, Reed
Canary Grass
(*Phalaris arundinacea*
L.), and Native Plants
in Wisconsin Wet
Meadows

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ABSTRACT: Twelve wet meadows in Dane County, Wisconsin showed vegetation patterns that correlate with hydrologic disturbance and presence of a clonal invasive grass, *Phalaris arundinacea* L., at two scales, 4500-m² (0.45 ha) “sites” and 1-m² plots. Sites with indicators of hydrologic disturbance had lower species richness and diversity than reference sites, and species richness, diversity, and mean coefficients of conservatism (Mean C) were inversely related to the abundance of *Phalaris* on sites. Within 1-m² plots, 5.5 ± 0.4 (SE) species coexisted with *Phalaris*, while about twice as many coexisted with two widespread native graminoids: 11.5 ± 0.3 with *Carex stricta* Lam. and 10.6 ± 0.3 with *Calamagrostis canadensis* (Michx.) Beauv. Cover of *Phalaris* was approximately six times higher in plots on sites with disturbance indicators than on reference sites. Overall, plots with either *Phalaris* or hydrologic disturbance had 2/3 the species of plots lacking *Phalaris* on reference sites, as well as lower diversity and Mean C. These results suggest a strong negative effect of hydrologic disturbance or presence of *Phalaris* on the quantity and quality of species in a wetland. When *Phalaris* and disturbance indicators co-occurred, the difference was more severe. Plots with *Phalaris* on disturbed sites had 1/3 the species of reference plots and the lowest diversity and Mean C. Species were grouped into seven “response types” based on apparent sensitivity to the presence of *Phalaris* and hydrologic disturbance. Only the clonal grass *Phragmites australis* (Cav.) Trin. ex Steud. responded positively to the combination of *Phalaris* and hydrologic disturbance.

Index terms: *Carex stricta*, invasive species, mean coefficient of conservatism (Mean C), sedge meadows, species richness

INTRODUCTION

Soil hydrologic conditions are considered the most important factor in the establishment and maintenance of specific types of wetlands and wetland processes (Mitsch and Gosselink 1993, Silvertown et al. 1999, Keddy 2000). The source of water for a wetland determines both the water chemistry and hydroperiod (Brinson 1993, e.g., Hunt et al. 1999) and influences the types of plant species that can establish and grow there (Goslee et al. 1997, Godwin et al. 2003, Kraemer 2003).

Urbanization causes both major and subtle changes in the hydrologic regimes of wetlands. Construction of stormwater sewers or drainage ditches can increase surface flow into wetlands or decrease water table depth. Increased area of impervious surfaces in the watershed may increase the frequency and severity of flooding (Watson et al. 1981, Pitt 1996). At the same time, groundwater-fed wetlands can be profoundly affected by municipal pumping of groundwater and diversion of recharge (infiltration) by impervious surfaces in urbanized areas – phenomena that often appear to be decoupled from influences on wetlands (Brinson 1993).

Few studies link specific hydrologic disturbances with vegetation characteristics, but hydrologic changes are suspected to

be responsible for the spread of some invasive species (Galatowitsch et al. 1999). Galatowitsch et al. (2000) found landscape-scale associations between stormwater runoff and introduced perennials in the prairie pothole region of Minnesota. The introduced perennials are often undesirable invasive species, either exotic in origin (e.g., *Lythrum salicaria* L.) or possibly hybrids of exotic and native strains (e.g., *Typha X glauca*, *Phalaris arundinacea* L.).

In July of 2000, we surveyed vegetation in three reference-wet meadows and in nine wet meadows with visible indicators of hydrologic disturbances (e.g., drainage ditches, stormwater basins, proximate municipal wells) in Dane County, Wisconsin. Our objectives were: (1) to determine if hydrologic disturbances correlated with patterns in the distribution and abundance of plant species, and (2) to describe species associations both on the scale of whole sites (measuring 4500-m², or 0.45 ha) and within 1-m² plots.

We hypothesized that lower species richness and diversity would occur on sites with indicators of hydrologic disturbances present. Likewise, we predicted that invasive species would correlate with low diversity at the scale of both sites and plots. Finally, we asked if mean coefficient of conservatism (Mean C), a measure of floristic

quality, was related to presence of *Phalaris arundinacea* and/or disturbance.

METHODS

Twelve wet meadows were grouped into two categories: (1) reference sites, for which no indicators of hydrologic disturbance were visible, and (2) sites with indicators of hydrologic disturbance apparent either within the site or in adjacent areas (Table 1). The indicators were existing structures, including stormwater sewer outlets and basins, drainage ditches, and nearby municipal wells.

Landscape Setting

All sites are located within the Yahara River watershed near Madison, Wisconsin (Figure 1). All are slightly (0.5 to 1.5 m) above the levels of the present chain of Yahara Lakes (Mendota, Wingra, Monona, Waubesa; Table 1). Fine-grained glacio-lacustrine deposits from the extensive glacial lake(s) that formed at the close of the Pleistocene cover much of the lower portion of the landscape; these deposits form aquitards that encouraged wetland formation, especially in the shallow bays of the post-glacial Yahara Lakes. Houghton

Mucks (Typic Medisaprists) and Palms Mucks (Terric Medisaprists) are common in former bays. Slightly above these and along drainageways, lineal wetlands form over the glacio-lacustrine deposits but do not form histosols because they are only intermittently saturated. Common series include Orion (Aquic Udifluvents) and Wacousta (Typic Haplaquolls).

Site Descriptions

Three study sites were located in the Cherokee Marsh wetland complex north of Lake Mendota. Originally a continuous wetland

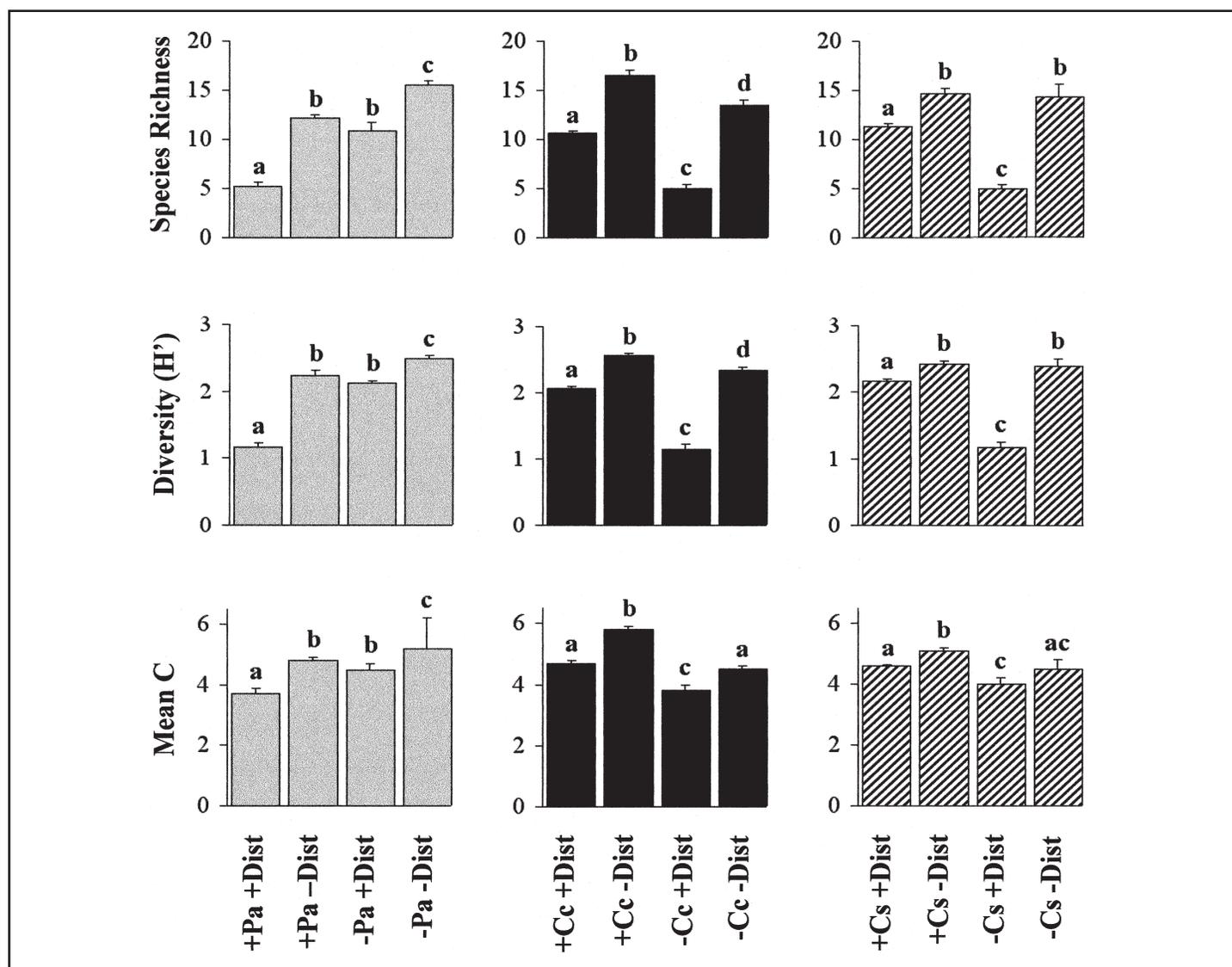


Figure 1. Summary of vegetation patterns in relation to presence/absence (\pm) of *Phalaris arundinacea* (\pm Pa), or *Calamagrostis canadensis* (\pm Cc), or *Carex stricta* (\pm Cs) and \pm disturbance indicators. Data are for 1-m² plots. All nine one-way ANOVAs were significant at $P < 0.0001$. Within graphs, different letters indicate means that differed significantly following LSD tests. Sample sizes: +Pa +Dist n=115; +Pa -Dist n=26; -Pa +Dist n=155; -Pa -Dist n=64; +Cc +Dist n=167; +Cc -Dist n=34; -Cc +Dist n=103; -Cc -Dist n=56; +Cs +Dist n=146; +Cs -Dist n=76; -Cs +Dist n=124; -Cs -Dist n=14.

of ca. 2000 ha, the area now suffers from filling for an airport, agricultural drainage ditches, and stormwater drainageways. A 50-ha core area remains unaltered except for a drainageway (Cherokee Marsh-CM). Along the boundary of the undisturbed core and the last drainage ditch, we established side-by-side study sites with Cherokee Ditch (CD) proximate and Cherokee Fen (CF) distal to the ditch.

Two study sites were located in the Pheasant Branch wetland complex at the west end of Lake Mendota. Located at the terminus of a natural drainageway, the Pheasant Branch Pond (PBP) site suffered from post-settlement sediment deposition and recent stormwater augmentation from suburban development. In contrast, the Pheasant Branch Fen (PBF) site is located just below the nose of a hill and thus escapes large stormwater flows.

Located at the edge of Lake Wingra, the Wingra Marsh (WM) site is sometimes flooded by stormwater from a nearby golf course and surrounding residential developments. Nearby city water supply and private irrigation wells may also affect the site. Southeast Marsh (SEM) was once part of a connected wetland complex around Lake Wingra, but a berm protecting a sinking housing development coupled with increased stormwater inputs have converted portions of it into a de facto detention pond that can experience a one meter fluctuation in water levels in a 24 h period (unpubl. data). The Arboretum Pond (AP) is located about 1.5 m above Lake Wingra along a natural drainageway that receives conditioned water via a series of detention areas.

The Nine-Springs valley drains into the Yahara River between Lakes Monona and

Waubesa. Deep freshwater lake deposits suggest that it was once a small, narrow lake, but it is now an extensive peatland with numerous large springs along its edges. A road floats across the peat in one area funneling all spring and storm flow through one undersized culvert. One study site above the road and alongside the straightened stream (Nine-Springs Ditch – NSD) and one below the road and a few meters away from the ditch (Syene Road Meadow – SRM) were chosen for contrast. Another site (Nine-Springs Meadow – NSM) suffers from adjacent filling and agricultural development (ponds, ditches) while nearby several areas escaped these intrusions (Nine-Springs Fen – NSF).

During July 10-20, 2000, two teams sampled each of the 12 sites with 1-m² plots using a square PVC frame. The two-person teams sampled 30 plots per site for

Table 1. Descriptions of 12 wet meadows sampled in July 2000, Dane County, Wisconsin, USA. Hydrologic disturbances were present on or adjacent to the site. Reference sites, then sites with indicators of disturbance, are listed alphabetically. Houghton Muck – Typic Medisapristis; Palms Muck – Terric Medisapristis; Waucosta – Haplaquolls; Orion – Udifluvents.

Site Name (abbreviation)	Latitude Longitude	Elevation (m)	Soil Series	Hydrologic Disturbance
Cherokee Fen (CF)	43°10'00" 89°19'45"	259	Houghton	none evident (reference site)
Nine Springs Fen (NSF)	43°01'30" 89°24'15"	259	Houghton	none evident (reference site)
Pheasant Branch Fen (PBF)	43°07'30" 89°24'15"	259	Houghton	none evident (reference site)
Arboretum Pond (AP)	43°02'15" 89°25'30"	259	Waucosta/Orion	overflow from stormwater basin
Cherokee Ditch (CD)	43°10'00" 89°19'45"	259	Houghton	drainage ditch
Cherokee Marsh (CM)	43°10'15" 89°19'15"	259	Houghton	surface runoff
Nine Springs Ditch (NSD)	43°01'45" 89°24'00"	258	Houghton	city wells, ditch, surface runoff
Nine Springs Meadow (NSM)	43°01'30" 89°24'00"	258	Houghton	drainage tiles, ditch
Pheasant Branch Pond (PBP)	43°07'30" 89°28'45"	259	Houghton	overflow from stormwater basin
Southeast Marsh (SM)	43°02'30" 89°24'30"	258	Palms	overflow from stormwater basin
Syene Road Meadow (SRM)	43°01'45" 89°23'45"	258	Houghton	city wells
Wingra Marsh (WM)	43°07'30" 89°26'00"	258	Houghton	city wells, surface runoff

a total of 360 plots. Ten plots per site were double-sampled by the two teams to assess the quality of data (Kercher et al. 2003). Plots were placed along a 90-m transect line stretched across the approximate center of a site. Every 3 meters a team walked a random perpendicular distance (from 1 to 25 m) away from the transect line and laid down a plot. Half of the plots were placed to the right of the line and half to the left.

Survey Methods and Data Analysis

Within plots, all taxa present were recorded and their abundance was estimated using nine cover classes in a Log₂ system (< 0.5%, 0.5-1%, 1-2%, 2-4%, 4-8%, 8-16%, 16-32%, 32-64%, and > 64%; Gauch 1982). Data were analyzed using cover-class midpoints. Nomenclature followed

the PLANTS Database (USDA, NRCS 2002).

Species richness (S), Shannon-Wiener diversity (H') and mean coefficient of conservatism, or Mean C (Swink and Wilhelm 1994), were calculated for each plot and site. Coefficients of conservatism came from a statewide system (Bernthal 2003) where botanical experts assigned coefficients to individual plant species ranging from 0 (weedy) to 10 (found only in undegraded natural communities). Exotic species, including *Phalaris arundinacea*, were not rated and thus did not affect our calculations of Mean C.

For analytic purposes, we divided the plots into four categories based on presence of the invasive grass *Phalaris arundinacea* (Pa) and indicators of disturbance: (1) plots

containing *Phalaris* in sites with indicators of hydrologic disturbance (+Pa +Dist; n = 115), (2) plots lacking *Phalaris* in sites with indicators of hydrologic disturbance (-Pa +Dist; n = 155), (3) plots containing *Phalaris* in reference sites (+Pa -Dist; n = 26), and (4) plots lacking *Phalaris* in reference sites (-Pa -Dist; n = 64). For each of the 30 most frequently encountered taxa in the 360 plots (except *Phalaris*), chi-square analyses were used to test for homogeneity of occurrence within the four categories of plots, using a Bonferroni-corrected alpha of 0.0017. Using both cover estimation and presence/absence data, plots were subjected to Bray-Curtis ordinations in PC-Ord (McCune and Mefford 1997), with overlays of individual taxa, plot species richness (S), Shannon-Wiener diversity (H'), and mean coefficient of conservatism (Mean C).

Table 2. Site-scale summary results for 12 wet meadows sampled in July 2000, Dane County, Wisconsin, USA: (1) the top two most frequently encountered taxa on each site and number of occurrences (out of n=30 plots per site); (2) the two taxa on each site with the highest sum of cover classes (maximum cover per taxon per site=270); (3) total species richness (S); (4) Shannon-Wiener diversity (H'); and (5) mean coefficient of conservatism (C). Summary results are based on the 30 1-m² plots per site. Site abbreviations are explained in Table 1; authorities of taxa are given in Table 4. * denotes a reference site, all other sites had indicators of hydrologic disturbance

Site	Most Frequently Encountered Taxa (number of occurrences)	Taxa With Highest Cover (sum of cover classes)	Conservatism and Diversity		
			S	H'	C
CF*	<i>Solidago gigantea</i> (29) <i>Carex stricta</i> (28)	<i>Thelypteris palustris</i> (153) <i>Carex stricta</i> (130)	54	2.6	5.5
NSF*	<i>Carex stricta</i> (30) <i>Aster puniceus</i> (25)	<i>Carex stricta</i> (208) <i>Aster puniceus</i> (92)	56	2.3	4.2
PBF*	<i>Aster puniceus</i> (25) <i>Equisetum arvense</i> (25)	<i>Aster puniceus</i> (106) <i>Equisetum arvense</i> (85)	68	2.4	4.3
AP	<i>Carex stricta</i> (29) <i>Impatiens capensis</i> (29)	<i>Carex stricta</i> (200) <i>Impatiens capensis</i> (134)	65	2.4	4.2
CD	<i>Aster puniceus</i> (28) <i>Solidago canadensis</i> (28)	<i>Calamagrostis canadensis</i> (121) <i>Thelypteris palustris</i> (108)	57	2.5	4.1
CM	<i>Typha</i> spp. (28) <i>Lysimachia thyrsoiflora</i> (26)	<i>Typha</i> spp. (151) <i>Lysimachia thyrsoiflora</i> (99)	29	1.8	4.3
NSD	<i>Phalaris arundinacea</i> (29) <i>Phragmites australis</i> (22)	<i>Phalaris arundinacea</i> (218) <i>Phragmites australis</i> (149)	11	0.7	3.2
NSM	<i>Phalaris arundinacea</i> (30) <i>Solidago gigantea</i> (6)	<i>Phalaris arundinacea</i> (263) <i>Eupatorium maculatum</i> (22)	14	0.5	4.4
PBP	<i>Impatiens capensis</i> (30) <i>Carex stricta</i> (28)	<i>Carex stricta</i> (164) <i>Impatiens capensis</i> (128)	40	2.1	4.0
SM	<i>Carex stricta</i> (28) <i>Calamagrostis canadensis</i> (28)	<i>Carex stricta</i> (165) <i>Calamagrostis canadensis</i> (151)	31	1.7	4.4
SRM	<i>Solidago canadensis</i> (29) <i>Carex stricta</i> (29)	<i>Solidago canadensis</i> (153) <i>Rubus strigosus</i> (131)	43	2.3	4.4
WM	<i>Impatiens capensis</i> (30) <i>Calamagrostis canadensis</i> (25)	<i>Phalaris arundinacea</i> (165) <i>Impatiens capensis</i> (126)	31	1.5	4.1

Plots were also divided into \pm disturbance categories to examine the patterns of S, H', and Mean C, for plots with and without two other major dominant species sampled in our study: the native sedge *Carex stricta* Lam. and the native grass *Calamagrostis canadensis* (Michx.) Beauv. One-way ANOVAs, two-tailed t-tests, and simple linear regressions were performed in Minitab (Minitab, Inc. 2000), using $\alpha = 0.05$.

RESULTS

Site Scale

The survey found 116 species. Site species richness (based on $n = 30$ plots) ranged from 11 species at Nine Springs Ditch to 68 at Pheasant Branch Fen; site diversity (H') ranged from 0.5 at Nine Springs Meadow to 2.6 at Cherokee Fen; and Mean C ranged from 3.2 at Nine Springs Ditch to 5.5 at Cherokee Fen (Table 2). The nine hydrologically disturbed sites had 35.7 ± 6.0 (mean \pm SE) species, which was significantly fewer than in reference sites (59.3 ± 4.4 , $t = 3.203$, $df = 10$, P

$= 0.01$). Disturbed sites also had lower diversity than reference sites (mean 1.7 ± 0.2 versus 2.4 ± 0.1 , $t = -2.672$, $df = 10$, $P = 0.02$), but there was no statistically significant difference between Mean C on disturbed and reference sites (mean 4.1 ± 0.1 vs. 4.6 ± 0.4 , respectively, $t = -1.66$, $df = 10$, $P = 0.13$).

Most sites were dominated by widely distributed native species, including *Carex stricta*, *Calamagrostis canadensis*, the annual forb *Impatiens capensis* Meerb., and the perennial forbs *Aster puniceus* L. and *Solidago* spp. (Table 2). Four of the nine disturbed sites were dominated by *Phalaris arundinacea*, *Typha* spp., and/or *Phragmites australis* (Cav.) Trin. ex Steud., all of which are tall, clonal perennial taxa that are known to be invasive throughout large areas of North America (Galatowitsch et al. 1999; Table 2). There were moderate to strong negative correlations between the frequency of *Phalaris* on sites and site species richness and diversity ($r = -0.62$ and -0.76 , respectively), and there was a moderate negative correlation between

frequency of *Phalaris* and site Mean C values ($r = -0.47$).

Plot Scale

Within 1-m² plots, species richness ranged from 1 to 22 species (mean \pm SE, 10.0 ± 0.3 , $n = 360$); species diversity (H') ranged from 0 to 2.9 (mean 1.9 ± 0.04), and Mean C ranged from 1 to 7.8 (mean 4.6 ± 0.07). The widespread tussock sedge, *Carex stricta*, was the most frequently encountered species and had the highest total cover summed across all 360 plots, while *Phalaris* was the fifth most frequently encountered species but had the second highest total cover and the highest average cover in plots where it occurred (Table 3). The native bluejoint grass, *Calamagrostis canadensis*, was frequently encountered, but it had, on average, less than half the cover of *C. stricta* and about one-fifth the cover of *Phalaris* when present in plots (Table 3).

The one-way ANOVAs for species richness, H', and Mean C in the four plot

Table 3. The 20 most frequently encountered species sampled in 360 1-m² plots within 12 wet meadows in Dane County, Wisconsin, July 2000 (in order of descending frequency), the number of plots where each was present, percent frequency, sum of cover classes (sum cc's), rank by total cover, and average cover for plots in which the species was present. Authorities of taxa are given in Table 4.

Species	No. plots present	Percent frequency	Sum cc's	Rank by cover	Ave. % cover where present
<i>Carex stricta</i>	222	62%	1136	1	18
<i>Calamagrostis canadensis</i>	201	58%	707	3	8.1
<i>Impatiens capensis</i>	162	45%	672	4	5.8
<i>Eupatorium maculatum</i>	146	41%	513	5	4.3
<i>Phalaris arundinacea</i>	141	39%	894	2	35.7
<i>Lycopus uniflorus</i>	124	34%	231	11	1
<i>Aster puniceus</i>	120	33%	418	6	3.4
<i>Solidago gigantea</i>	114	32%	348	7	2.5
<i>Lycopus americanus</i>	98	27%	212	12	1.2
Moss spp.	95	26%	181	14	1.4
<i>Lysimachia thyrsiflora</i>	77	21%	201	13	1.9
<i>Solidago canadensis</i>	75	21%	289	9	6.5
<i>Mentha arvensis</i>	72	20%	137	21	0.9
<i>Thelypteris palustris</i>	69	19%	306	8	8.1
<i>Campanula aparinoides</i>	67	19%	102	26	0.6
<i>Cornus stolonifera</i>	59	16%	239	10	7.9
<i>Glyceria striata</i>	56	16%	89	29	0.3
<i>Bromus ciliatus</i>	56	16%	66	37	0.7
<i>Rumex orbiculatus</i>	55	15%	162	18	3.1
<i>Viola cucullata</i>	51	14%	68	36	0.4

types ($\pm Pa \pm Dist$) were highly significant ($F \geq 92.6$ for all, $df = 359$, $P << 0.0001$; Figure 1). Plots without *Phalaris* in disturbed sites (-Pa +Dist), and plots with *Phalaris* in reference sites (+Pa -Dist), had similar moderate numbers of species, H' , and Mean C, and both plot types had significantly fewer species, lower H' , and lower Mean C than plots without *Phalaris* in reference sites. Plots with *Phalaris* in disturbed sites (+Pa +Dist) had the lowest species richness, H' , and Mean C of the four plot types (Figure 1).

When the plots were partitioned into those in reference versus disturbed sites and those containing or lacking *Carex stricta* ($\pm Cs \pm Dist$), the one-way ANOVAs for species richness, H' , and Mean C were again all significant ($P << 0.0001$; Figure 1). This was also the case for *Calamagrostis canadensis* ($\pm Cc \pm Dist$). Plots that contained *C. stricta* (or *C. canadensis*) and were in reference sites generally had the highest values (Figure 1). Plots that contained *C. stricta* (or *C. canadensis*) and were in disturbed sites, or plots that lacked *C. stricta* (or *C. canadensis*) and were in reference sites, usually had high or moderate values. Plots that lacked *C. stricta* (or *C. canadensis*) and were in disturbed sites always had the lowest species richness, H' , and Mean C (Figure 1).

Species richness within individual 1-m² plots was significantly negatively related to the cover of *Phalaris*; this was true both for plots in disturbed sites ($r = -0.59$, $F = 59.8$, $df = 114$, $P << 0.0001$) and for plots in reference sites ($r = -0.47$, $F = 6.7$, $df = 25$, $P = 0.016$), with an overall correlation coefficient $r = -0.67$ ($F = 110.2$, $df = 140$, $P << 0.0001$). However, the mean cover of *Phalaris* was about six times higher in plots in disturbed sites ($42.4\% \pm 2.8$, $n = 115$) than in plots in reference sites ($6.9\% \pm 2.5$, $n = 26$; $t = 5.86$, $df = 139$, $P < 0.0001$). Species richness also had a significant negative relationship to cover of *Carex stricta* both in plots in disturbed sites and in plots in reference sites (overall, $r = -0.21$, $F = 9.94$, $df = 221$, $P < 0.002$), but mean cover of *C. stricta* did not differ for plots in disturbed versus reference sites (overall mean cover = $18.0\% \pm 1.3$; $t = -0.07$, $df = 220$, $P = 0.95$). Species richness

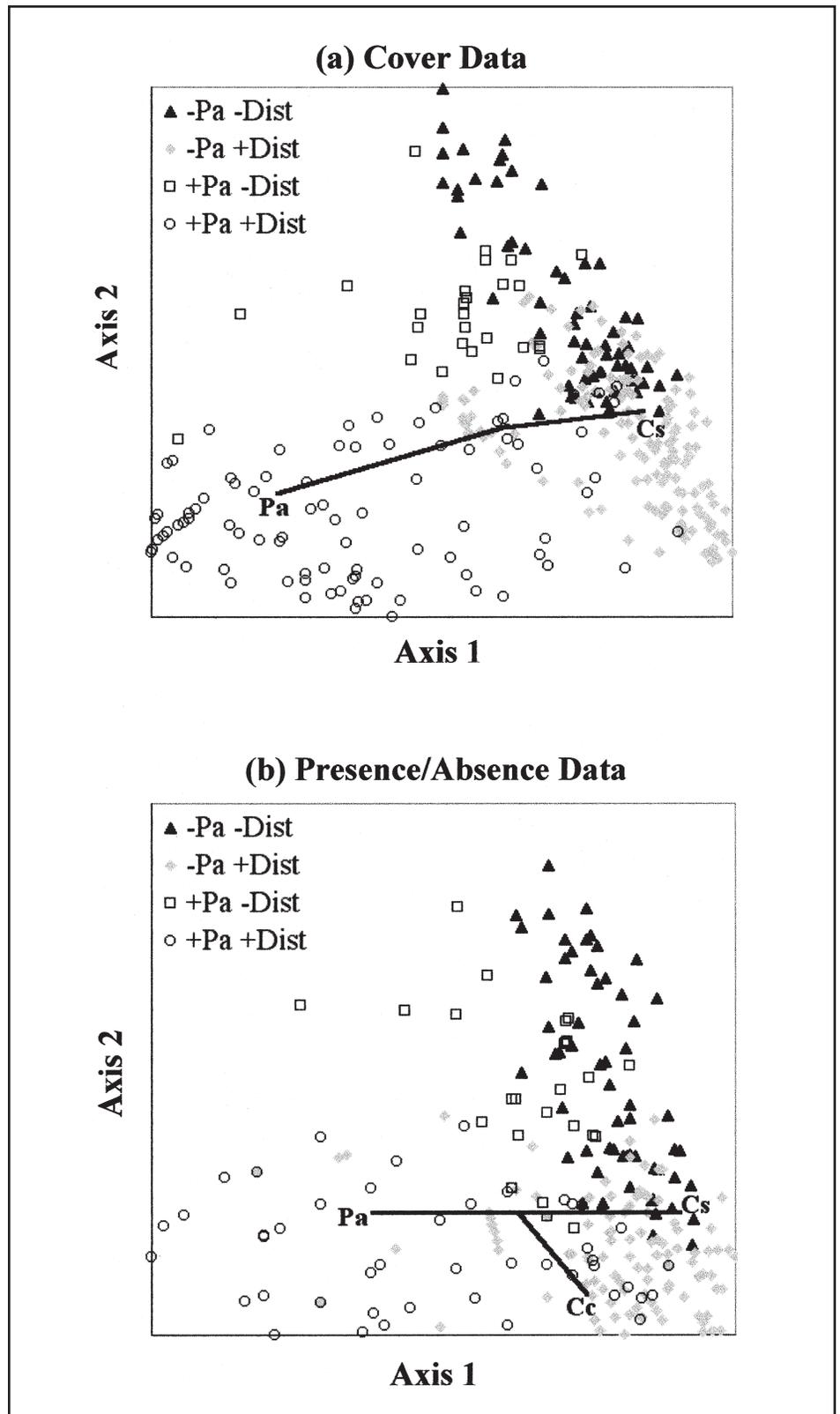


Figure 2. Bray-Curtis ordination of 360 1-m² plots sampled in July of 2000, divided into plots with and without *Phalaris arundinacea* ($\pm Pa$) on sites with and without visible indicators of hydrologic disturbance ($\pm Dist$). Results are shown for Axes 1 vs. 2 using quantitative cover data (a) and presence/absence data (b). Line overlays show the correlations of *Phalaris arundinacea* (Pa), *Calamagrostis canadensis* (Cc), and *Carex stricta* (Cs) with Axes 1 and 2. Line length indicates the strength of the correlation (joint plot cutoff $r^2 = 0.400$).

was unrelated to cover of *Calamagrostis canadensis* within both plots in disturbed sites and plots in reference sites (overall, $r = 0.05$, $F = 0.46$, $df = 200$, $P = 0.46$), and mean cover of *C. canadensis* did not differ among plots in disturbed versus reference sites (overall mean cover = $8.1\% \pm 1.0$; $t = 0.47$, $df = 199$, $P = 0.64$). On average, 5.5 ± 0.4 species coexisted with *Phalaris* on the 1-m² scale, compared to 11.5 ± 0.3 for *Carex stricta* and 10.6 ± 0.3 for *Calamagrostis canadensis* ($n = 141$, 222 , and 201 , respectively).

The Bray-Curtis ordinations based on cover class data and presence/absence data were very similar (Figure 2). Although there were no discrete clusters in the resulting graphs, plots did tend to congregate with others of the same type (i.e., $\pm Pa \pm Dist$; Figure 2). Using the ordination produced with the cover data, *Phalaris* and *Phragmites australis* had negative correlations with Axis 1 ($r = -0.88$ and -0.38 , respectively), and *Carex stricta*, *Impatiens capensis*, *Calamagrostis canadensis*, and *Eupatorium maculatum* L. had the highest positive correlations with Axis 1 ($r = 0.67$,

0.53 , 0.48 , and 0.47 , respectively). *Phalaris* had a moderate negative correlation with Axis 2 ($r = -0.52$), while *Aster puniceus*, *Agrostis gigantea* Roth, *Equisetum arvense* L., *Poa pratensis* L., *Viola cucullata* Ait., and *Oligoneuron riddellii* (Frank ex Riddell) Rydb. had the highest positive correlations with Axis 2 ($r = 0.59$, 0.56 , 0.56 , 0.49 , 0.45 , and 0.44 , respectively). Plot species richness, H' , and Mean C were all positively correlated with both Axis 1 ($r = 0.62$, 0.76 , and 0.69 , respectively) and Axis 2 ($r = 0.64$, 0.63 , 0.51 , respectively).

Table 4. The 30 most frequently encountered taxa in 360 1-m² plots and their responses to the presence of *Phalaris arundinacea* (Pa) and/or hydrologic disturbance, listed alphabetically by response type. A greater than expected number of occurrences within a plot type is denoted with a "+", fewer occurrences than expected with a "-", and no substantial departure from expectation is given a "0." Response types are: (1) decreased with Pa, (2) decreased with disturbance, (3) decreased with Pa but increased with disturbance when Pa is absent, (4) decreased with the combination of Pa and disturbance, (5) increased with the combination of Pa and disturbance, (6) no clear pattern or, (7) not significant. All chi-square tests were significant at $P < 0.0001$, except for those in response category 7.

Taxon	-Pa -Dist N=64	-Pa +Dist N=155	+Pa -Dist N=26	+Pa +Dist N=115	Response Type
<i>Bromus ciliatus</i> L.	+	0	-	-	1
<i>Campanula aparinoides</i> Pursh	+	0	-	-	1
<i>Eupatorium maculatum</i> L.	+	+	-	-	1
<i>Lycopus uniflorus</i> Michx.	+	+	-	-	1
Moss spp.	0	+	-	-	1
<i>Thelypteris palustris</i> Schott	+	0	-	-	1
<i>Aster puniceus</i> L.	+	-	+	-	2
<i>Equisetum arvense</i> L.	+	-	+	-	2
<i>Glyceria striata</i> (Lam.) A.S. Hitchc.	+	-	+	-	2
<i>Oligoneuron riddellii</i> (Frank ex Riddell) Rydb.	+	-	+	-	2
<i>Solidago gigantea</i> Ait.	+	-	+	-	2
<i>Viola cucullata</i> Ait.	+	-	+	-	2
<i>Calamagrostis canadensis</i> (Michx.) Beauv.	0	+	-	-	3
<i>Epilobium coloratum</i> Biehler	-	+	-	-	3
<i>Impatiens capensis</i> Meerb.	-	+	-	-	3
<i>Lysimachia thyrsoflora</i> L.	-	+	-	-	3
<i>Rumex orbiculatus</i> Gray	-	+	-	-	3
<i>Carex lasiocarpa</i> Ehrh.	+	0	0	-	4
<i>Carex stricta</i> Lam.	+	+	+	-	4
<i>Cornus stolonifera</i> Michx.	+	0	0	-	4
<i>Lycopus americanus</i> Muhl. ex W. Bart.	+	0	+	-	4
<i>Pilea pumila</i> (L.) Gray	0	+	0	-	4
<i>Solidago canadensis</i> L.	0	0	+	-	4
<i>Phragmites australis</i> (Cav.) Trin. ex Steud.	-	-	0	+	5
<i>Mentha arvensis</i> L.	-	+	+	-	6
<i>Carex lacustris</i> Willd.	0	0	0	0	7
<i>Cirsium muticum</i> Michx.	0	0	0	0	7
<i>Lathyrus palustris</i> L.	0	0	0	0	7
<i>Rubus strigosus</i> Michx.	0	0	0	0	7
<i>Typha latifolia</i> L.	0	0	0	0	7

Species Patterns

Most species showed significant deviations from their expected abundance within the four major plot types (\pm Pa, \pm Dist), based on chi-square tests of homogeneity (Table 4). The 30 taxa we tested could be grouped into seven “response types,” which include: (1) taxa that were less common than expected only in plots containing *Phalaris*, (2) taxa that were less common than expected only in plots in disturbed sites, (3) taxa that were more common than expected only in plots lacking *Phalaris* in disturbed sites, (4) taxa that were less common than expected only in plots containing *Phalaris* in disturbed sites, (5) taxa that were more common than expected in plots containing *Phalaris* that were in disturbed sites (only the clonal invasive grass *Phragmites australis* fell into this category), (6) taxa with no clear pattern despite a significant chi-square test, and (7) taxa with no significant pattern (Table 4).

DISCUSSION

We hypothesized that species richness and diversity would be lower on sites with visible indicators of hydrologic disturbance than on apparently undisturbed reference sites. Likewise, we predicted that invasive species would correlate with low diversity on 0.45 ha “sites” and within 1-m² plots. Our results support both hypotheses. Disturbed sites had lower overall species richness and diversity, and there were negative

relationships between the abundance of the invasive grass *Phalaris arundinacea* and measures of site quality. At the 1-m² scale, we found that plots containing *Phalaris* in reference sites (+Pa -Dist) and plots lacking *Phalaris* in disturbed sites (-Pa +Dist) had roughly 2/3 the species richness of plots that occurred in reference sites and lacked *Phalaris* (-Pa -Dist). Plots that both contained *Phalaris* and occurred in disturbed sites (+Pa +Dist), however, had only 1/3 the species of -Pa -Dist plots. Our correlational study suggests independent, and possibly interactive, effects of hydrologic disturbance and presence of *Phalaris* on vegetation diversity and quality (Figure 3 and see below).

Two common native graminoids, *Carex stricta* and *Calamagrostis canadensis*, displayed patterns of species richness, H', and Mean C that differed greatly from those of *Phalaris*. Plots in sites that lacked indicators of hydrologic disturbance in which *C. stricta* or *C. canadensis* occurred had the highest quantity and quality of taxa, while plots in disturbed sites that lacked either of the two native species had the lowest values. Thus, while fewer species and lower floristic quality are associated with *Phalaris*, more species of higher quality co-occur with *C. stricta* and *C. canadensis*. At least in the case of *Phalaris* versus *C. stricta*, this pattern may be due to the greater microtopographic variability created by *C. stricta* tussocks (Werner and Zedler 2002). Further support that *Phalaris*

reduces plant diversity comes from management experiments (e.g., Paveglio and Kilbride 2000).

We asked if mean coefficient of conservatism (Mean C), one measure of floristic quality, was related to presence of *Phalaris* and/or disturbance within our 12 wet meadows. A closely related measure, floristic quality index (FQI), has been criticized for its subjectivity and sensitivity to differences in sampling intensity, season, or habitat type (Bowles et al. 2000, Francis et al. 2000, Matthews 2003). Although Mean C is still based on the subjective assignment of coefficients to taxa by experts, it has been suggested that Mean C yields more intuitive results with no hidden information and with little effect of species richness/sampling intensity (Rooney and Rogers 2003). In our survey, we found that Mean C declined with disturbance or presence of *Phalaris* within 1-m² plots, and was lowest when disturbance and *Phalaris* were combined (note that our results for Mean C were not confounded by the presence of *Phalaris*, since it was not assigned a community coefficient). This pattern parallels those for species richness and diversity, and we detected a significant positive relationship between Mean C and species richness and diversity ($r=0.51$ and 0.52 , respectively; $P < 0.0001$ for both) for plots though not for sites ($r=0.36$ and 0.46 ; $P = 0.24$ and 0.13 , respectively). Matthews (2003) likewise found a significant positive relationship between species richness and Mean C for diverse wetland types censused in Illinois, USA ($r = 0.44$ in that study). This correlation may indicate concomitant but independent declines in species richness and quality, or it may reflect multicollinearity of these variables.

Taxa responded in several different ways to the presence of *Phalaris* and disturbance. Some taxa (response type 1) were less common than expected only when *Phalaris* was present (i.e., the forbs *Campanula aparinoides* Pursh, *Eupatorium maculatum*, and *Lycopus uniflorus* Michx., the fern *Thelypteris palustris* Schott, the grass *Bromus ciliatus* L., and mosses), suggesting competitive exclusion of these taxa by the taller, clonal *Phalaris*. Other taxa (response type 2) were less common than expected

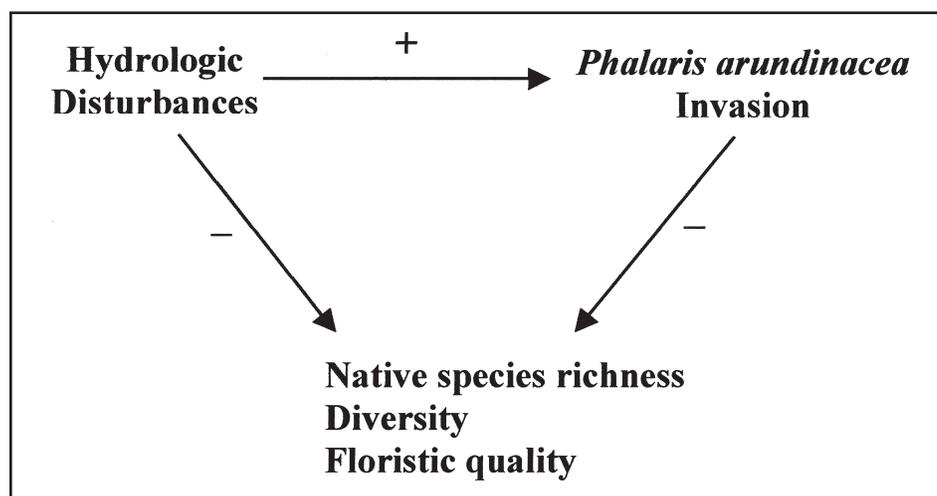


Figure 3. Conceptual model suggesting the interrelationships of hydrologic disturbances, *Phalaris arundinacea*, and native species. “+” and “-” signs indicate positive and negative relationships, respectively.

only in plots in sites with indicators of hydrologic disturbance (i.e., the forbs *Aster puniceus*, *Oligoneuron riddellii*, *Solidago gigantea* Ait. and *Viola cucullata*, the grass *Glyceria striata* (Lam.) A.S. Hitchc., and the horsetail *Equisetum arvense*), suggesting the primacy of hydrologic alterations over competition with *Phalaris* in influencing the distribution of these taxa.

Most taxa had more complicated patterns. Several (response type 3) appeared to thrive with disturbance, as long as *Phalaris* was not present (i.e., the grass *Calamagrostis canadensis*, and the forbs *Epilobium coloratum* Biehler, *Impatiens capensis*, *Lysimachia thyrsiflora* L., and *Rumex orbiculatus* Gray); and several (response type 4) were as common as expected in plots with either *Phalaris* or disturbance alone, but were especially rare in plots with both factors combined (i.e., the sedges *Carex lasiocarpa* Ehrh. and *Carex stricta*, the forbs *Lycopus americanus* Muhl. ex W. Bart., *Pilea pumila* (L.) Gray, and *Solidago canadensis* L., and the shrub *Cornus stolonifera* Michx.). Only *Phragmites australis* had positive associations with both *Phalaris* and disturbance (response type 5), and, not surprisingly, this species is very similar to *Phalaris* in that it is a tall, clonal perennial grass that is invasive in wetlands (Galatowitsch et al. 1999). This suggests that the two species have similar responses to disturbed hydrologic regimes (but see Choi and Bury 2003) and are probably in the early stages of competition or facilitating one another in our sites. However, *Typha latifolia* L., another tall, widespread clonal perennial graminoid, showed no discernible tendency to increase with disturbance and/or *Phalaris* in our study.

Our survey of 12 wet meadows points to a shift from more to less diverse communities that are dominated by clonal invasive species, especially *Phalaris arundinacea*, due to changes that have altered the hydrologic regimes of wetlands, a hypothesis that is also supported by other field studies. Owen's (1999) hydrologic study of an urban wetland in southern Wisconsin showed that, in less than 25 years, *Phalaris* and *Typha* spp. (including *T. latifolia*, *T. angustifolia* L., and *T. x glauca*) had in-

creased their cover in the wetland; *Phalaris* had expanded in areas that experienced the largest variations in water levels, ranging from flashy spring and summer flooding due to urban stormwater runoff to very dry conditions during long periods of no inflow, while *Typha angustifolia* had expanded in the wettest areas. A study of wetlands in northwestern Indiana documented *Phalaris* expansion primarily into artificially drained urban wetlands, *Typha angustifolia* expansion in impounded wetlands, and invasion of *Typha* litter mounds by *Phragmites australis* (Choi and Bury 2003). A survey of wetlands in the prairie pothole region of Minnesota found positive associations between presence of stormwater runoff and, to a lesser extent, presence of ditches and dominance by introduced perennials including both *Phalaris arundinacea* and *Typha angustifolia* (Galatowitsch et al. 2000). We found evidence in support of the hypothesis that both surface and groundwater alterations contribute to the spread of invasive perennial species. *Typha* spp. were not sampled with high frequency on our sites but did dominate Cherokee Marsh, a site that receives inputs of stormwater runoff. *Phragmites australis* was likewise infrequently sampled but was co-dominant with *Phalaris* at Nine Springs Meadow, a site with indicators of both groundwater (city wells, a drainage ditch) and surface water (major road) alterations. *Phalaris*, the most common invasive species in our survey, dominated three of the 12 wet meadows. One of these sites (Nine Springs Meadow) has been drained, while the other two sites had indicators of both decreased groundwater and increased surface flow.

In sites lacking disturbance, we saw 21% fewer species, 11% lower diversity, and 8% lower Mean C in plots containing *Phalaris*, while in disturbed sites, we saw 52% fewer species, 18% lower diversity, and 45% lower Mean C in plots containing *Phalaris*. Elsewhere, we suggested that hydrologic disturbance simultaneously makes sites more invasible and *Phalaris* more aggressive (Maurer et al. 2003). *Phalaris* is known to tolerate a range of hydrologic regimes (Lefor 1987, Rice and Pinkerton 1993, Figiel et al. 1995, Owen 1999, Miller and Zedler 2003, Kercher, unpubl. data). Either increased surface water flow or de-

creased groundwater influence could make wet meadows more susceptible to *Phalaris* invasion by reducing growth of sensitive native species. The effect of increased surface water has been demonstrated by Kercher and Zedler (2004) in a mesocosm study, which showed that floods lasting four weeks or longer caused several sensitive native species to decline and more tolerant *Phalaris* plants to grow and spread rapidly into the large gaps created during the die-off of the natives. Canopy gaps could also increase opportunities for invasion from seed (Lindig-Cisneros and Zedler 2002). At the same time, nutrients carried in surface runoff or released with lowered water tables may favor the vegetative expansion and growth of *Phalaris* over that of native species (Green and Galatowitsch 2001, 2002; Kercher and Zedler 2004). Direct tests of our conceptual model (Figure 3) are underway in mesocosms, and further research is warranted for other wetland communities affected by both hydrologic disturbances and invasive species.

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Suzanne Kercher recently received a Ph.D. in Botany from the University of Wisconsin-Madison working on this project and experiments that tested the effects of various disturbances on invasion of wetlands by reed canary grass. She is currently a fellow in the Botany Department and teaches botany at Edgewood College in Madison, Wisconsin.

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U.S. GEOLOGICAL SURVEY Fact Sheet 076-03

Effects of Urban Development on Floods

By C. P. Konrad

Over the past century, the United States has become an increasingly urban society. The changes in land use associated with urban development affect flooding in many ways. Removing vegetation and soil, grading the land surface, and constructing drainage networks increase runoff to streams from rainfall and snowmelt. As a result, the peak discharge, volume, and frequency of floods increase in nearby streams. Changes to stream channels during urban development can limit their capacity to convey floodwaters. Roads and buildings constructed in flood-prone areas are exposed to increased flood hazards, including inundation and erosion, as new development continues. Information about streamflow and how it is affected by land use can help communities reduce their current and future vulnerability to floods.

HYDROLOGIC EFFECTS OF URBAN DEVELOPMENT

Streams are fed by runoff from rainfall and snowmelt moving as overland or subsurface flow. Floods occur when large volumes of runoff flow quickly into streams and rivers. The peak discharge of a flood is influenced by many factors, including the intensity and duration of storms and snowmelt, the topography and geology of stream basins, vegetation, and the hydrologic conditions preceding storm and snowmelt events.

Land use and other human activities also influence the peak discharge of floods by modifying how rainfall and snowmelt are stored on and run off the land surface into streams. In undeveloped areas such as forests and grasslands, rainfall and snowmelt collect and are stored on vegetation, in the soil column, or in surface depressions. When this storage capacity is filled, runoff flows slowly through soil as subsurface flow. In contrast, urban areas, where much of the land surface is covered by roads and buildings, have less capacity to store rainfall and snowmelt. Construction of roads and buildings often involves removing vegetation, soil, and depressions from the land surface. The permeable soil is replaced by impermeable surfaces such as roads, roofs, parking lots, and sidewalks that store little water, reduce infiltration of water into the ground, and accelerate runoff to ditches and streams. Even in suburban areas, where lawns and other permeable landscaping may be common, rainfall and snowmelt can saturate thin soils and produce overland flow, which runs off quickly. Dense networks of ditches and culverts in cities reduce the distance that runoff must travel overland or through subsurface flow paths to reach streams and rivers. Once water

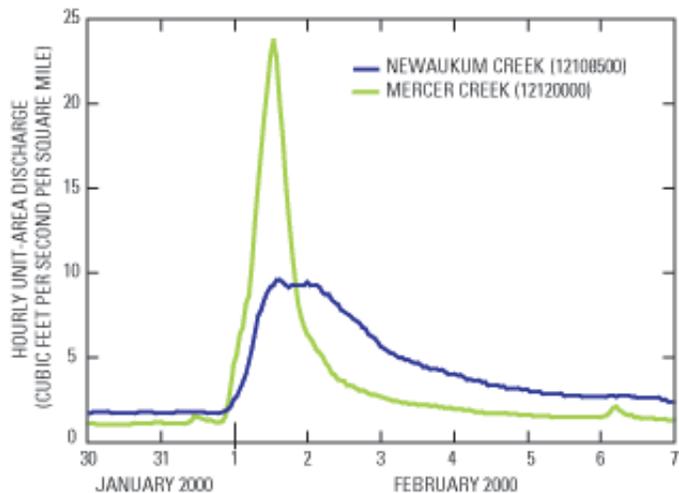


Flooding in Hickory Hills, Illinois, prompted the construction of a reservoir to control runoff from upstream areas. Source: Loren Wobig, Illinois Office of Water Resources.

enters a drainage network, it flows faster than either overland or subsurface flow.

With less storage capacity for water in urban basins and more rapid runoff, urban streams rise more quickly during storms and have higher peak discharge rates than do rural streams. In addition, the total volume of water discharged during a flood tends to be larger for urban streams than for rural streams. For example, streamflow in Mercer Creek, an urban stream in western Washington, increases earlier and more rapidly, has a higher peak discharge and volume during the storm on February 1, 2000, and decreases more rapidly than in Newaukum Creek, a nearby rural stream. As with any comparison between streams, the differences in streamflow cannot be attributed solely to land use, but may also reflect differences in geology, topography, basin size and shape, and storm patterns.

The hydrologic effects of urban development often are greatest in small stream basins where, prior to development, much of the precipitation falling on the basin would have become subsurface flow, recharging aquifers or discharging to the stream network further downstream. Moreover, urban development can completely transform the landscape in a small stream basin, unlike in larger river basins where areas with natural vegetation and soil are likely to be retained.



Streamflow in Mercer Creek, an urban stream in western Washington, increases more quickly, reaches a higher peak discharge, and has a larger volume during a one-day storm on February 1, 2000, than streamflow in Newaukum Creek, a nearby rural stream. Streamflow during the following week, however, was greater in Newaukum Creek.

HYDRAULIC EFFECTS FROM CHANGES TO STREAM CHANNELS AND FLOODPLAINS

Development along stream channels and floodplains can alter the capacity of a channel to convey water and can increase the height of the water surface (also known as stage) corresponding to a given discharge. In particular, structures that encroach on the floodplain, such as bridges, can increase upstream flooding by narrowing the width of the channel and increasing the channel's resistance to flow. As a result, the water is at a higher stage as it flows past the obstruction, creating a backwater that will inundate a larger area upstream.

Sediment and debris carried by floodwaters can further constrict a channel and increase flooding. This hazard is greatest upstream of culverts, bridges, or other places where debris collects. Small stream channels can be filled with sediment or become clogged with debris, because of undersized culverts, for example. This creates a closed basin with no outlet for runoff. Although channels can be engineered to convey floodwater and debris quickly downstream, the local benefits of this approach must be balanced against the possibility of increased flooding downstream.

Erosion in urban streams represents another consequence of urban development. Frequent flooding in urban streams increases channel and bank erosion. Where channels have been straightened and vegetation has been removed from channel banks, streamflow velocities will increase, allowing a stream to transport more sediment. In many urban areas, stream-bank erosion represents an ongoing threat to roads, bridges, and other structures that is difficult to control even by hardening stream banks.



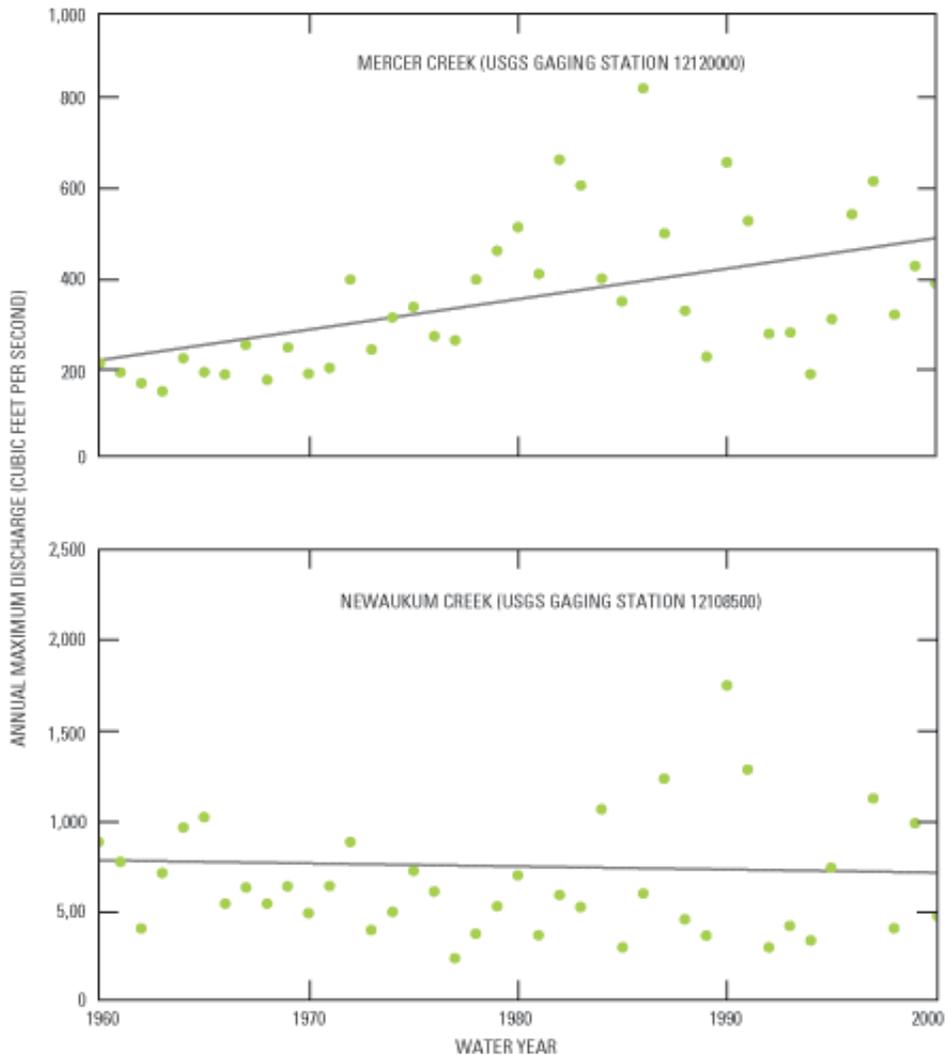
Road washed out by a flood in West Virginia. Source: A. Rothstein, Farm Security Administration.

EFFECTS OF URBAN DEVELOPMENT ON FLOOD DISCHARGE AND FREQUENCY

Common consequences of urban development are increased peak discharge and frequency of floods. Typically, the annual maximum discharge in a stream will increase as urban development occurs, although the increase is sometimes masked by substantial year-to-year variation in storms, as is apparent in the annual maximum discharge for Mercer Creek from 1960 to 2000. In comparison, the annual maximum discharge for rural Newaukum Creek varied during the period but showed no clear trend.

The effects of development in urban basins are most pronounced for moderate storms following dry periods. For larger storms during wet periods, the soil in

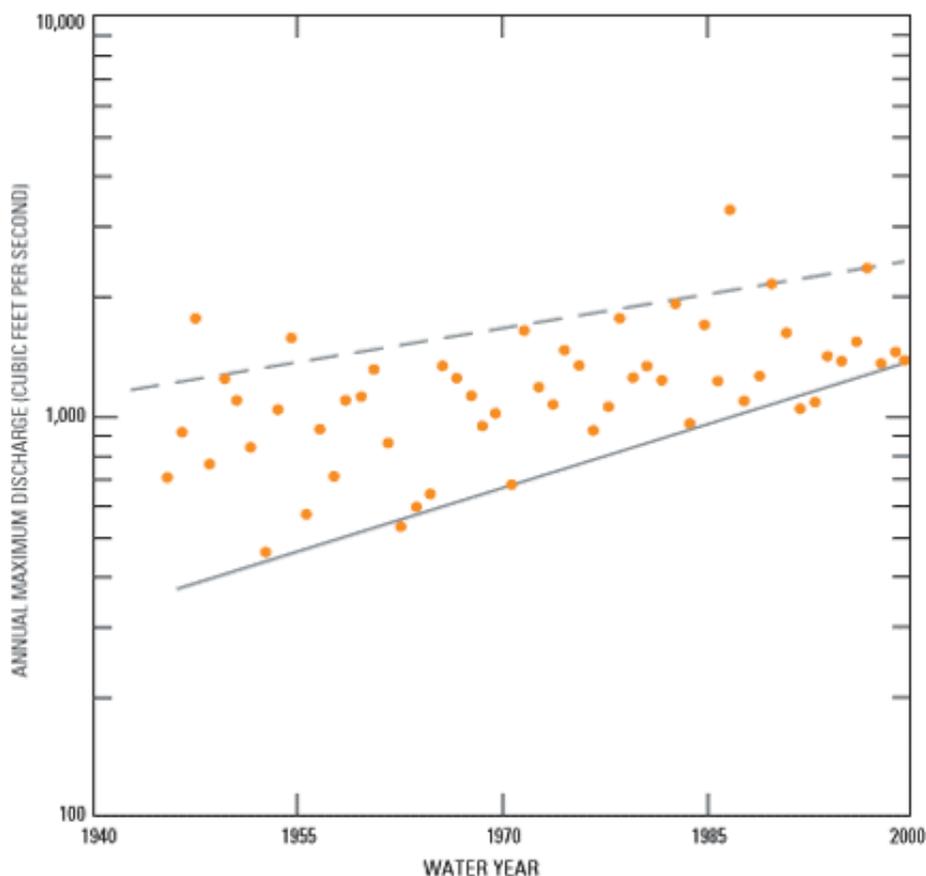
rural basins becomes saturated and additional rainfall or snowmelt runs off much as it does in an urban basin.



Annual maximum discharge increased with urban development in Mercer Creek from 1960 to 2000, but remained essentially the same in nearby rural Newaukum Creek during that period.

The relative increase in peak discharge is greater for frequent, small floods than infrequent, large floods.

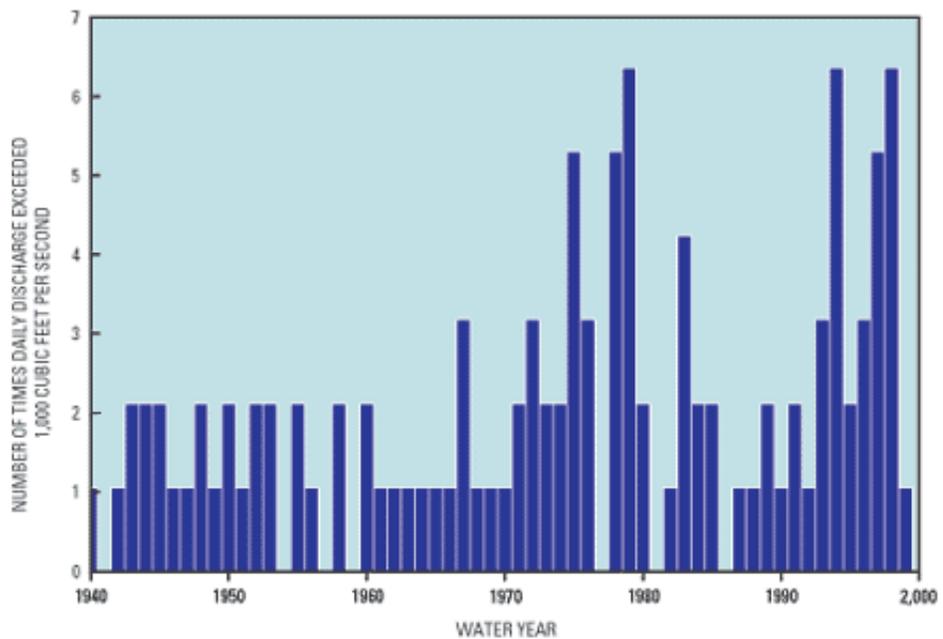
Flood Frequency	Chance that flood's peak discharge will be exceeded in any year	Increase in flood peak discharge because of urban development
2-year	50 percent	100 to 600 percent
10-year	10 percent	20 to 300 percent
100-year	1 percent	10 to 250 percent



The relative increase in annual maximum discharge in Salt Creek, Illinois, (USGS gaging station 05531500) has been greater for small floods (solid line, less than 95 percent of the annual peaks for the period of record) than for large floods (dashed line, more than 95 percent of the annual peaks for the period of record).

The effect of urban development in the last half of the 20th century on small floods is evident in Salt Creek, Illinois. With the exception of an unusually large flood in 1987, large floods have increased by about 100 percent (from about 1,000 cubic feet per second to about 2,000 ft³/s) while small floods have increased by about 200 percent (from about 400 ft³/s to 1,200 ft³/s). Nonetheless, even a small increase in the peak discharge of a large flood can increase flood damages.

The frequency of moderate flooding can increase substantially after development. The annual frequency that daily discharge exceeded 1,000 ft³/s on the Northeast Branch of the Anacostia River in Maryland increased from once or twice per year in the 1940s and 1950s to as much as six times per year in the 1990s.



The number of times per year that daily discharge in the Northeast Branch of the Anacostia River, Maryland, (USGS gaging station 01649500) was greater than 1,000 ft³/s has increased over time.

REDUCING FLOOD HAZARDS IN URBAN AREAS

There are many approaches for reducing flood hazards in basins under development. Areas identified as flood-prone have been used for parks and playgrounds that can tolerate occasional flooding. Buildings and bridges have been elevated, protected with floodwalls and levees, or designed to withstand temporary inundation. Drainage systems have been expanded to increase their capacity for detaining and conveying high streamflows; for example, by using rooftops and parking lots to store water. Techniques that promote infiltration and storage of water in the soil column, such as infiltration trenches, permeable pavements, soil amendments, and reducing impermeable surfaces have also been incorporated into new and existing residential and commercial developments to reduce runoff from these areas. Wet-season runoff from a neighborhood in Seattle, Washington, was reduced by 98 percent by reducing the width of the street and incorporating vegetated swales and native plants in the street right-of-way.



Floodwalls along Willow Creek in Rosemont, Illinois. Source: Kevin D. Richards, U.S. Geological Survey.

In response to frequent flooding along the Napa River in California, the local community integrated many of these approaches into a single plan for flood protection that is expected to reduce flood damage while helping to restore the river ecosystem. The plan involves bridge reconstruction, levee setbacks, a floodwall, moving of vulnerable structures, detention basins, larger stormwater conveyances, and a high-flow bypass channel.

The U.S. Geological Survey in cooperation with the City of Charlotte and Mecklenburg County, North Carolina, developed a flood information and notification system (FINS) to address the need for prompt notification of flood conditions in urban areas where streams rise and fall rapidly. FINS is based on a large network of streamflow gaging and rainfall stations that broadcast information within minutes of being recorded via radio telemetry. The system automatically notifies the National Weather Service and emergency responders in the region when rainfall and streamflow indicate the likelihood of flooding, giving these agencies additional time to issue warnings and evacuate areas if necessary.

CONCLUSIONS

Urbanization generally increases the size and frequency of floods and may expose communities to increasing flood hazards. Current streamflow information provides a scientific foundation for flood planning and management in urban areas. Because flood hazard maps based on streamflow data from a few decades ago may no longer be accurate today, floodplain managers need new peak streamflow data to update flood frequency analyses and flood maps in areas with recent urbanization. Streamflow-gaging stations provide a continuous record of streamflow that can be used in the design of new urban infrastructure including roads, bridges, culverts, channels, and detention structures. Stormwater managers can use streamflow information in combination with rainfall records to evaluate innovative solutions for reducing runoff from urban areas. Real-time streamflow-gaging stations, which make streamflow and rainfall data available via the internet and other communications networks as they are recorded, offer multiple benefits in urban watersheds. In particular, they provide flood managers with information that can guide flood control operations and emergency actions such as evacuations and road closures.

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U.S. Geological Survey stream gaging and the National Streamflow Information Program: <http://water.usgs.gov/nsip>

Current streamflow conditions around the U.S.: <http://water.usgs.gov/waterwatch/>

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Water quality implications from three decades of phosphorus loads and trophic dynamics in the Yahara chain of lakes

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Abstract

Trophic responses to phosphorus (P) loads spanning 29–33 years were assessed for the eutrophic Yahara chain of lakes: Mendota (area = 39.6 km², mean depth = 12.7 m, flushing rate = 0.23 yr⁻¹); Monona (13.7 km², 8.3 m, 1.3 yr⁻¹); Waubesa (8.5 km², 4.7 m, 4.3 yr⁻¹); and Kegonsa (13.0 km², 5.1 m, 3.0 yr⁻¹). During extended drought periods with low P loads, summer (Jul–Aug) total P (TP) concentrations declined substantially in all 4 lakes, with Mendota achieving mesotrophic conditions (<0.024 mg L⁻¹). In years when P loads were high due to major runoff events, summer TP in the lakes was high (especially in shallower Waubesa and Kegonsa); in some summers dissolved inorganic P was elevated, indicating algae growth was not P limited. Summer TP returned to normal levels following both low and high load years, signifying the lakes were responsive to P load changes. The proportion of P input loads passed via a lake's outlet to the next lake downstream increased as flushing rates increased. Because Monona, Waubesa, and Kegonsa received 60, 83, and 76% of their surface water P load from the respective upstream lake's outlet, reducing P loads in Mendota's large watershed was predicted to produce significant water quality benefits downstream. Modeling indicated a significant grazing effect of *Daphnia* on summer TP and Secchi transparency readings for Mendota and Monona. Finally, using drought loads as targets, our study established P loading reductions needed to improve water quality in all 4 Yahara lakes.

Key words: agricultural runoff, *Daphnia*, Lake Mendota, nonpoint pollution, phosphorus loads, Secchi disk, total phosphorus, Yahara lakes

Introduction

Eutrophication of lakes worldwide is linked to over-fertilization by phosphorus (P), which stimulates blooms of blue-green algae (Sas 1989, Schindler 2006, Smith et al. 2006, Carpenter 2008). The Yahara River chain of 4 lakes (Mendota, Monona, Waubesa, and Kegonsa in downstream order; Fig. 1) near Madison, Wisconsin, USA, exemplifies those eutrophication problems because blue-green algal blooms have been legion for more than a century. The first problems from blue-green algae were in the lower 3 Yahara lakes, which received Madison's partially treated wastewater until the effluent was diverted in 1958 (Lathrop 2007). Mendota's algal bloom problems

began shortly after World War II when wastewater inputs of P from upstream communities increased coincident with an increase in agricultural and urban nonpoint pollution from Mendota's watershed (Lathrop 1992, Lathrop 2007, Carpenter et al. 2006). After upstream community wastewater discharges to Mendota ended in 1971, agricultural and urban runoff produced even higher levels of P in the lake in subsequent years.

Nonpoint pollution reduction programs first began in the 1970s and continue today, with little perceived change in the frequency or severity of blue-green algal blooms in Mendota or the other 3 Yahara lakes (Lathrop et al. 1998, Carpenter et al. 2006, Lathrop 2007). However, a heightened awareness of injurious and potentially deadly

toxins associated with blue-green algae has intensified governmental and citizen efforts to reduce P inputs to the Yahara lakes as the primary mechanism to improve water quality. The Yahara CLEAN Project was launched in 2008 as a joint partnership to achieve that end.

To help focus these lake clean-up efforts, we developed and analyzed long-term P loading and lake response data to estimate the effects of specific P loading reduction targets for the 4 Yahara lakes. Modeling also indicated an important role for algal grazing by *Daphnia* in these summer trophic state determinations and helped support our load reduction targets considering potential food web alterations expected to result from invasive species. Finally, our analyses quantified the benefit of reducing P loads to upstream lakes because those reductions cascade to downstream lakes via decreased loads in upstream lake outlet waters. Analyses that examine the response of lake trophic conditions to external P loading have been widely

applied to individual lakes for decades, but fewer studies have analyzed lake loading relationships in chains of lakes (Elser and Kimmel 1985, Choulik and Moore 1992, Hillbricht-Ilkowska 2002, Epstein et al. 2013). Our study has proved important for local lake P control efforts, but our approach is also applicable to other lake systems.

Methods and approaches

Phosphorus loadings

Lake Mendota: We developed 33 years of annual P loads to Lake Mendota for 1976 through 2008 using approaches updated from previous analyses (Lathrop et al. 1998, Carpenter and Lathrop 2008). Our new lake response modeling used an annual loading time step from 1 November of the previous year through 31 October of the stated year instead of a mid-April annual time step used in

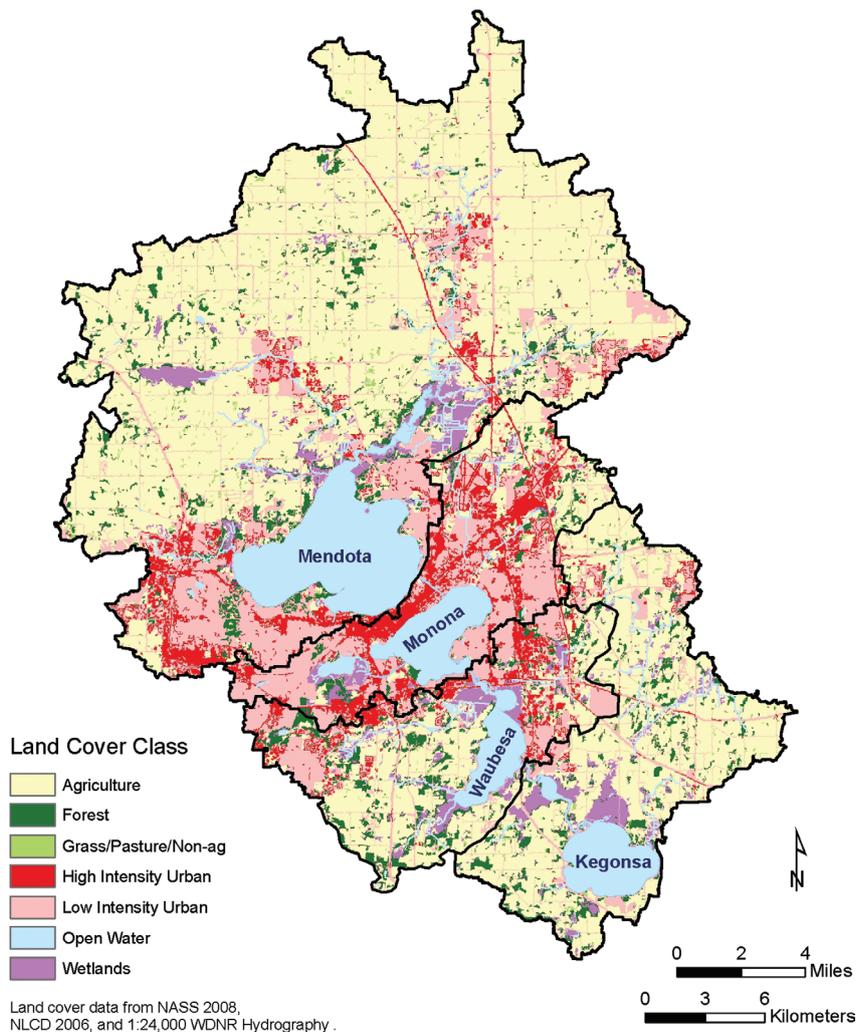


Fig. 1. The Yahara River chain of lakes (Mendota, Monona, Waubesa, Kegonsa) near Madison in southern Wisconsin, USA. (Source: Dane Co. Land and Water Resources Dept.)

our earlier analyses. This new loading time step allowed the lake's P status (water column P concentration or mass) on 1 November of each year (i.e., after fall turnover commenced) to be used as a hindcast predictor of each summer's water quality and eliminated the problem of loads before and after mid-April falling into different load years. Thus, annual loads using the 1 November time step were more precisely linked to each summer's water quality. For our lake response modeling, in-lake water quality data were available for 29–33 years of annual P loads.

P loads for rural and urban subbasins (hydrologic units) in all 4 Yahara lake drainage basins were estimated by Montgomery Associates Resource Solutions using the 2005 version of the SWAT model (Nietsch et al. 2005, Gassman et al. 2007), the latest model version available at the time of the consulting firm's contract work. The popular, nationally used model proved an effective inventory tool for land use practices, potential pollution sources, and subwatershed areas for the Yahara lakes. Using local daily precipitation data and land use information provided by Dane County and the City of Madison, the model predicted monthly water export and sediment and P loads for each subbasin during the 33 loading study years (1976–2008).

We did not use the P-loading data predicted by SWAT 2005 for Lake Mendota's rural subwatersheds because the model did not have subroutines to accurately predict P loads during late-winter runoff events when the ground is frozen and winter spreading of manure occurs, a widespread practice in the Mendota watershed with a large number of dairy operations. Instead, we developed P loads based on 2 of Mendota's subwatershed tributaries (Yahara River and Pheasant Branch) that had long-term US Geological Survey (USGS) monitoring data for P loads. Previous analyses indicated the January–March runoff period represented 43–48% of the long-term annual P load in these 2 subwatersheds (Lathrop 2007).

Similar to our earlier analyses of P loads in the Lake Mendota watershed, we used monthly monitored subwatershed loads to predict monthly P loads in other subwatersheds (Sixmile Creek and Token Creek) based on predictive relationships developed from more extensive monitoring data available for 1976–1980 (Lathrop 1998). While we recognize that changing land management practices within each subwatershed could alter these predictive relationships over time, late-winter runoff events and seasonal droughts would be systemic throughout the lake's entire watershed. For rural areas without historical monitoring data, P loads were extrapolated from each year's monitored subwatershed loads.

We computed P loads for urban storm sewer basins draining directly to Lake Mendota using water flow volumes predicted by SWAT for the 33 loading years for

each basin, multiplied by each basin's P export coefficient computed by SLAMM modeling (Pitt and Voorhees 2002) performed by USGS for the City of Madison in the early 2000s. A comparison of monthly SWAT modeling results with USGS long-term flow monitoring data for Mendota's Spring Harbor storm sewer basin indicated that SWAT produced reliable annual flow volumes for urban basins. The SLAMM modeling provided P loading and water volume data for each urban basin using "average year" precipitation data for 1981 and 2000 land use data to run the model. From the SLAMM modeling results, an average P concentration for each urban basin was then computed that reflected the characteristics of each basin. We then calculated P loads for each urban basin for all 33 loading years in our analyses by multiplying SWAT's predicted annual water volumes times each basin's average P concentration. While this approach did not account for any urban land use changes during 1976–2008, the approach did incorporate yearly variations in runoff volumes used in calculating the annual urban P loads.

Outlet P loads for Lake Mendota were computed by multiplying discharge volumes for the lake outlet times mid-lake surface water P concentration data. Daily outlet flows were calculated from equations using gate and lock opening records for 1976–1997 (Lathrop et al. 1998). Since 2003, daily flows have been measured by USGS in the Yahara River downstream of the lake outlet. For 1998–2002, monthly outlet flow volumes were predicted from Yahara River flows at Waubesa's outlet where a long-term USGS gauging station is located. Lake P concentration data that corresponded to the daily or monthly outlet flows were interpolated from surface P concentrations measured in samples collected generally biweekly during spring and summer, every 2–4 weeks during fall, and at least once during winter when the lakes were ice covered.

Lake Monona: The largest portion of the annual P load to Lake Monona came from the outlet of upstream Lake Mendota. For the mostly urban land draining directly to Monona, we computed P loads using the same methods as for Mendota's urban basins: the SLAMM-derived P export concentration for each urban basin was multiplied by the SWAT-derived water discharge volumes predicted for each year during 1976–2008. Because these were end-of-pipe P loading estimates, however, P loads to all urban basins discharging to Lake Wingra, a shallow 1.3 km² lake in the western part of Monona's direct drainage basin, were attenuated before the water entered Monona. To adjust for this, we multiplied P concentration data available for Lake Wingra times the SWAT-derived annual water volumes for all urban basins discharging directly to Wingra to produce a more realistic estimate of annual P loads leaving Wingra and entering Monona from the west end of its urban

drainage basin. No other adjustments were made for urban P loads entering Monona, although a limited amount of monitoring data from 1976 for the Starkweather Creek subwatershed on Monona's northeast side indicated some attenuation of P loads may be occurring in that relatively flat subwatershed.

We computed Monona's annual outlet P loads for 1976–2008 by multiplying monthly flow volume estimates times interpolated lake P concentration data, as for Mendota. Monthly flow volumes were predicted from Lake Waubesa outlet flow records using a relationship developed from historical monthly flow data for the outlet of Monona.

Lake Waubesa: Outlet P loads from Lake Monona constituted the largest P-loading source to Lake Waubesa. To compute Waubesa's direct drainage P loads for 1976–2008, we used SWAT P loading results because no nearby subwatershed monitoring data were available. The SWAT loading bias for winter manure runoff as described for Mendota was expected to be less important for Waubesa because watershed inventory data indicated that little manure is produced in Waubesa's direct drainage area. Additionally, even with a large error in the P loading estimates for Waubesa's direct drainage area, its P load was relatively small compared to the river load coming from upstream Lake Monona. For Waubesa's outlet P loads, we multiplied USGS monitored daily discharge volumes times interpolated lake P concentration data for 1980–2008. We did not compute Waubesa outlet loads prior to 1980 due to the lack of reliable lake P data.

Lake Kegonsa: Outlet P loads from upstream Lake Waubesa constituted the largest P-loading source to Lake Kegonsa during 1980–2008. We calculated the direct drainage loads to Kegonsa for those same years using the SWAT modeling results, as for Waubesa. Outlet P loads for Kegonsa were based on interpolated lake P concentration data for 1980–2008 and monthly flow volumes predicted from Waubesa outlet flow records.

Other P loading sources: In addition to P loads entering the 4 lakes via streams and storm sewers, P can also enter via dry fallout and precipitation directly on the lake surfaces, and from groundwater inputs, with dry fallout being the most important of the 3 sources. Early estimates for these sources were developed for Lake Mendota (Lathrop 1979) and treated as a constant annual input of P in our loading analyses. We applied estimates for these sources to the lower Yahara lakes based on a unit lake surface area conversion from Mendota's estimate (excluding groundwater, which has much less inflow to the lower Yahara lakes).

Volumetric P loads: Because the 4 Yahara lakes have widely differing surface areas and water depths and volumes (Table 1), we also calculated volumetric P loads ($\text{g m}^{-3} \text{ yr}^{-1}$) by dividing each lake's annual load by that lake's water volume. This allowed more direct comparisons of the magnitude of annual P loads each lake received during 1976–2008.

Lake outlet pass-through load factors

One important set of analyses estimated the P load reductions that would cascade to a downstream lake following upstream lake P-load reductions. For Mendota, these reductions would come from watershed management practices; for the lower 3 Yahara lakes, P loading reductions to each lake could result from practices installed in the direct drainage basin or from less P leaving the upstream lake's outlet.

To determine these lake outlet "pass-through" factors, we plotted the annual outlet P loads versus the annual total input P loads for each lake and verified that all the lake input:outlet relationships were linear. We then developed simple linear regression equations where the regression slope coefficient for each lake's input:outlet relationship was that lake's pass-through factor. Thus, for a P load reduction realized for a given lake, a percentage of that load reduction would result in a reduction in P leaving the lake's outlet to provide downstream water quality benefits.

In-lake water quality

To help set summertime water quality goals for the Yahara lakes, we used Carlson's (1977) Trophic State Index (TSI) in which separate equations for in-lake total phosphorus (TP) concentrations and Secchi disk transparency readings allowed the boundary between mesotrophy and eutrophy (TSI = 50) to be computed. These boundaries corresponded to $\text{TP} = 0.024 \text{ mg L}^{-1}$ and to Secchi transparency = 2.0 m; thus, when the lakes experienced summer TP concentrations $< 0.024 \text{ mg L}^{-1}$ or Secchi transparencies $> 2.0 \text{ m}$, then mesotrophic conditions occurred as defined by the separate indices. When the lakes had $\text{TP} > 0.024 \text{ mg L}^{-1}$ or Secchi transparencies $< 2.0 \text{ m}$, the lakes had eutrophic (or in some cases hypereutrophic) conditions. Because the TSI values for TP and Secchi were independently derived, the 2 indices did not always agree on a lake's trophic state on any given sampling date or time period. For example, a Secchi-TSI could indicate the lake was mesotrophic while the TP-TSI could indicate the lake was eutrophic.

To portray long-term water quality trends in the 4 Yahara lakes, we compiled available long-term Secchi disk readings and surface water TP concentrations for the summer months when algal blooms are most problematic.

Table 1. Physical characteristics of the Yahara lakes.

	Mendota	Monona	Waubesa	Kegonsa
Direct drainage area (km ²)	553	119	124	155
Lake area (km ²)	39.6	13.7	8.5	13.0
Total watershed area (km ²)	593	725	858	1026
Maximum lake depth (m)	25.3	22.6	11.3	9.8
Mean lake depth (m)	12.7	8.3	4.7	5.1
Lake volume (m ³ × 10 ⁶)	505	110	39.5	66.8
Mean flushing rate (yr ⁻¹)	0.23	1.3	4.3	3.0

Reliable TP concentration data have been regularly collected in the lakes since 1980 (Lathrop 2007); Secchi disk transparency data have been routinely collected since 1976 in Mendota and Monona, and since 1980 in Waubesa and Kegonsa. All data are accessible through the North-Temperate Lakes Long-Term Ecological Research project (<http://lter.limnology.wisc.edu/>). Because the Yahara lakes all exhibited a strong clear-water phase during late spring and early summer (i.e., Jun), we standardized our summer lake water quality dataset by using data collected between 30 June and 7 September to represent “July–August” summer conditions. We chose this date range to ensure comparable data were analyzed each year. Results are presented through 2012 to detect more recent water quality trends.

Water quality variables such as summer surface TP and Secchi transparency are highly variable from day to day in eutrophic lakes; the Yahara lakes are no exception. Phosphorus load and algal grazing by zooplankton are important variables that control year-to-year water quality conditions, but day-to-day variability can be high even at fixed conditions of P load and grazing. To address this variability, we computed probabilities of meeting the water quality goal for mesotrophy using both the TP and Secchi TSI indices. Thus, our lake response modeling focuses on the probability of mesotrophy occurring in the lakes (i.e., the probability of having TP <0.024 mg/L or Secchi transparency >2.0 m on any given Jul–Aug day).

Phosphorus load simulation: Our modeling process involved first simulating the probability distribution of P loads for a given change in mean annual loading, and then simulating the probability distribution of water quality conditional on the P load distribution. The approach is similar to that used by Lathrop et al. (1998); however, here we employ a more extensive time series and predict summer surface-water TP and Secchi transparency instead of blue-green algal biomass as the water quality responses.

To generate simulated P load distributions, we first fit autoregressive models to the observed time series for annual P loads to lakes Mendota and Monona. We then

computed predicted loads using the Bayesian posterior distribution (Gelman et al. 2004), a Student t-distribution similar to the distribution of predictions from an ordinary linear regression (Gelman et al. 2005). Simulated load distributions were random samples from these Bayesian posterior distributions. Statistical moments (mean, variance, range, autocorrelation) were similar for the predicted distributions and the actual observed distributions.

To simulate different loading conditions, we rescaled the predicted load distributions so that the mean was a specified multiplier of the observed mean for 1976–2008 with a range of multipliers from 0.2 to 2.0, with increments of 0.1. For example, when the load multiplier is 1.0 (corresponding to 0% change from current conditions), the simulated loads match the mean of the observed loads. When the load multiplier is 2.0, the simulated loads have a mean twice as large as the observed loads. When the load multiplier is 0.5, the simulated loads have a mean half (or 50%) of the observed loads. For each load multiplier, we computed 5000 years of simulated P loads. These values were then used as input to compute distributions of lake water quality variables.

Lake water quality simulation: We computed regression models to predict surface water TP concentrations and Secchi transparency for lakes Mendota and Monona from P load and an algal-grazing index of the dominant *Daphnia* species of zooplankton present in the lake each spring–summer (Lathrop et al. 1996). The grazing index was 1 if the larger-bodied *Daphnia pulicaria* was the dominant grazer that year, and 0 if the smaller-bodied *Daphnia galeata mendotae* was the dominant grazer. *D. pulicaria* is an effective algal grazer known to increase water clarity in lakes (Kasprzak et al. 1999, Lathrop et al. 1999). Each regression model yields a posterior probability distribution for surface water TP or Secchi transparency given the distribution of annual P loads and presence or absence of *D. pulicaria*. This posterior distribution is a Student t-distribution similar to the distribution of predictions from a linear regression (Gelman et al. 2004).

Given a sample of simulated P loads and the presence or absence of *D. pulicaria*, we computed a random sample of water quality using the posterior distribution of the water quality regression. By integrating Bayesian posterior distributions for surface water TP and Secchi transparency, we computed the probabilities of TP <0.024 mg L⁻¹ and Secchi transparency >2.0 m (i.e., mesotrophic conditions) for each value of the P load multiplier (or percent change in mean annual P load) with and without dominance by *D. pulicaria*. We interpreted these results as the probability of mesotrophic conditions for each scenario of P load and grazer dominance in lakes Mendota and Monona.

We also conducted similar modeling analyses for lakes Waubesa and Kegonsa, but results are not reported here because lake TP and Secchi transparency were not responsive to P loads for many reasons. First, the volumetric P loads for those lakes were considerably larger than for Mendota and Monona, which may explain why Waubesa and Kegonsa had elevated dissolved reactive (inorganic) P concentrations (DRP) during many summers (Lathrop 2007). Elevated DRP is an indicator that algal growth was not limited by P; thus, water quality in the lower 2 Yahara lakes during 1980–2008 was unresponsive to variations in annual P loads because the loads in most years were so large. In addition, the lower 2 lakes are relatively shallow (compared to Mendota and Monona) and therefore are subject to high internal recycling rates of P from the bottom sediments throughout the summer. Furthermore, *Daphnia* data were not available to compute a grazing index for Waubesa and Kegonsa; therefore, any variance due to grazing could not be accounted for in regression models.

Results

P loads to the Yahara lakes

Trends in Mendota's monitored subwatershed P loads:

The most reliable indicators of trends in annual P load to Lake Mendota were from its monitored subwatersheds where daily P loads have been calculated since 1976 for Pheasant Branch, and for 1976–1980 and since 1990 for the Yahara River (Fig. 2). Annual P loads (Nov–Oct) in both subwatersheds exhibited considerable year-to-year variation that included 2-year droughts (1987–1988, 2002–2003, 2011–2012) and years of extreme runoff events causing massive flooding (1993, 2008) as well as years with significant January–March runoff loadings (1993, 1994, 1997, 2005, 2009; Lathrop 2007). We included available loading data for 2009–2012 to indicate more recent P loading trends. From 1976 through 2012, the annual P loads varied considerably in the 2 monitored tributaries to Lake Mendota. Since 1990 when both sub-

watersheds have been monitored continuously, Pheasant Branch P loads trended slightly downward, possibly due to the construction of an in-stream sedimentation pond in 2001 (Gebert et al. 2012), while the Yahara River P loads exhibited no changing trend.

Outlet P loads: The annual outlet P loads for all 4 Yahara lakes were highly correlated and exhibited significant interannual variability (Fig. 3). In general, because of greater river flows sequentially down the Yahara River chain, the outlet P loads for the lake immediately downstream were slightly higher than for the upstream lake. In some years, Kegonsa's outlet P load was notably higher than the other lake outlet loads, which reflected Kegonsa's higher outlet flow rates combined with its usually highest lake P concentrations. The outlet P loads for the 4 lakes also mirrored the periods of major droughts and extreme runoff events in the long-term record. For the 1987–1988 drought, the full effect on outlet P loads was delayed to 1988–1989 due to less water leaving Mendota (and the other lakes) at the end of the drought. The 2-year drought of 2002–2003 also produced relatively low outlet P loads for the lakes in 2003; however, outlet P loads for years preceding that drought were generally much higher than during years preceding the late 1980s drought.

Volumetric P loads: The long-term record of volumetric annual P loads for each of the 4 Yahara lakes were plotted as a set of probability distributions (Fig. 4). For each lake, the distribution of volumetric annual loads is skewed due to a few extremely high load years (e.g., 1993 and 2008). The most important finding of this analysis is that the P loads to each lake were substantially larger with greater load modes (and means) and variance for each successive downstream lake; Waubesa's and Kegonsa's load distributions were relatively similar but had large modes and variance compared with Mendota's loads, with Monona being intermediate. Even comparing Mendota's and Monona's volumetric annual P loading distributions for 1976–2008, the P loads to Monona were higher than any loads calculated for Lake Mendota except for the most extreme loading years of 1993 and 2008. Conversely, the drought P loads to Mendota were lower than any loads recorded for Monona. We believe these volumetric P loading comparisons help explain why the lower lakes, especially Waubesa and Kegonsa, were less responsive to variations in P loading during the long-term record. The quantity of P flowing into those lakes was probably so large that algae growth was not P limited during many summers.

Average P loads for the Yahara lakes: Mendota had the highest average input load followed by Monona, Kegonsa,

and Waubesa (Table 2); however, the importance of the river load from the upstream lake was evident for the lower 3 Yahara lakes. Excluding dry fallout and other minor sources of P load, Mendota's outlet P load constituted 60% of Monona's total surface water input load (outlet plus direct drainage loads). For Waubesa, the upstream outlet river load was 83% of the combined surface water sources; for Kegonsa, the river load was 76% of the combined sources.

Lake outlet pass-through load factors

All input:outlet P load relationships for the 4 Yahara lakes were approximately linear, although individual lakes had different regression slope coefficients or outlet pass-through factors (Fig. 5; Table 2). Thus, a percentage of the P loading reduction realized by implementing effective land management practices in the direct drainage basin of a given lake is predicted to occur in that lake's outlet P load flowing to the next lake downstream. For P load reductions to Lake Mendota, the reduced P load cascades to all 3 lower Yahara lakes. For example, using our empirically derived pass-through factors, a 10,000 kg reduction in P load to Mendota on average is predicted to produce a P load reduction of 2650 kg to Monona (10,000 kg × 0.265). That P load reduction to Monona is predicted to result in a 1550 kg load reduction to Waubesa (2650 kg × 0.586), and in turn a 1450 kg reduction to Kegonsa (1550 kg × 0.935). Kegonsa's outlet P load to the lower Yahara River is also predicted to decrease by 1130 kg (1450 kg × 0.779). These P load reductions are averages at steady-state; in some years the pass-through benefits will be larger and in other years they will be smaller. Nonetheless, the average steady-state reductions are instructive and demonstrate the pass-through benefits of improving upstream water quality.

As expected, the outlet pass-through load factors were inversely related in ranked order to each lake's long-term mean flushing rate. Thus, Lake Mendota with the slowest flushing rate (0.23 yr⁻¹) retained the most P entering the lake each year. Lake Waubesa with the fastest flushing rate (4.3 yr⁻¹) had relatively little P retained in the lake. Lakes Monona and Kegonsa with flushing rates of 1.3 and 3.0 yr⁻¹, respectively, corresponded in similar order to the amount of P retained in the 4 lakes.

Summer lake water quality

Analyses of summer water quality conditions represented July and August when blue-green algal blooms were the most troublesome during the summer recreation season. Using both TP and Secchi TSI indicators of July–August water quality, Mendota and Monona generally exhibited

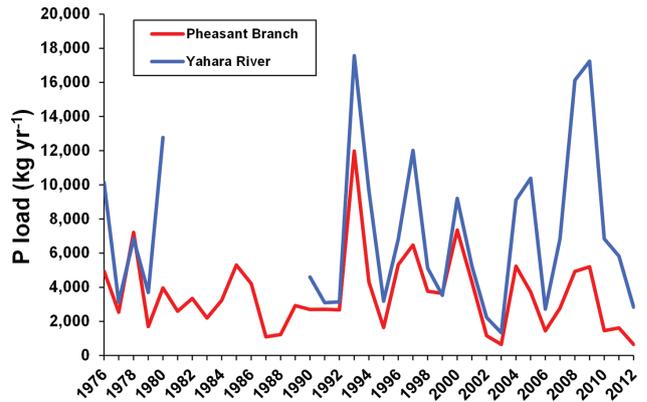


Fig. 2. Annual P loads (kg yr⁻¹) for the Pheasant Branch and Yahara River monitored subwatersheds draining to Lake Mendota, 1976–2012 (Nov–Oct). Loading data: 1976–1989 from Lathrop (1998); 1990–2011 from USGS.

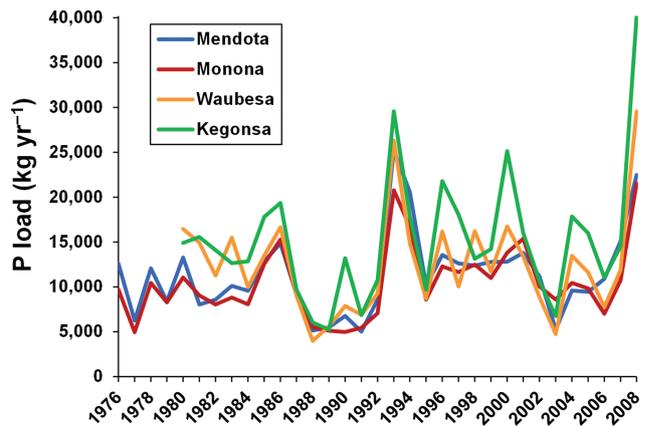


Fig. 3. Outlet P loads (kg yr⁻¹) for the 4 Yahara lakes, 1976–2008.

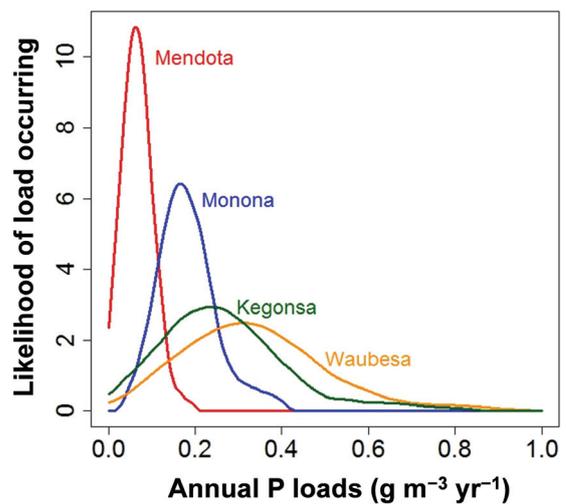


Fig. 4. Likelihood distributions of normalized annual P loads (g m⁻³ yr⁻¹) for the 4 Yahara lakes based on 1976–2008 loading data (Kegonsa 1980–2008). P loads are normalized by dividing each lake's set of annual P loads by the lake's volume.

eutrophic conditions while Waubesa and Kegonsa exhibited highly eutrophic conditions. Median TP concentrations of all July–August median values for 1980–2012 in the 4 Yahara lakes were: Mendota (0.032 mg L⁻¹), Monona (0.034 mg L⁻¹), Waubesa (0.064 mg L⁻¹), and Kegonsa (0.077 mg L⁻¹). Median July–August Secchi disk readings were: Mendota (1.9 m), Monona (1.6 m), Waubesa (0.9 m), and Kegonsa (0.9 m).

Each year's median July–August TP concentrations for 1980–2012 was highly correlated for Mendota and Monona and for Waubesa and Kegonsa (Fig. 6). While Mendota and Monona often had median TP concentrations well into the eutrophic TP-TSI region, TP was low enough in some summers to reach mesotrophic conditions (<0.024 mg L⁻¹). Both lakes notably exhibited mesotrophic TP conditions in 1988 in response to the 2-year drought. Although summer TP concentrations in Waubesa and Kegonsa were much higher than in Mendota and Monona, TP dropped close to the mesotrophic boundary in response

to the late 1980s drought. Conversely, when the lakes experienced extreme P loads (e.g., 1993 and 2008), July–August TP concentrations returned to more normal levels in 1–2 years when loads declined.

In summers when TP concentrations were high, DRP concentrations were often well above analytical detection, especially in Waubesa and Kegonsa, but also occasionally in the deeper lakes (Fig. 7). Thus, during summers when TP was high due to high P loadings (external and internal), algal growth was likely not limited by P because the turnover rate of DRP would not have been as rapid as when DRP was undetectable; DRP-starved algae would have removed it as fast as it became available. This finding was in contrast to other seasons when DRP has been high in the Yahara lakes (Lathrop 2007, Hoffman et al. 2013).

July–August TP concentrations during 1980–2012 suggested a declining trend in TP had occurred, with the greatest decline in Mendota and the least in Kegonsa,

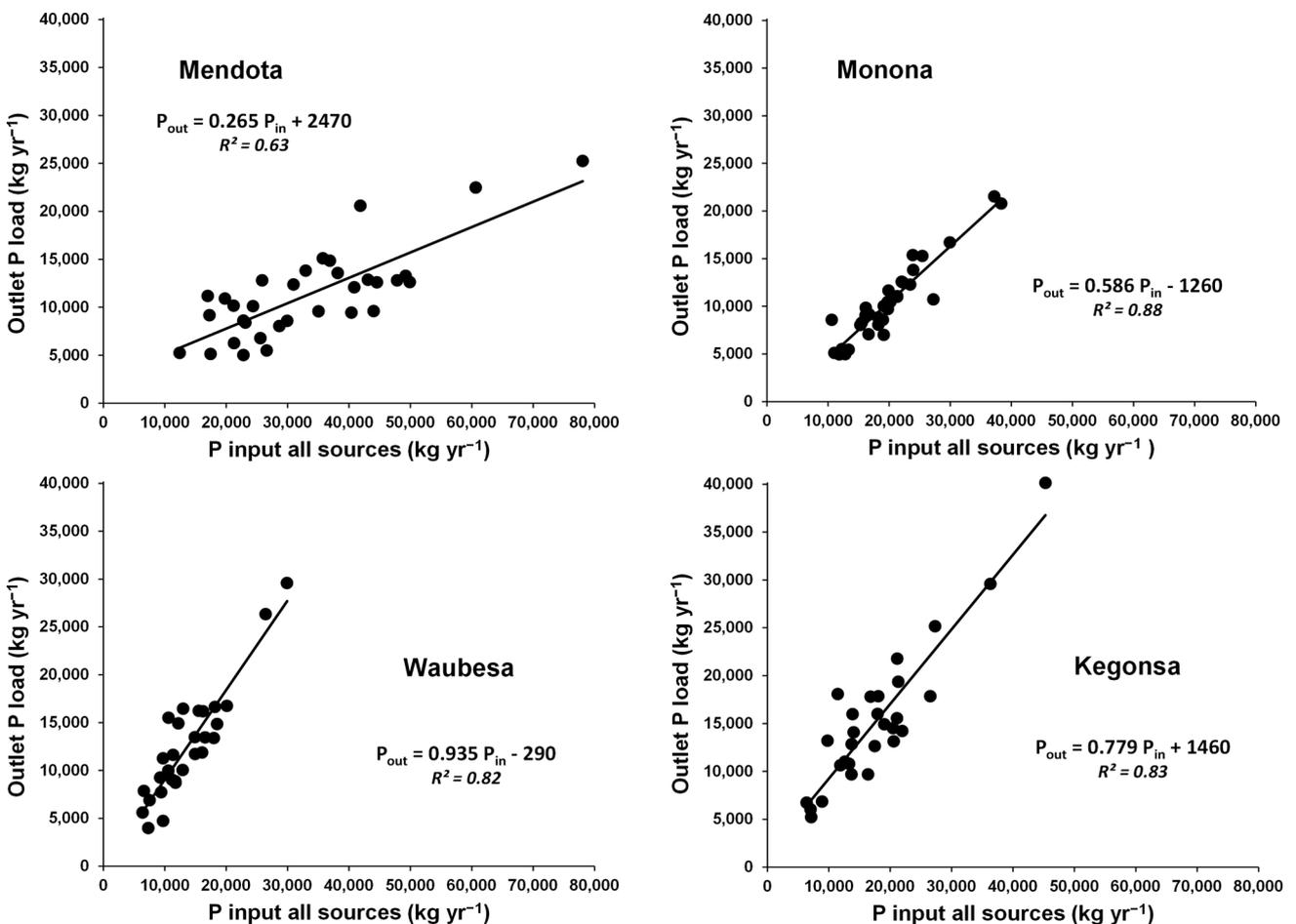


Fig. 5. Annual outlet P loads vs. annual P input loads for each of the 4 Yahara lakes. Each lake's outlet pass-through loading factor is the slope of the linear regression derived from each set of P loads. Mendota and Monona analyses are from 1976–2008 annual loading data; Waubesa and Kegonsa analyses are from 1980–2008 data.

Table 2. Summary of annual input and outlet P loads for the 4 Yahara lakes for 1976–2008, including average P loads during late 1980s drought, outlet P loads as proportion of P input loads, P load reduction targets, and 50% P load reduction scenario for the 4 lakes.

	Mendota	Monona	Waubesa ¹	Kegonsa ¹
<u>P Load Summary:</u>				
Long-term average P load entering lake from all sources (kg yr ⁻¹) ²	33,400	20,000	13,300	17,700
Average load entering lake from direct drainage sources (kg yr ⁻¹)	29,600	7500	2100	4000
Average load entering lake from upstream lake outlet (kg yr ⁻¹)	–	11,400	10,400	12,500
Load estimate from other sources (kg yr ⁻¹) ³	3800	1100	700	1100
Average load leaving lake outlet (kg yr ⁻¹)	11,400	10,400	12,500	15,200
Lake outlet load as proportion of total input load ⁴	0.265	0.586	0.935	0.779
Average total input load during late 1980's drought (kg yr ⁻¹) ⁵	17,400	11,700	6800	7100
Average P load reduction needed to meet drought target load (kg yr ⁻¹)	16,000	8300	6500	10,600
Target load reduction as percent of all loading sources	48%	42%	49%	60%
Target load reduction as percent of direct drainage load sources	54%	–	–	–
<u>P Load Reduction Scenario:</u>				
50% load reduction from direct drainage sources to lake (kg yr ⁻¹)	14,800	3750	1050	2000
Load reduction passed through from upstream lake reduction (kg yr ⁻¹) ⁶	–	3920	4490	5180
Total load reduction to lake (kg yr ⁻¹)	14,800	7670	5540	7180
Total load reduction as percent of load reduction needed to meet drought target	93%	92%	85%	68%

¹Waubesa outlet P load and all Kegonsa P loads are for 1980–2008.

²Long-term average P load to Mendota is 34,500 kg yr⁻¹ if a 1984 fertilizer spill of 4000 kg P in the lake's watershed is included in average.

³Other P sources include previously derived average estimates for dry fallout and precipitation (minor). For Mendota, the average estimate for other sources also includes a small P input from groundwater; the 1984 fertilizer spill in the lake's watershed is excluded in the average estimate.

⁴Proportion is slope coefficient of linear regression of each lake's outlet load versus total input load for all loading years.

⁵Drought effect is average of 1987–1988 P loads for Mendota and 1988–1989 for other 3 lakes.

⁶Pass-through P load reduction is total load reduction to upstream lake multiplied by that lake's outlet:input load proportion.

but the trends were not statistically significant due to the high annual variability in TP. While in-lake water quality conditions exhibited the same general trend as watershed P loadings to the lakes during this same time period, we believe the relatively rapid TP response of the lakes (including Mendota) to extremely high or low P loads provides strong evidence that the lakes would respond quickly to major P load reductions.

Median July–August Secchi disk transparency readings were highly variable for Mendota and to some extent for Monona (Fig. 8); Secchi readings were significantly lower with relatively little variability for much more eutrophic Waubesa and Kegonsa. For Mendota, median Secchi readings were in the mesotrophic TSI condition for almost half the years. Monona exhibited mesotrophic Secchi conditions during just 3 summers while Waubesa and Kegonsa did not approach the

mesotrophic Secchi boundary during the study period. Mendota and Monona's greatest Secchi readings during 1976–2012 occurred in 1988 in association with the 2-year drought.

Lake response modeling

Lake Mendota: Our modeling results indicated that the probability of July–August days with mesotrophic water quality conditions in Lake Mendota would increase if the average distribution of P loads to the lake were to decline, although the results were different for the TP (<0.024 mg L⁻¹) and Secchi (>2.0 m) TSIs (Fig. 9 and 10). Our results also indicated that food web dynamics that affect algal grazing by *Daphnia* zooplankton had a strong influence on the probability of mesotrophic conditions in Lake Mendota.

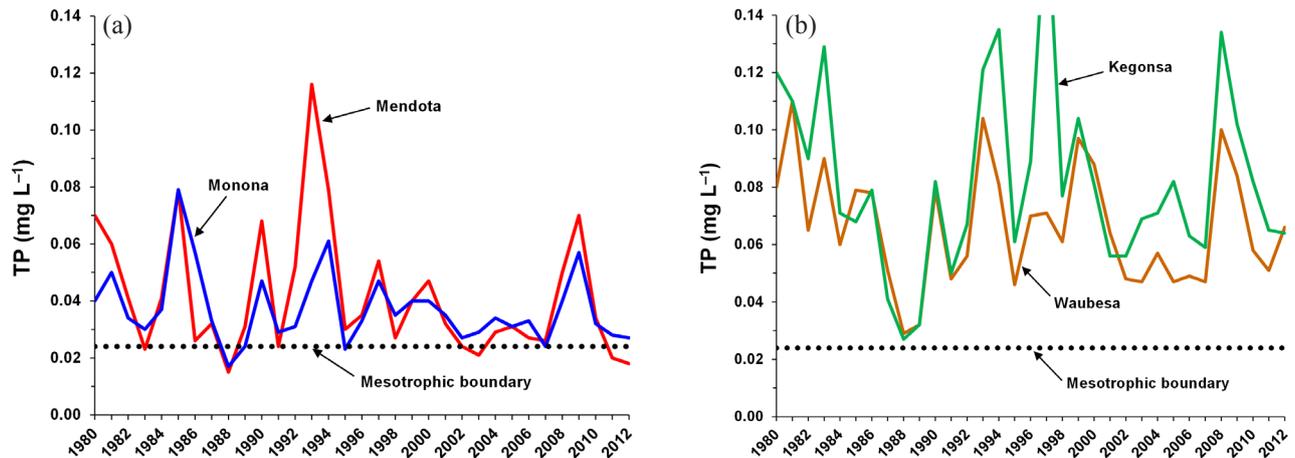


Fig. 6. Total P concentrations in the surface waters of lakes plotted as the median of each year's July–August summer values during 1980–2012. TP < 0.024 mg L⁻¹ signifies mesotrophy; TP > 0.024 mg L⁻¹ signifies eutrophy: (a) lakes Mendota and Monona; (b) lakes Waubesa and Kegonsa.

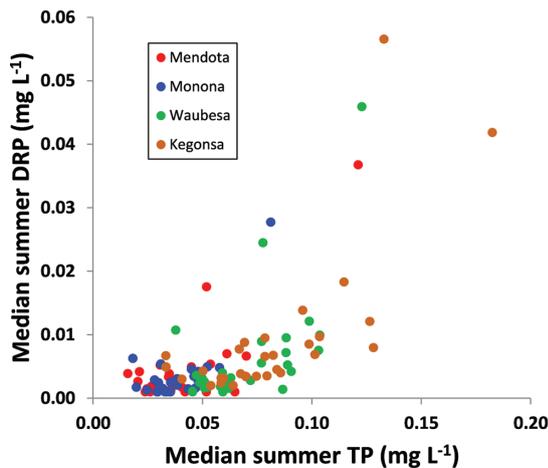


Fig. 7. Median summer TP vs. median summer dissolved reactive P (DRP) for the 4 Yahara lakes, 1980–2008.

Under current loading conditions, combined with grazer dominance of the large-bodied *D. pulicaria* grazer, the probability of lake TP in the mesotrophic state was slightly less than 0.2, or almost 2 of 10 July–August days on average over many years (Fig. 9). If average future P loads were reduced by 50% with the same grazer dominance, then the probability of mesotrophy during July–August was predicted to be almost 4 of 10 days using the TP-TSI indicator. Conversely, if average future P loads substantially increased, then the lake would exhibit eutrophic conditions on most July–August days.

The importance of algal grazing by *Daphnia* was identified in our modeling results for Lake Mendota. Prior studies indicated that when *D. pulicaria* was effectively eliminated in a particular year due to predation by large densities of planktivorous fish, then the lake was only populated for short periods in late spring by the smaller-bodied *D. galeata mendotae*, a zooplankton species that

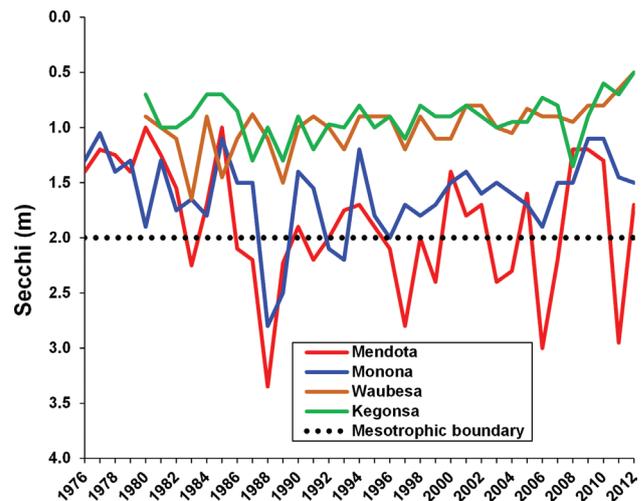


Fig. 8. Secchi disk transparency readings for the 4 Yahara lakes plotted as the median of each year's July–August summer values during 1980–2012. Secchi >2.0 m signifies mesotrophy; Secchi <2.0 m signifies eutrophy.

significantly reduced grazing pressure on algae (Lathrop et al. 1996, 1999, 2002). Thus, under current P load conditions and without the presence of the large grazer, the probability of lake TP being in the mesotrophic state is only about 0.05 (i.e., 1 of 20 days) on average over many summers (Fig. 9). Under these same reduced algal grazer conditions but with a 50% P load reduction, the TP mesotrophic probability increases to about 0.15 (i.e., 3 of 20 days), which is close to the probability under the current distribution of P loads with the large grazer present (i.e., 0.2). In other words, our TP-TSI modeling results indicate that a 50% P load reduction could be negated by a food web shift causing the loss of the large-bodied *D. pulicaria* grazer in the lake.

Our modeling results for the Secchi-TSI indicate that Lake Mendota was mesotrophic 6 of 10 summer days on

average when the large grazer was present (Fig. 10). During summers when the large grazer was absent, the lake was mesotrophic only 2 of 10 days. Thus, the Secchi-TSI indicator recorded substantially higher probabilities of mesotrophy than the TP-TSI indicator. Our modeling results also indicated that Secchi-TSI probabilities would only increase about 1 additional day of 10 if future P loads were reduced by 50% for either *Daphnia* grazer condition.

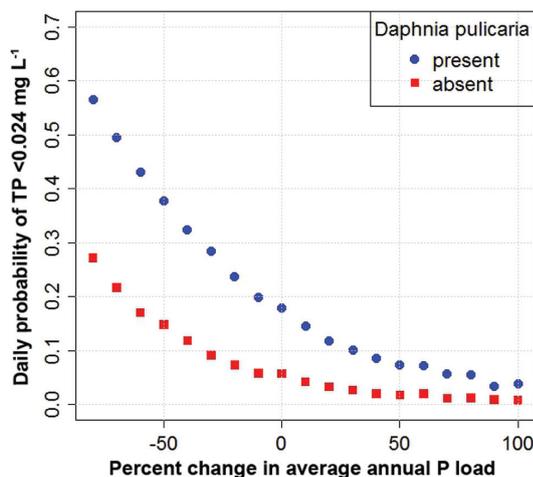


Fig. 9. Daily probability of Lake Mendota having a surface water TP concentration $<0.024 \text{ mg L}^{-1}$ (mesotrophy) during July–August relative to the long-term average P load condition and the presence or absence of the large-bodied *Daphnia pulicaria* grazer. A 0% change in average annual P load represents the 1976–2008 period. The percent change in P load is relative to the current long-term average load with its associated annual load variability.

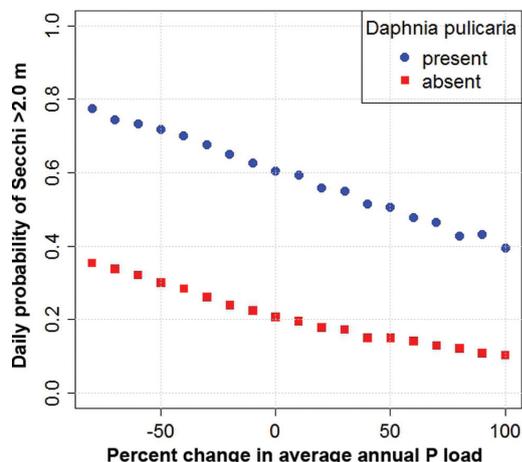


Fig. 10. Daily probability of Lake Mendota having a Secchi disk transparency $>2.0 \text{ m}$ (mesotrophy) during July–August relative to the long-term average P load condition and the presence or absence of the large-bodied *Daphnia pulicaria* grazer. A 0% change in average annual P load represents the 1976–2008 period. The percent change in P load is relative to the current long-term average load with its associated annual load variability.

Lake Monona: Modeling results for both TP and Secchi TSI indicators of mesotrophy in Lake Monona were generally similar to results for Lake Mendota with some important differences (Fig. 11 and 12). Monona’s TP-TSI probability of mesotrophy is predicted to increase from 0.2 to 0.3 (i.e., from 2 to 3 of 10 days) with an average P load reduction of 50% from current loads when the large-bodied *Daphnia pulicaria* is present; the probability increases from 0.1 to 0.2 when the large *Daphnia* grazer is absent (Fig. 11). For the Secchi-TSI indicator, a 50% P load reduction is predicted to increase mesotrophy probabilities from about 0.35 to 0.45 when the large grazer is present, and from about 0.25 to 0.35 when the large grazer is absent (Fig. 12). Thus, modeling results for both TSI indicators suggest a 50% P load reduction would only produce a net gain of about 1 of 10 days of mesotrophy in Lake Monona for either algal grazing condition.

Drought P loading targets

Because all 4 Yahara lakes responded with dramatically reduced in-lake P concentrations during the late 1980s drought, we believe the average annual P loads estimated for that drought period provide a good P loading target for management efforts (Table 2). The drought loading targets can then be used to determine what percentage reduction in average P load is needed from each lake’s total load, as well as direct drainage sources for Mendota. For Mendota, average P loads would need to be reduced by 48% based on all P loading sources, or 54% based on direct drainage sources, to meet the drought loading target. Similarly, the P load reduction from all sources to meet the drought target is estimated to be 42% for Monona, 49% for Waubesa, and 60% for Kegonsa.

Scenario for P load reductions

We developed a scenario that reduced the average P load by 50% from each lake’s direct drainage loading sources by utilizing all the P loading information and lake outlet pass-through factors generated in our study (Table 2). In the scenario, the load reduction was greatest in the Mendota watershed because that lake’s drainage source load represents nearly 70% of the direct drainage loads for all 4 lakes combined. In addition, this scenario demonstrated the cascading benefit to downstream lakes by reducing P loads to lakes farther upstream. For the 50% direct drainage load reduction scenario, Mendota’s pass-through load reduction to Monona is about equal to Monona’s direct drainage load reduction that would be achieved by management practices installed in that lake’s urban basin (excluding storm sewer basins draining directly to Lake Wingra due to its P load attenuation effect). For Waubesa, the pass-through load

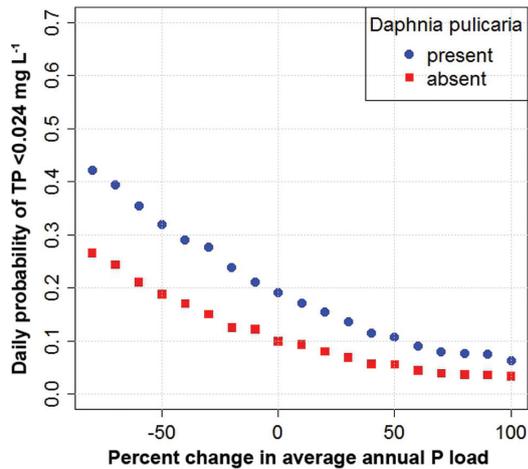


Fig. 11. Daily probability of Lake Monona having a surface water TP concentration $<0.024 \text{ mg L}^{-1}$ (mesotrophy) during July–August relative to the long-term average P load condition and the presence or absence of the large-bodied *Daphnia pulicaria* grazer (see Fig. 9).

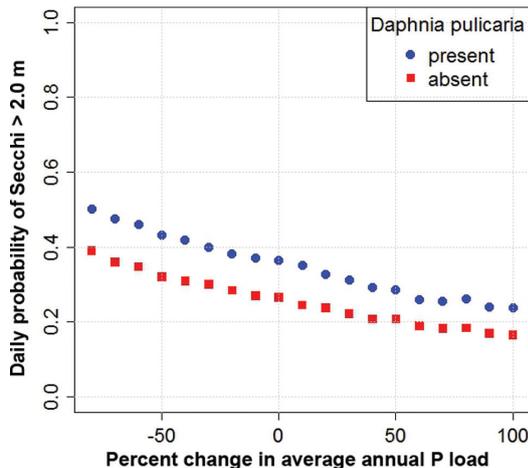


Fig. 12. Daily probability of Lake Monona having a Secchi disk transparency $>2.0 \text{ m}$ (mesotrophy) during July–August relative to the long-term average P load condition and the presence or absence of the large-bodied *Daphnia pulicaria* grazer (see Fig. 10).

reduction from Monona is 4 times Waubesa's direct drainage load reduction. For Kegonsa, the pass-through reduction from Waubesa is about 2.5 times the direct drainage load reduction.

For Mendota and Monona, the total load reduction to each lake predicted in the scenario represents 92–93% of the target load reduction needed to achieve the late 1980s drought loading target for each lake. For Waubesa and Kegonsa, the reductions represent 85 and 68% of the respective target load reductions needed. Thus, to meet P loading reduction goals for the lower Yahara lakes, substantial P loading reductions are needed in the Mendota watershed; our recommendation is a reduction of 50% as a stated goal for the Yahara CLEAN Project. Given the

importance of pass-through load reductions to Waubesa and Kegonsa relative to direct drainage load reductions, priority should be given to reducing Mendota's P loading sources, followed by Monona's P sources. The 50% average annual P load reduction goal for Mendota is still much higher than the estimated average surface water input load from Mendota's watershed prior to European settlement in the early 1800s (Soranno et al. 1996).

Reducing outlet pass-through P loads relative to downstream direct drainage loads is also critical because P coming from a lake outlet is likely almost all "biologically available" for algal growth. Phosphorus originating from direct drainage sources is not all biologically available, however, because some of the P is strongly bound to sediments in runoff and not easily released in a biologically available form. Thus, even more priority should be given to reducing P sources in Mendota's watershed for the pass-through benefits downstream.

Discussion

Long-term P loading data substantiated the occurrence of summer blue-green algal blooms in the 4 Yahara lakes after all wastewater inputs were diverted more than 50 years ago. Phosphorus loads to Lake Mendota, the headwater lake in the Yahara chain of lakes, were directly tied to agricultural and urban nonpoint pollution carried by runoff in streams and storm sewers from the lake's large watershed. As a result, annual loads to Mendota since 1976 have been highly variable, ranging from relatively low P loads during drought years with little runoff to years with extreme runoff events that produced massive P loads. Large P loads also occurred in some years during January–March (Lathrop 2007) when the ground was frozen, thus allowing snowmelt and/or water from relatively light rains to run off from Mendota's rural subwatersheds where raw manure had been extensively applied.

Annual P loads to downstream Monona, Waubesa, and Kegonsa also exhibited high variability. Runoff from lands draining directly to each lake contributed to annual loads, but the principal source of loading to each lake was from the outlet of the respective upstream lake. For Waubesa and Kegonsa, the upstream lake outlets contributed on average about 80% of the P load from all surface water inputs to each lake. For Monona, about 60% of its surface water P load came from Mendota. These outlet loads were affected by the amount of water flowing in the Yahara River as well as P concentrations in the upstream lakes. Because Waubesa and Kegonsa are much shallower and smaller in surface area and volume than Mendota (with Monona being intermediate), the volumetric P loads were much larger for the shallower lakes. In addition, Waubesa and Kegonsa may be subject

to greater internal P loading due to the large area of epilimnetic waters in contact with bottom sediments.

Thus, lake depth and lake flushing rate dictated the high P input load passing through Waubesa and Kegonsa compared with Mendota (with Monona being intermediate). These relationships also confirmed that management practices to reduce P loads should be emphasized in Mendota's watershed, with second priority given to Monona's direct drainage basin. Improved water quality upstream cascades down the Yahara lake chain—a finding that has helped convince downstream lake users that money spent for management practices in Mendota's watershed would benefit their lakes.

While the annual P loads to all 4 lakes were variable, in-lake TP concentrations during summer (Jul–Aug) corresponded consistently and relatively rapidly to the magnitude of those loads. When P loads were unusually high, summer TP was also high. In such summers, DRP was also elevated (especially in Waubesa and Kegonsa), a sign that algal growth was not P limited at that time. When annual loadings subsequently declined, however, lake TP also declined. Conversely, when P loads were low from prolonged droughts such as in 1987–1988, lake TP declined and even reached mesotrophic conditions ($<0.024 \text{ mg L}^{-1}$) in Mendota.

This same drought caused low river flows and reduced TP in Mendota, diminishing loads to the lower 3 lakes in 1988–1989. Monona also achieved mesotrophy, but shallower Waubesa and Kegonsa did not, even though TP declined to its lowest level ($\sim 0.030 \text{ mg L}^{-1}$) since 1980 in the lower 2 lakes. This rapid response of all the Yahara lakes to changes in P loads is encouraging, indicating that immediate improvements can be expected in the lakes if management can successfully decrease P loads.

While the Yahara lakes' water quality improves with drought-induced reductions of P loading, aggressive management is needed to sustain improvements in water quality. Long-term trends in water quality are not significant despite considerable effort to mitigate eutrophication (Lathrop 2007). Trends toward greater impervious surface in the watershed, higher densities of livestock, and more extreme rainfall and runoff events may partially offset the benefits of management actions to date. Thus, P load reductions of at least 50% in each of the 4 direct drainage basins are recommended to improve water quality, with most emphasis on the relatively large watershed of Lake Mendota; however, much deeper cuts to future P loads may be needed if trends in land use and runoff patterns continue.

Although lake TP concentrations were linked to P loads, and hence were a good indicator of a lake's trophic state, Secchi disk readings sometimes produced different results, partly explained by the types of blue-green algal blooms that occur in the middle of the lake

where limnological measurements were made. When TP concentrations were low, algal densities were also low and Secchi readings were relatively deep; both TP and Secchi TSIs signified mesotrophy. When TP levels were moderate to high, however, water clarity varied depending on the degree of *Daphnia* grazing on algae.

If large-bodied *Daphnia pulicaria* were absent, then smaller species of blue-green algae could dominate, reducing water clarity and causing the water to appear green throughout the whole lake. If *D. pulicaria* were present, then the smaller algae were removed by grazing, allowing larger filamentous and colonial blue-green algae to grow and dominate because they are not effectively controlled by grazing. Because many of these larger blue-green species have gas vacuoles that cause the algae to be buoyant, moderate winds can clear the middle of the lake as the algae are pushed to downwind shorelines where noxious floating scums can sometimes pile up. Our modeling results are consistent with this grazing effect.

Because Secchi readings are strongly affected by *Daphnia* grazing on algae, which in turn is mediated by food web dynamics controlled by fish and invertebrate predation, Secchi-TSIs can indicate mesotrophy when TP-TSI values indicate eutrophy. The recent invasion by the spiny water flea (*Bythotrephes longimanus*, a predator on *Daphnia*) or the potential invasion by zebra mussels (*Dreissena polymorpha*, which enhance algal grazing) could strongly affect Secchi-TSIs. We therefore believe summer TP concentrations (or TP-TSI values) are a more useful indicator of lake water quality improvements due to P loading reductions. Secchi transparency readings (or Secchi-TSI values), which are more easily understood by lake users, can indicate food web dynamics in the lake, including changes that might occur from invasive species or fishery management.

The Yahara lakes, like many lakes in agricultural watersheds, are eutrophied by large nonpoint inflows of P. The response of the lakes to drought indicates that sharp, if temporary, reductions in P load cause notable improvements in water quality. Thus, P reduction has significant benefits despite the long history of excessive P inputs, a finding that offers some hope of mitigating eutrophication in these and other lakes subject to agricultural runoff. Our long-term data also indicate that management of fisheries and exclusion of invasive species are important determinants of water quality. Increased algal grazing by *Daphnia* can produce clearer water even during summer, although large colonial and filamentous blue-green algae that are not grazed may pile up as noxious floating scums on downwind shorelines if P loads are too high.

While the importance of P load reduction and intensive grazing are known from many lakes, the mitigation of eutrophication by a reduction of nonpoint pollution is

difficult (Jeppesen and Sammalkorpi 2002, Sondergaard et al. 2007). Substantial and sustained commitments to nonpoint P load abatement are required to remedy eutrophication in the Yahara lakes, as with many other lakes around the world.

Acknowledgements

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A Balanced Diet for Lake Erie

Reducing Phosphorus Loadings and Harmful Algal Blooms

A Report of the Lake Erie Ecosystem Priority
February 2014

For More Information

For more information on the Lake Erie Ecosystem Priority or the International Joint Commission (IJC), please visit the IJC's website: www.ijc.org. Information also can be obtained by contacting any of the following IJC offices:

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Signed this 12th day of February, 2014, pursuant to Article 7 of the Great Lakes Water Quality Protocol of 2012, which gives the International Joint Commission the responsibility to provide advice and recommendations to the United States and Canadian governments on matters covered on the Annexes to the Agreement. This report addresses the challenge of nutrient pollution in Lake Erie.

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Foreword

The problem of excess nutrients in Lake Erie and resulting algal blooms has challenged scientists and troubled the public for more than 50 years. Stirred by public concern, governments responded with vigor to the problem in the 1960s and 1970s, resulting in measurable reductions in phosphorus inputs and a steep reduction in algal blooms. By the mid-1980s, the rapid recovery of Lake Erie was a globally-known success story.

However, Lake Erie is once again severely threatened. It is the shallowest of the Great Lakes, the warmest and the most susceptible to eutrophication and the effects of climate change. The recent accelerating decline of this lake, manifested as impaired water quality, massive, summer-long algal blooms, hypoxia and fish kills, has focused binational attention on the need for urgent actions to reduce external inputs of phosphorus. While Lake Erie's health suffers from multiple stressors, the rising proportion of dissolved reactive phosphorus is seen as the primary cause of this decline.

The return of severe Lake Erie algal blooms in the 2000s has again galvanized public concern and a governmental response. The worst algal bloom ever experienced on the lake occurred in 2011, prompting the International Joint Commission (IJC) to make binational investigation into the science and opportunities for action by governments to reduce algal bloom-causing pollution a priority.

The IJC recognizes and applauds the commitment of the United States and Canadian governments to restoring the lake's health. The United States Great Lakes Restoration Initiative is providing substantial funding to Lake Erie Basin restoration. The Canadian Great Lakes Nutrient Initiative is also contributing substantially to understanding the sources of excess nutrients and measures to reduce them. However, in carrying out the Lake Erie Ecosystem Priority, the IJC finds that more needs to be done.

The IJC offers its analysis and recommendations in this report in a spirit of cooperation, recognizing that today's challenges to Lake Erie's health are formidable and require the leadership and guidance of the United States and Canadian governments and collaboration by all sectors of society to again make the recovery of Lake Erie a globally-known success story.

Acknowledgements

This report is the product of a binational cooperative effort that involved more than 60 scientists, engineers, planners and technical experts in Canada and the United States. The IJC expresses its sincere appreciation to these individuals for their contributions to the planning, applied research and analysis that went into the preparation of this report. Their collaborative efforts have produced findings and recommendations that will enable the governments of Canada and the United States to more effectively address the challenges facing Lake Erie and the millions of citizens who depend on and enjoy its waters.

The current Commission would like to acknowledge and recognize the role of former Canadian Commissioners Lyall Knott, Pierre Trepanier and Joe Comuzzi (Chair) in establishing the study of Lake Erie as a Commission priority in 2012.

The IJC also acknowledges and thanks the many members of the public who participated in the outreach events in 2012 and 2013 and who provided valuable comments on Lake Erie's challenges and possible actions to address those challenges.

A detailed list of contributors to this report is provided in Appendix I.

We note, however, that the findings and recommendations in this report are solely the responsibility of the IJC.

*This report is dedicated to the memory of Dave Dolan (1949-2013) of the University of Wisconsin, with thanks for a lifetime of work improving our understanding of the Great Lakes. Dave contributed significantly to the **Taking Action on Lake Erie** scientific work group.*



2011 Algal Bloom, Lake Erie, Western Basin

NASA

Executive Summary

In 2011, Lake Erie experienced its largest algal bloom in history. In 2012, the International Joint Commission (IJC) established the **Lake Erie Ecosystem Priority (LEEP)** in response to a growing challenge: lake-wide changes in Lake Erie related to problems of phosphorus enrichment from both rural and urban sources, compounded by the influence of climate change and aquatic invasive species. These changes have resulted in impaired water quality, with impacts on ecosystem health, drinking water supplies, fisheries, recreation and tourism, and property values. This report presents the IJC's key findings and recommendations from the LEEP study.

The IJC is an independent binational organization created by Canada and the United States under the *Boundary Waters Treaty of 1909*. Under the Treaty, the two countries cooperate to prevent and resolve disputes relating to the use and quality of the many lakes and rivers along their shared border. The Great Lakes Water Quality Agreement (the Agreement) assigns the IJC a role in assessing progress, engaging the public and providing scientific advice to help the two countries restore and maintain the chemical, physical, and biological integrity of the waters of the Great Lakes.

Background

The smallest and shallowest of the five Great Lakes, Lake Erie has long experienced changes as a result of human activities and natural forces. With 11.6 million people living in its basin, and a watershed dominated

by big cities and sprawling farmland with little forest cover, Lake Erie is severely impacted by human activities.

In the decades leading up to the 1970s, loadings of nutrients, particularly phosphorus from municipal sewage treatment plants and other anthropogenic sources, visibly degraded Lake Erie. This excessive nutrient enrichment, known as eutrophication, resulted in severe algal fouling of the lake, which in turn created aesthetic, taste and odor problems, reduced available oxygen and led to fish die-offs. Great Lakes eutrophication prompted the governments of Canada and the United States to sign the Agreement in 1972, establishing a binational commitment to reduce nutrient loadings and clean up the lakes.

Following the signing, governments on both sides of the international border made significant investments to upgrade and expand municipal sewage treatment plants. In addition, governments took action to reduce phosphorus concentrations in household detergents. By the mid-1980s, Lake Erie phosphorus loadings were reduced by more than half from 1970s levels, and many of the problems associated with eutrophication were reduced or eliminated, confirming that reducing phosphorus loadings led to improved water quality. Lake Erie's recovery was a globally-recognized success story.

However, by the early 2000s, problems with excess nutrient enrichment appeared again in Lake Erie, and have since continued to worsen. In recent years, the problem of harmful and nuisance algal blooms has be-

come widespread. In 2011, heavy spring rains flushed a large amount of phosphorus into western Lake Erie. This was soon followed by warm temperatures, creating a mass of algae that extended more than 5,000 km² (about 1,930 mi²), three times larger than the next largest bloom previously recorded.

Although eutrophication is again a serious threat to Lake Erie water quality, the sources and remedies are different from those of the 1960s and 1970s. While sewage plants still contribute some phosphorus to Lake Erie, diffuse runoff from rural and urban lands is a leading factor in eutrophication. Of particular concern is runoff of dissolved reactive phosphorus, the portion of total phosphorus that is most readily available to support algae growth and thus a primary cause of renewed algal blooms. Addressing runoff requires strategies tailored to particular land uses, rather than controls on sewage plants alone.

The LEEP Study

The core objective of LEEP is to provide advice to federal, state, provincial and local governments in their development of policy and management practices to help restore the lake's ecosystem by reducing nutrient loads and resulting harmful algal blooms.

To reach this objective, the IJC established study teams of independent experts, who worked to develop a better scientific understanding of the causes and controls of phosphorus loading into Lake Erie. The LEEP work plan focused on *scientific* priorities, though it included *socio-economic* and *regulatory* themes as part of a comprehensive approach. Each theme was addressed by a series of binational working groups led by various IJC advisory boards and councils or by IJC staff.

Engaging the public was an important component of the LEEP project from the start. More than 400 individuals and organizations participated in roundtables, open houses and public meetings hosted by the IJC in communities across the Lake Erie Basin in both Canada and the United States in 2012 and 2013. In

addition, a draft of the report was made available for public review and comment. The more than 130 comments provided by lakeside residents, anglers, boaters, farmers and other concerned residents and organizations helped strengthen the analysis and recommendations in the LEEP report.

Phosphorus Loading to Lake Erie

Phosphorus is the key nutrient limiting the amount of phytoplankton and attached algae in Lake Erie.

The primary sources of phosphorus loadings to Lake Erie in the decades leading up to the 1972 Agreement were municipal sewage plants. Today, however, external phosphorus loads occur largely as runoff from diffuse land uses such as fertilized farm fields, lawns and impervious surfaces including streets and parking lots.

Of the 2011 loadings, it is estimated that more than one-half came from tributaries into Lake Erie that are monitored, such as in larger agricultural areas and rural communities. Unmonitored areas, typically coastal communities and smaller agricultural areas adjacent to shorelines, and direct point sources were estimated to each account for about 16%, while Lake Huron and atmospheric sources each accounted for between 4-6% of external loadings.

Agricultural operations are a major source of phosphorus loadings into Lake Erie. These loadings result primarily from fertilizer application and manure. The bulk of this input occurs during spring snowmelt and heavy rainstorms, when significant amounts of phosphorus can be transported by runoff water.

Phosphorus from urban areas is associated with construction activities, stormwater runoff, combined sewer overflow discharges, lawn and garden activities, leaves from deciduous trees and pet waste. Pinpointing exact amounts of phosphorus loadings from the multitude of urban land uses is often difficult.

The atmosphere is another source of phosphorus loading. Atmospheric deposition represented an

estimated 6% of the total external load to Lake Erie in 2011. Phosphorus can find its way from the airshed into lake ecosystems through inputs to the watershed from rain or snowfall and by wind-transported particles.

Data-driven models show the existence of “hot spots” – locations in sub-basins within the major watersheds – that contribute a disproportionate share of the total amount of dissolved reactive phosphorus entering Lake Erie. The single largest source of dissolved reactive phosphorus that generates harmful algal blooms in the western basin of Lake Erie is the Maumee River.

A Lake Experiencing Profound Changes

Lake Erie continues to experience serious changes as a result of phosphorus loading, compounded by the growing influence of climate change. Precipitation patterns in the Lake Erie Basin under climate change are characterized by less frequent but more intense storms. Such intense events lead to higher nutrient runoff from agricultural and urban lands, and increased overall nutrient loads to Lake Erie. Depending on the timing of runoff, future nutrient loading, coupled with warmer water temperatures, could lead to increased severity and frequency of algal blooms.

Algal Blooms

Some species of algae and cyanobacteria (‘blue-green algae’) in Lake Erie can constitute harmful and nuisance algal blooms. Free-floating mats of cyanobacteria *Microcystis* and *Anabaena* predominate in the lake’s western basin and have the potential to produce toxins that pose a significant risk to fish, wildlife and human health. Some areas of the western basin also are affected by dense bottom mats of *Lyngbya*, which is a non-toxic but odorous cyanobacteria that has been reported in the Maumee Basin and other areas. In the eastern basin, large shoreline blooms of the attached filamentous green algae *Cladophora* foul recreational beaches, clog municipal and industrial water intakes, impair water quality and pose potential microbial health risks to wildlife, household pets and humans.

Hypoxia

Hypoxia refers to a condition where the dissolved oxygen content of water is reduced to very low levels. This can occur during the summer months in deeper lake basins such as the central basin of Lake Erie, where the water column stratifies in layers and the warmer oxygenated waters at the surface are separated from the colder, denser bottom water. High external nutrient inputs stimulate the production of excessive organic material (algae and other organisms) in the sunlit surface layers, and the subsequent decay of this material in the bottom waters rapidly depletes the supply of oxygen, creating “dead zones,” where dissolved oxygen levels are so low that fish and other aquatic life cannot survive. Hypoxic conditions also lead to the release of phosphorus from sediments, known as ‘internal loading,’ which also may contribute to the development of algal blooms.

Climate change could exacerbate the magnitude, duration and frequency of hypoxia in Lake Erie. Warmer future conditions are expected to facilitate an earlier and longer period of stratification (or layering) during summers, causing algal growth and hypoxic conditions to begin sooner and persist over an extended time period.

Fish

Lake Erie fisheries have important ecological, recreational and commercial value. Each species of fish has preferred food choices and temperature ranges, and all fish depend upon adequate dissolved oxygen.

The decomposition process of algal blooms can significantly reduce dissolved oxygen supplies, undermining native fish populations. When algae die, the decomposition process uses much of the dissolved oxygen in the bottom waters. A changing climate – warmer temperatures, less ice cover and increased frequency of intense precipitation events – could exacerbate algal blooms, reduce water clarity and exacerbate future hypoxia.

Over the longer term, phosphorus loading together with future climatic conditions could alter Lake Erie's rich and diverse fish community. Cold-water species and species sensitive to low oxygen and reduced water clarity would be expected to decline, while species more tolerant to warm water likely would thrive.

Human Health and Socio-economic Conditions

Individuals swimming, waterskiing, or boating in harmful algal blooms can be exposed to toxins. Although the likelihood of people being seriously affected by a bloom is low, minor skin irritation can occur with contact. As well, gastrointestinal discomfort and, in very rare but severe cases, acute liver failure can occur if water from a bloom is ingested. In the Great Lakes basin, only Lake Erie has had documented cases of human illness and animal (dog) deaths related to harmful algal blooms.

Public concerns about the impact of harmful algal blooms on drinking water in Lake Erie were heightened in the summer of 2013 when residents in Carroll Township, Ohio, were advised not to drink water from their local treatment plant due to high levels of microcystin - the first time a toxin associated with algae led to a plant shutdown in the state. In cases where harmful algal blooms appear, municipal water treatment facilities drawing water supplies from Lake Erie may need to carry out additional monitoring and treatment before the water is safe for human consumption.

Limited data constrain efforts to estimate the economic effects of Lake Erie algal blooms throughout the entire lake basin. Using Ohio data as a proxy for the broader Lake Erie Basin, the LEEP study identified important economic costs associated with effects on property values, regional tourism, beach tourism and recreational and commercial fishing.

Regulation and Policy

The IJC reviewed nutrient management statutes and programs among all eight Great Lakes states, Ontario and Quebec. Related recommendations were developed for the LEEP report, based in part on the most effective initiatives identified.

Improving the Health of Lake Erie: Opportunities for Action

New Loading Targets

The LEEP study developed response curves to predict levels of algal blooms and hypoxia as a function of phosphorus loading. These load-response curves, in turn, were used to identify new loading targets, as part of a comprehensive management plan to address these issues in Lake Erie.

The LEEP study concluded that to reduce algal blooms and areas of hypoxia significantly requires substantial reductions in phosphorus loads below current levels, and that the focus should be on reducing dissolved reactive phosphorus loads. Furthermore, in setting future targets, it will be important to recognize that harmful algal blooms and hypoxia targets likely will require separate considerations – solving one problem will not necessarily solve the other. Greater reductions in dissolved reactive phosphorus will be needed to address the hypoxia problem.

Best Management Practices¹:

The LEEP study involved a comprehensive review of more than 240 sources on the implementation and effectiveness of *best management practices* (BMPs) that could be considered for implementation within the Lake Erie Basin to reduce phosphorus loads. BMPs cover a range of proven, practical methods, techniques and other actions that allow individuals and organizations to prevent or reduce the risks of water pollution resulting from their activities.

¹ In Canada, best management practices typically are referred to as beneficial management practices.

The control of phosphorus in agricultural operations must focus on changes in agricultural practices that have been implemented in recent decades, such as increased prevalence of fall application of nutrients, applying two years' worth of fertilizer in a single application, and broadcast application. The goal is to increase the efficiency of phosphorus use at the farm scale. Promising approaches include improvements in the management of soil, manure, and mineral fertilizer, and agricultural and conservation practices that balance inputs and outputs of phosphorus within watersheds across the Lake Erie Basin. Extreme weather events can confound the effectiveness of agricultural BMPs.

Within urban areas, there are many diffuse sources of phosphorus. Therefore, BMPs will need to be highly varied and targeted for implementation in a wide range of urban activities.

Data and Knowledge Gaps

Accurately monitoring phosphorus loadings and identifying the most important sources allows for effective priority-setting of actions to restore the health of Lake Erie. The LEEP study identified several gaps with respect to monitoring of phosphorus loadings and their effects on the ecology of Lake Erie. These gaps include:

- an uneven distribution of tributary monitoring across the Lake Erie Basin;
- an absence of continuous monitoring near the mouth of the Detroit River;
- limited monitoring of the lake's nearshore zone; and,
- routine monitoring of critical wet weather events – an issue of increasing importance under climate change.

Knowledge research gaps include:

- how different physical, chemical, and biological factors interact to create the conditions that can trigger harmful and nuisance algal blooms;

- how different fish communities of the lake may respond under the warming trends and altered precipitation patterns associated with continued climate change; and,
- how much various BMPs actually reduce phosphorus loading, and how much they cost.

In addition, there is a need for timely and more comprehensive economic data that would allow for a better understanding of the economic impacts of algal blooms across the Lake Erie Basin.

Recommendations

Responsibility for the development and implementation of plans, programs, policies and related activities to address Lake Erie water quality rests with the governments of the United States and Canada and Ontario and the Lake Erie Basin states (Ohio, Michigan, Indiana, Pennsylvania and New York). The IJC serves in an advisory role to the governments, and offers its recommendations in a spirit of cooperation.

The IJC believes that current knowledge is sufficient to justify immediate additional efforts to reduce external loading of nutrients to Lake Erie. Phosphorus, especially the bioavailable dissolved reactive fraction, is a primary concern. Efforts must deal with both agriculture and urban sources. The highest priority for remedial action should be the Maumee River watershed.

The participation of the province of Ontario and Lake Erie Basin states is essential to realizing improved Lake Erie health. Due to their location around the lake and land use, some states have deeper phosphorus reductions to make than others. For example, while Lake Erie's western and central basins require urgent targeted phosphorus reductions, the states of Pennsylvania and New York State contribute phosphorus loads only to the eastern basin. Efforts to reduce phosphorous inputs into the eastern basin will have little impact on algal bloom and hypoxic conditions occurring upstream. However, reduced phosphorus

inputs into the eastern basin will benefit the local environment as well as Lake Ontario, which receives 80% of its flow from Lake Erie.

Based on the LEEP study's analysis and key findings, the IJC recommends the following actions:

Setting Phosphorus Reduction Targets

1. The Governments of the United States and Canada should adopt new targets for maximum acceptable phosphorus loadings in Lake Erie:

- to reduce the frequency and severity of harmful algal blooms in the western Lake Erie Basin to an acceptable level (None/Mild blooms), the total phosphorus load target for the Maumee River for the spring (March-June) period should be established as 800 metric tonnes (MT), a 37% reduction from the 2007-2012 average; for dissolved reactive phosphorus, the target for the spring period should be 150 MT, a 41% decrease from the 2007-2012 average; extended over the course of a full year, the total phosphorus target should be 1,600 MT, a 39% decrease from the 2007-2012 average;
- when the rest of the watersheds in the western Lake Erie Basin are included, the total phosphorus load target for the spring should be 1,600 MT and the dissolved reactive phosphorus target should be 300 MT; extended over the course of a full year, the total phosphorus target should be 3,200 MT;
- to decrease the central Lake Erie Basin hypoxic area by 50% to about 2,000 km² (772 mi²) and 10 hypoxic days a year, the target total phosphorus load for the western basin and central basin should be 4,300 MT, a 46% reduction from the 2003-2011 observed average load and 56% below the current target;
- when expressed as annual dissolved reactive phosphorus load, the target for achieving the same hypoxic area (2,000 km²) and number of hypoxic days (10) in the central Lake Erie Basin should be 550 MT. This new level represents a 78% reduction from the 2005-2011 average dissolved reactive phosphorus load; and,

- total phosphorus and dissolved reactive phosphorus targets should be phased in over a nine-year period (2014-2022) by setting transitional targets on a three-year basis to coincide with the triennial cycle and assessment of progress outlined in the 2012 Agreement.

2. To establish and implement new targets of phosphorus loadings:

- the governments of the United States and Canada should develop domestic action plans including both regulatory and non-regulatory measures to reduce nutrient pollution of Lake Erie sooner than the 2018 goal set in the 2012 Agreement;
- the governments of Michigan, New York, Ohio, Pennsylvania and Ontario should apply a public trust framework consisting of a set of important common law legal principles shared by both countries, as an added measure of protection for Lake Erie water quality; governments should apply this framework as an added decision-making tool in policies, permitting and other proceedings; and,
- the governments of Michigan and Ohio should, under the *United States Clean Water Act*, list the waters of the western basin of Lake Erie as impaired because of nutrient pollution; this would trigger the development of a tri-state phosphorus total maximum daily load (TMDL) involving those states and Indiana, with U.S. Environmental Protection Agency oversight.

Reducing Phosphorus Loading into Lake Erie from Agricultural Sources and Septic Systems

3. The Governments of the United States, Canada, Ontario, Michigan, Indiana, Ohio, Pennsylvania and New York should immediately expand the focus of existing and planned incentive-based agri-environmental programs beyond particulate phosphorus to include an emphasis on best management practices that are most likely to reduce dissolved reactive phosphorus, such as reducing the amount of phosphorus applied to fields, slowing the movement of water to the field drainage system, and detaining flows at field drainage outlets.
4. Future phosphorus management efforts of the Governments of the United States, Canada, Ontario, Michigan, Indiana, Ohio, Pennsylvania and New York should focus on:
 - avoiding agricultural applications of phosphorus in autumn;
 - reducing the load delivered during the spring period (March 1 to June 30); and,
 - those sub-watersheds that are delivering the most phosphorus into the lake, including the Maumee River.
5. The Governments of the United States, Canada, Ontario, Michigan, Indiana, Ohio, Pennsylvania, New York and local agencies should increase the scale and intensity of agricultural best management practices programs that have been shown to reduce phosphorus runoff.
6. The Governments of the United States, Canada, Ontario, Michigan and Ohio should:
 - commit to the goal of a 10% increase by 2030 beyond current levels of coastal wetland areas in the western basin of Lake Erie to reduce nutrient pollution and promote biodiversity (an increase of about 1,053 ha or 2,600 acres);
 - allocate adequate funding to support this significant first step in coastal wetland restoration, in concert with non-governmental funders; and,
 - set a science-based goal for protection and restoration of wetlands inland from the Lake Erie coastal zone and develop appropriate strategies to meet the goal.
7. The Governments of the United States, Canada, Ontario, Michigan, Indiana, Ohio, Pennsylvania and New York should strengthen and increase the use of regulatory mechanisms of conservation farm planning to reduce nutrient loadings.
8. The Governments of the United States, Canada, Ontario, Michigan, Indiana, Ohio, Pennsylvania, and New York should accelerate 4Rs (Right source, Right rate, Right time and Right place) outreach/extension programs, and phase in mandatory certification standards for agrology advisors, retailers and applicators to ensure fertilizer is applied based on the 4Rs.
9. United States and Canadian federal policies should link the cost and availability of crop insurance purchases or premiums to farm conservation planning and implementation of nutrient management practices.
10. The Governments of Ontario, Michigan, Indiana, Ohio, Pennsylvania and New York should ban the application of manure, biosolids and commercial fertilizers containing phosphorus from agricultural operations on frozen ground or ground covered by snow for lands that drain to Lake Erie.
11. The Governments of Ontario and Michigan should:
 - enact legislation requiring inspection of septic systems at regular intervals, and at the time of property sale or land severance, to identify and assure upgrade/replacement of failing and potentially failing systems; and,
 - expand state/provincial and community education

initiatives promoting homeowner awareness of the need for septic system maintenance, including regular pumpout, and upgrade/replacement.

Reducing Phosphorus Loading into Lake Erie from Urban Sources

12. The Governments of the United States, Canada, Ontario, Indiana, Michigan, New York, Ohio and Pennsylvania should work with municipalities to promote and accelerate the use of green infrastructure (such as filter strips, rain gardens, bio-swales, and engineered wetlands) in urban stormwater management in the Lake Erie Basin by:

- providing funding, regulatory direction and technical support to municipalities and, where feasible and appropriate as an alternative to more expensive stormwater controls, authorize green infrastructure in United States municipal water discharge permits and Ontario environmental compliance approvals; and,
- encouraging the adoption of local ordinances/by-laws promoting green infrastructure.

13. The Governments of Ontario, Ohio and Pennsylvania should prohibit the sale and use of phosphorus fertilizers for lawn care, with the exception of the establishment of new lawns during the first growing season or in cases where soil testing indicates a need for phosphorus.

Strengthening Monitoring and Research in the Lake Erie Basin

14. The Governments of the United States and Canada should commit sustained funding to enhance and maintain monitoring networks in the Lake Erie Basin, focusing on:

- tributaries throughout the Lake Erie Basin, including key sub-basins and wet weather events to

capture seasonal differences from a wider range of basin tributaries;

- dissolved reactive phosphorus which, in addition to total phosphorus and other parameters, will need to be regularly monitored at all appropriate sites;
- establishment of water quality monitoring stations to quantify the nutrient dynamics from Lake Huron through St. Clair River and Lake St. Clair;
- establishment of a continuous, long-term water quality monitoring system at the outlet of the Detroit River that measures critical nutrient parameters; and,
- an evaluation of the cumulative effectiveness of urban and rural best management practices.

15. The Governments of the United States and Canada should support research to strengthen understanding of:

- the dynamics of harmful algal blooms through a comprehensive limnological approach to studying entire bloom communities;
- how open-lake disposal of dredged sediments from the Toledo navigational channel affects phosphorus loadings in Lake Erie;
- environmentally sustainable methods of sediment disposal;
- how various factors, such as the interaction of lake water with land-based runoff and tributary discharges, can be used to predict the conditions associated with nuisance blooms under current and future climate change scenarios;
- how Lake Erie's diverse and productive fish communities could respond under the warming trends and altered precipitation patterns associated with continued climate change; and,
- the economic effects of Lake Erie algal blooms throughout the entire lake basin.

16. The Governments of the United States and Canada and organizations involved in lake management should improve data management through greater coordination and sharing.



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Runoff of soil and fertilizer



Brenda Culler, Ohio DNR

Chapter 1 Introduction to the Lake Erie Ecosystem Priority Report

1.1 Purpose of the Report

This report presents the findings and recommendations of the **Lake Erie Ecosystem Priority** (LEEP), which the International Joint Commission (IJC) initiated in 2012 as part of its three-year priority cycle to provide advice to federal, state/provincial and local governments for developing policy and management approaches to address lake-wide challenges with respect to declining water quality, algal blooms, hypoxia and associated ecosystem, human health and economic impacts.

The IJC is an independent binational organization created by Canada and the United States under the *Boundary Waters Treaty of 1909*. Under the Treaty, the two countries cooperate to prevent and resolve disputes relating to the use and quality of the many lakes and rivers along their shared border. At the request of both governments, under the Great Lakes Water Quality Agreement² (the Agreement), the IJC also has a role in advising the two countries on restoration and maintenance of the chemical, physical, and biological integrity of the waters of the Great Lakes.

Intended Audiences

The LEEP report was prepared to provide advice to the governments of Canada and the United States regarding the protection and restoration of Lake Erie. The findings and recommendations of the report also will be of direct interest to a broad audience of agencies, water users, residents, organizations and decision-makers concerned about water quality and the future of Lake Erie.

The report represents a synthesis of extensive scientific analysis. Readers wanting more detailed information are encouraged to review the original scientific and technical papers prepared as part of the study.³

1.2 Background to the Report

The Great Lakes basin, from the headwaters of Lake Superior to the outlet of Lake Ontario, is home to more than 45 million people in Canada and the United States. The five Great Lakes, created 10,000 years ago at the end of the last period of continental glaciation, make up the largest surface freshwater system on Earth. These waters support food crop irrigation, electrical power generation and transportation of raw materials and finished goods. They maintain rich

² For more information on the Great Lakes Water Quality Agreement, see: www.binational.net or ijc.org

³ LEEP papers are available at: www.ijc.org/en/_leep/Technical_Documents

wetlands and fisheries. They provide bountiful sources of drinking water and recreational opportunities for millions of people.

Yet human use of the lakes has degraded water quality and ecosystems. As the smallest (measured by volume) and shallowest of the five Great Lakes, Lake Erie has long experienced changes as a result of human activities and natural forces.

In the decades leading up to the 1970s, loadings of nutrients, especially phosphorus from municipal sewage treatment plants and other runoff sources, visibly degraded the lake. This excessive nutrient enrichment – also known as eutrophication – resulted in severe algal fouling of the lakes, which in turn created aesthetic, taste and odor problems, and fish die-offs. Although eutrophication was apparent at many locations around the Great Lakes, it was particularly evident in Lake Erie. This eutrophication led the governments of Canada and the United States to sign the Agreement in 1972, most recently amended in 2012, establishing a binational commitment to clean up the lakes.

Following the signing of the Agreement more than 40 years ago, governments on both sides of the border made significant investments to upgrade and expand municipal sewage treatment plants. In addition, governments took action to reduce phosphorus concentrations in household detergents. By the mid-1980s, Lake Erie phosphorus loadings were reduced by more than half from 1970s levels, and many of the problems associated with eutrophication were reduced or eliminated (Lake Erie Nutrient Science Task Group, 2009).

By the early 2000s, however, problems with nutrient enrichment and oxygen depletion appeared again, and have since continued to worsen. In recent years, the problem of harmful and nuisance algal blooms⁴ has once again become widespread. In 2011, heavy rains in the spring flushed a large amount of phosphorus, including large proportions of dissolved reactive phosphorus (DRP) – the portion of total phospho-

rus that is most readily available to support algae growth – from agricultural runoff, into western Lake Erie. Warm temperatures soon followed, creating a mass of algae that extended for more than 5,000 km² (about 1,930 mi²). **The 2011 algal bloom was the largest in the lake's history, three times larger than the next largest bloom previously recorded. Trends in agricultural practices, such as fertilization application timing (proximity to storm events) and tillage practice (no-till), and meteorological conditions, including heavy spring rainfall and warm and quiescent summer weather, contributed to the bloom (Michalak et al., 2013).**

The problems of nutrient enrichment in Lake Erie are compounded by the influence of climate change on temperature and precipitation regimes and ecosystem changes caused by aquatic invasive species such as *dreissenid* mussels (Lake Erie Nutrient Science Task Group, 2009). As a result of these influences, Lake Erie has experienced a decline in water quality over the past decade, with impacts on ecosystem health, drinking water supplies, recreation and tourism, and property values.

⁴ Excessive and relatively rapid growth of algae. Blooms can occur naturally as the result of a change in water temperature and current or as a result of an excess of nutrients in the water.

Great Lakes Water Quality Agreement and the International Joint Commission

The Agreement is widely regarded as one of the world's most successful binational environmental agreements. Originally signed by Canada and the United States in 1972, the agreement has been revised four times, with each revision responding to evolving priorities:

- The original 1972 Agreement set general and specific water quality objectives and mandated programs to meet them. It gave priority to point source pollution from sewage treatment plants and industrial sources, as well as changes to allowable levels of phosphorus in household detergents. Point source pollution was dramatically reduced and many visible and noxious pollution problems were alleviated, including harmful algal blooms in Lake Erie.
- The 1978 version of the Agreement adopted an ecosystem approach (one which considers the interaction of air, land, water and living things, including humans) and called for a broad range of pollution-reduction programs, including virtual elimination of the input of persistent toxic substances.
- The Agreement was amended in 1983 to enhance efforts to reduce phosphorus inputs to the Great Lakes. Scientists from both countries worked together to set the target loads for each lake that would need to be met to achieve the water quality objectives of the Agreement. Detailed plans to reduce phosphorus loading to receiving waters were developed and adopted by each jurisdiction in the basin.
- A 1987 amendment called for programs to restore both the quality of open waters and beneficial water uses in 43 of the most contaminated local areas in the basin. Conditions have improved significantly in a number of these 'Areas of Concern,' though only five have been restored and removed from the list.
- The 2012 Agreement contains several new Annexes responding to current and emerging challenges, including aquatic invasive species, climate change, habitat and species, and groundwater. It also shifts greater emphasis back to nutrients by requiring the development of specific lake objectives for water quality including nutrients (specifying interim targets), and the development of programs to accomplish those objectives.

The IJC continues to play an important role under the Agreement. In addition to engaging and informing the public, it analyzes information provided by the governments, assesses the effectiveness of programs in both countries and reports on progress.



2011 Algal Bloom, Lake Erie, Western Basin

NASA

1.3 Establishment of the Lake Erie Ecosystem Priority

In 2012, recognizing the urgency and importance of Lake Erie's faltering health, and the potential cost of further delay, the IJC established the Lake Erie ecosystem as a priority area for binational study. The IJC has spent much of the past two years developing a better scientific understanding of the causes and controls of phosphorus in Lake Erie. This report presents the outcome of this work.

While the report focuses on phosphorus, the IJC recognizes that stressors other than nutrients also can adversely affect the water quality and ecology of Lake Erie. These stressors include erosion of shorelines and streambanks, chemical contaminants, wetland loss, and hydrologic alteration through dams.

LEEP is intended to complement several important initiatives to reduce nutrient loadings into the Great Lakes already underway at the federal, state, provincial and municipal levels. These initiatives include the binational Lake Erie Lakewide Action and Management Plan (LAMP) and its related publications (for example, LAMP, 2011), Environment Canada's Great Lakes Nutrient Initiative, the United States' Great Lakes Restoration Initiative (coordinated by the United States Environmental Protection Agency [USEPA]), and Ohio's Lake Erie Phosphorus Task Force.

1.4 Study Approach

Key Themes

The LEEP work plan primarily addressed science, and secondarily socio-economic and regulatory themes as part of a comprehensive approach. The themes were addressed by binational working groups led by the IJC's Great Lakes Science Advisory Board, Great Lakes Water Quality Board, Council of Great Lakes Research Managers, and IJC staff.

The science theme addressed five interrelated concerns regarding Lake Erie algae outbreaks:

- current external and internal phosphorus loading;
- effects of climate change on phosphorus loading, algal blooms, wetlands and fish;
- effectiveness of agricultural and urban best management practices (BMPs);
- management models and targets for phosphorus, harmful algal blooms (HABs) and hypoxia; and,
- adequacy of phosphorus monitoring programs within the Lake Erie Basin.

The Great Lakes Science Advisory Board was tasked with the first four of these issues. It convened a *Taking Action on Lake Erie* (TAcLE) work group, composed of advisory board members and experts in the field. The work group carried out extensive literature reviews, conducted independent analyses and modeling, and prepared papers summarizing the findings

⁶ International Joint Commission Retreat in Montreal, QC, Canada (Winter 2012)

and conclusions. The fifth science issue, the adequacy of phosphorus monitoring programs within the Lake Erie Basin, was addressed by the Council of Great Lakes Research Managers. Draft science papers were reviewed at an experts' workshop in February 2013, after which the report authors revised the papers and presented them to IJC staff.

Under the *socio-economic* theme, the study commissioned an expert paper on the economic impact of excessive algal blooms and the costs and benefits of solutions.

Finally, under the *regulatory* theme, IJC staff prepared a paper on the legislative and regulatory framework affecting sources of nutrients entering Lake Erie, including policies in place at the United States and Canadian federal levels and in the Great Lakes states and the province of Ontario.

Public Engagement

Throughout the LEEP process, the IJC made extensive efforts to inform and engage the public in both

the United States and Canada. Early on, this process included a roundtable in March 2012, held in Ann Arbor, MI and attended by more than 60 people. The presentations and discussions improved the IJC's understanding of the challenges facing Lake Erie and helped to frame the LEEP work plan.

In the summer of 2012, a series of eight public meetings was held to invite input. Comments provided by lakeside residents, anglers, boaters, and other concerned residents were important contributions to the analysis and recommendations in the draft LEEP report that was released in August 2013 for public review and comment.

In September and October of 2013, more than 400 people attended a second set of public meetings, which were held in: Detroit, MI; Milan, Oregon and Cleveland, OH; Port Stanley, Leamington and Walpole Island First Nation, ON; and as part of the Great Lakes Week conference in Milwaukee, WI. Comments also were invited online through the IJC's website.⁵ Commenters represented a wide range of interests. The LEEP report includes many improvements suggested by the public.

Key Concerns Expressed During the LEEP Public Engagement Activities

Of the more than 130 comments received, several key concerns were expressed by the public:

- the need to deal with uncertainty surrounding the contribution of the Detroit River (and the City of Detroit sewage treatment plant) to phosphorus loads in Lake Erie;
- the role of agriculture as a driver of the problem and as a solution, including both agronomic practices and CAFO (Concentrated/Confined Animal Feeding Operations) management;
- the need for additional regulatory tools to reduce phosphorus loading that complement existing incentive-based programming;
- the need for more research into development and adoption of suitable best management practices for the Lake Erie watershed;
- an emphasis on dissolved reactive phosphorus-specific best management practices, but not at the expense of particulate phosphorus and sediment-focused best management practices;
- the importance of drinking water considerations (partially a result of the *Microcystis* toxin found in the Carroll Township water plant);
- the adoption of a Total Maximum Daily Load program for Lake Erie in the United States and an equivalent program in Canada;
- the need for protection and restoration of natural land cover, including wetlands, to reduce and filter sediment and nutrient runoff; and,
- the need to address failing septic systems as a source of nutrients.

⁵All public comments received during the LEEP process are posted at http://www.ijc.org/en/_leep/Comments.

1.5 Organization of the Report

The balance of this report is organized into the following three chapters:

Chapter 2 summarizes the impacts of phosphorus loading, compounded by the influence of climate change and aquatic invasive species, on the Lake Erie ecosystem, human health and socio-economic conditions.

Chapter 3 reviews existing and possible initiatives to address the impacts on the Lake Erie ecosystem from phosphorus loading. It discusses modeling efforts to identify new phosphorus loading targets that could be established to reduce the loadings into Lake Erie, and identifies BMPs to reduce phosphorus runoff from agricultural operations and urban development. It also identifies important gaps in monitoring and research.

Chapter 4 presents the IJC's recommendations for addressing the challenges facing Lake Erie.

The Appendix includes acknowledgements, previous recommendations, references, a glossary, and a conversion table for comparing metric and United States customary units.



Less frequent, but more intense thunderstorms will lead to increased nutrient runoff.



A common non-structural BMP is reducing phosphorus loads from lawn fertilizers.

Chapter 2 Understanding the Changing Lake Erie Ecosystem

The science component of the **Lake Erie Ecosystem Priority** (LEEP) focused on improving understanding of how phosphorus loadings are affecting water quality in Lake Erie. Science investigations explored the issues of harmful algal blooms (HABs)⁶ in the lake's western basin and oxygen depletion or hypoxia in the central basin. The socio-economic and regulatory components considered the impacts of these changes on human health, boating, recreational fishing and other activities.

Chapter 2 presents the results of these efforts to better understand why and how Lake Erie is changing. The chapter:

- provides a brief overview of the physical and socio-economic context of Lake Erie;
- describes trends in phosphorus loading to the lake, as well as the contributions from various sources; and,
- describes the effects of phosphorus loading, compounded by the influence of climate change and aquatic invasive species, on water quality in Lake Erie and on human health and socio-economic conditions in the basin.

2.1 Overview of the Lake Erie Ecosystem

Lake Erie is the shallowest and the smallest of all the Great Lakes⁷, with a total surface area of 25,700 km² (about 9,900 mi²) and an average depth of only 19 m (62 ft) (LAMP, 2012; GLIN). The lake is naturally divided into three distinct basins with different average depths: the western basin (7.4 m or 24.1 ft); the central basin (18.5 m or 60.1 ft); and, the eastern basin (24.4 m or 79.3 ft) (GLFC, 2003; Lake Erie LAMP, 2011). As a result, the lake waters warm rapidly in the spring and summer, and can freeze over in winter.

On an annual basis, about 80% of Lake Erie's total inflow comes from the St. Clair River, which conveys flows from the upper lakes of Superior, Michigan and Huron through the Detroit River into the lake's shallow western basin. About 11% of the inflow is from rain and snow. The balance comes from tributaries, the largest of which is the Maumee River (LAMP, 2011). Other major tributaries are the Sandusky, Cuyahoga, Grand, Raisin, and Huron rivers. The Detroit River also conveys flows from tributaries discharged into Lake St. Clair, including the Thames River. Lake Erie drains into Lake Ontario via the Niagara River.

⁶ Harmful algal blooms (HABs) result from the proliferation of blue-green algae (including cyanobacteria) in environmentally stressed systems, where conditions favor opportunistic growth of one or more noxious species, which displace more benign ones. These blooms are considered harmful because excessive growth can harm ecosystems and produce poisons (or toxins) that can cause illness in humans, domestic pets and wildlife.

⁷ As measured by volume. Lake Ontario has a smaller surface area (about 19,000 km² or 7,340 mi²) but is much deeper than Lake Erie.

Lake Erie's shoreline of 1,402 km (871 mi) and land basin of 58,800 km² (about 22,700 mi²) include parts of Indiana, Michigan, Ohio, Pennsylvania, New York and Ontario (CCGLHHD, 1977). The Lake Erie Basin is the most densely populated of the five Great Lake basins, with 17 metropolitan areas with populations of more than 50,000 and a total population of 11.6 million (LAMP, 2011).

Key Lake Erie users include: domestic, municipal and industrial water users; shipping; coastal zone residents and commercial interests; Tribes, First Nations and Métis; agricultural interests; recreational boating and tourism; and sport and commercial fishing interests.

With its fertile soils, the Lake Erie Basin is intensively farmed, with about 63% of the lake's watershed used for agriculture (Figure 2-1). Land use along the shoreline is dominated by: residential uses (39% in Canada and 45% in the United States); agriculture (21 and 14%, respectively); and, commercial uses (10 and 12%, respectively) (Environment Canada and USEPA, 1995).

The shallowness of the lake and its warm temperatures makes it the most biologically productive of all the Great Lakes. It supports a species-rich and diverse fish community, with more than 130 species documented. In addition to their important ecological roles, several species also support large recreational and commercial fisheries. For example, walleye (*Sander vitreus*) supports the lake's most valued recreational fishery and yellow perch (*Perca flavescens*), walleye and several other species support large commercial fisheries.

2.2 Phosphorus Loading

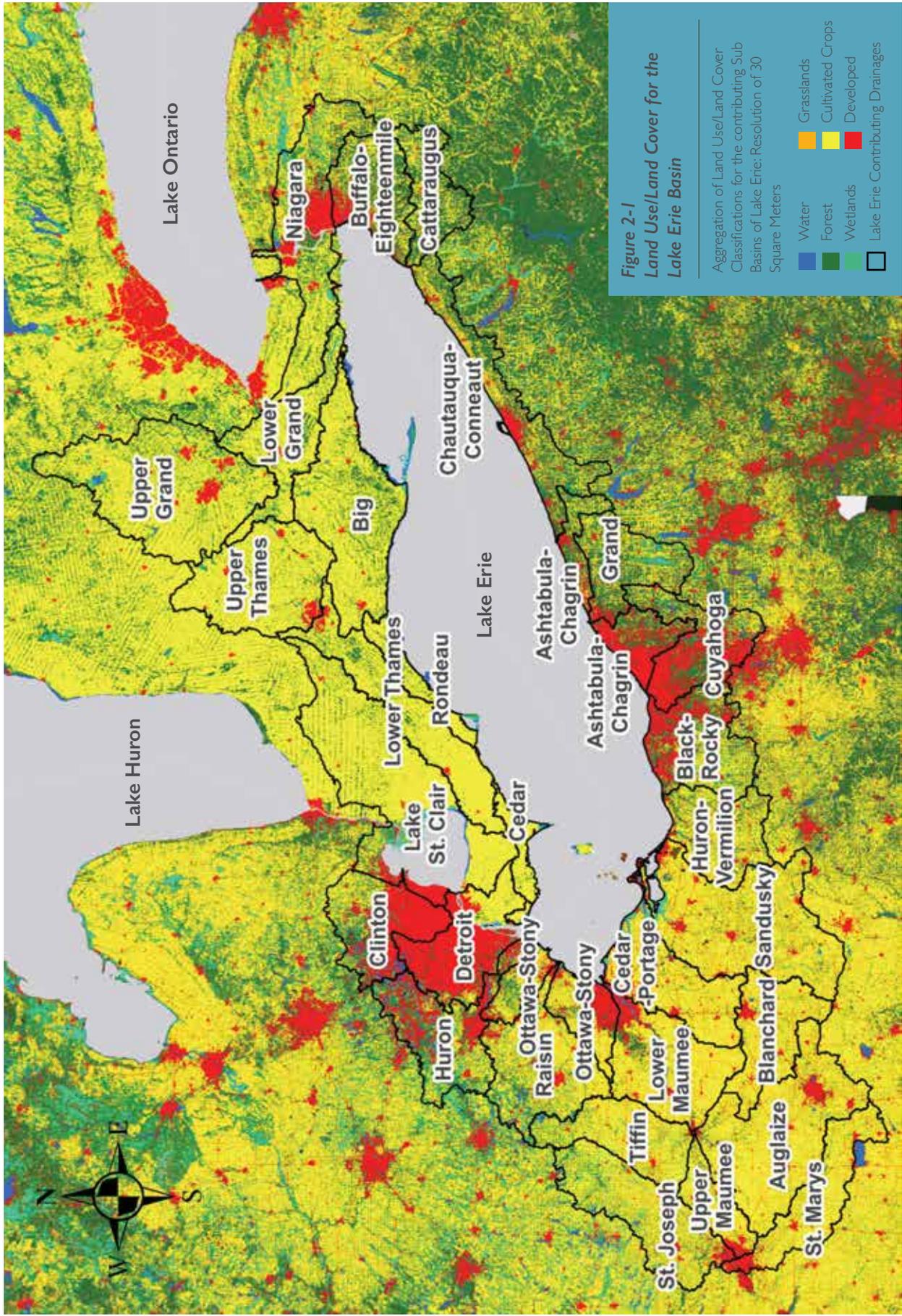
Phosphorus has long been recognized as the primary cause of nutrient enrichment (eutrophication) problems in most temperate zone lakes, including Lake Erie (Schindler 2012; Scavia *et al.*, 2014). Microscopic plants, the smallest forms of algae, comprise the base of the food web in any lake. Algae grow by converting available nutrients in the presence of sunlight to new plant material. The dominant types of nutrients

in Lake Erie are made up of nitrogen and phosphorus. **However, phosphorus is considered the limiting nutrient in the lake (that is, the nutrient that limits the growth of algae) because there is almost always sufficient nitrogen available for algal growth (Lake Erie Nutrient Science Task Group, 2009).**

Phosphorus is a chemical element that occurs both naturally in the environment and in many common commercial products. The major commercial application of phosphorus compounds is the production of fertilizers, used to replace the phosphorus that plants remove from the soil. Phosphorus is also an ingredient in many detergents, pesticides and other products.

To support the development of effective policy and management approaches to addressing lake-wide challenges in Lake Erie, LEEP sought to:

- provide the best available updated estimates of the total phosphorus (TP) load and bioavailable phosphorus (commonly referred to as DRP) for Lake Erie through to 2011, by tributary/watershed; and,
- evaluate the relative contributions from various sources to total loading.



Note: The map is based on harmonized Canadian Fundamental Drainage Areas (FDA) and the U.S. Watershed Boundary Dataset (WBD). The Canadian Units are 4-digit Sub Basins and the U.S. Units are 8-digit Sub Basins.

Source: IJC, modified from Great Lakes Aquatic Habitat Framework (GLAHF), University of Michigan.

2.2.1 Nutrient Limitation in Aquatic Ecosystems

Phosphorus and nitrogen, along with carbon and several other nutrients, including iron, manganese and zinc, are essential for algal growth. Nutrient limitation occurs when an essential nutrient is in short supply and algal growth is slowed or stopped, which often leads to changes in algal community composition and structure. Knowledge of which nutrients (and their forms) are primarily responsible for stimulating algal growth is important for devising solutions to issues of HABs and hypoxia associated with eutrophication. Different types of aquatic ecosystems tend to be limited by different nutrients. For example, algal growth in saltwater environments such as estuaries and coasts primarily is limited by nitrogen, while the open ocean generally is limited by either nitrogen or iron (Howarth and Marino, 2006). Rivers can be limited by either nitrogen or phosphorus, depending on river attributes such as stream size, flow rate, network complexity, and catchment land use and land cover.

Decades of nutrient inputs to watersheds from human sewage, livestock manure and commercial fertilizer typically result in lakes that are highly enriched in both nitrogen and phosphorus. For freshwater lakes across the temperate zone, the general view is that algal growth is controlled by phosphorus availability and that excessive loads of phosphorus lead to eutrophication (Schindler, 2012). Exceptions include some saline and montane lakes, where nitrogen can be limiting and prairie landscapes dominated by agriculture where phosphorus is replete (Baulch, 2013). Similarly, there is some evidence for nitrogen limitation or co-limitation, as well as other trace elements, with phosphorus in the context of mixed algal communities, near simultaneous limitation thresholds of nitrogen and phosphorus, and seasonal and spatial heterogeneity (DeBruyn et al., 2004; Lewis et al., 2011; Dolman et al., 2012).

In the western basin of Lake Erie, strong relationships have been observed between measurements of discharge and phosphorus loads from key tributaries and

the reoccurrence of HABs (Stumpf et al., 2012; Michalak et al., 2013) and between phosphorus loads and central basin hypoxia (Rucinski et al., 2014; Scavia et al., 2014). **Both bodies of research provide convincing evidence that the single most important solution for the restoration of Lake Erie water quality is the reduction of phosphorus inputs.**

Key Terms Used in the Report

1. *Total Phosphorus, Particulate Phosphorus and Dissolved Phosphorus*

- Total phosphorus (TP) is the sum of all fractions of phosphorus in a given quantity of water, including particulate and dissolved fractions.
- Particulate phosphorus (PP) refers to the fraction of phosphorus that is attached to suspended sediment and organic matter and dissolved phosphorus refers to the fraction that is dissolved in the water column. The dissolved fraction is generally referred to as soluble reactive phosphorus (SRP) or dissolved reactive phosphorus (DRP). This report uses DRP to reflect the more commonly used term in the Lake Erie watershed.
- Not all of the phosphorus entering a lake from its tributaries is readily available to support algal growth. Bioavailable phosphorus refers to the form of phosphorus that stimulates algal growth. Most of the phosphorus expressed as DRP is considered bioavailable (greater than ~90%); a much smaller portion of PP is described as bioavailable (less than ~30%).

2. *Point and Non-point Sources of Pollution*

- Point source pollution comes from specific locations in a river network or along the shoreline of a lake. Discharges from industrial activities and effluents from wastewater treatment plants are examples of point sources.
- Non-point source (NPS) pollution comes from many locations and origins distributed throughout a watershed as a result of land-based human activities such as agriculture, construction and forestry. Pollutants including sediments from soil and streambank loss, nutrients and bacteria from fertilizers and manures, pesticides and other chemical contaminants are transported by rainfall and snowmelt runoff over land and through groundwater systems before entering rivers and lakes. NPS pollution is also referred to as diffuse pollution.
- Atmospheric deposition is a source of NPS pollution.
- Pollution from built-up and urban regions, including residential areas, can be described as both point source and NPS depending on such factors as region size, density of buildings and people, and the extent and composition of green spaces and natural habitats.

3. *External and Internal Loading of Phosphorus*

- External loading refers to the quantity of phosphorus that enters a lake from external sources, including contributions from watersheds via river networks, direct discharges from human activities along lake shorelines, and atmospheric deposition.
- Internal loading refers to the quantity of phosphorus within in a lake that is derived from in-lake sources, primarily from profundal or lake-bottom sediments. Internal loading is facilitated by hypoxia (low oxygen levels) that periodically occurs near the sediment-water interface. Though all lakes have background levels of phosphorus, excessive nutrient loading means that the bulk of the phosphorus that comprises internal loading is originally from external sources.

Loadings vs. Concentrations

The amount of phosphorus in Lake Erie is generally expressed as *loadings* or *concentrations*:

- A **loading** is the mass of phosphorus entering the lake from one or more sources. It is expressed as the mass of phosphorus per given period of time (e.g., kg/day or metric tonnes/year). It typically is used to quantify inputs, such as from streams and rivers.
- A **concentration** is the mass of phosphorus in a given volume of water, generally expressed as milligrams or micrograms of phosphorus per litre. It is often used to characterize the trophic status of a lake or river.

For tributaries entering Lake Erie, loadings are calculated as the product of concentration (e.g., mg/L) and water discharge or flow rate (e.g., cubic feet per second [cfs] or liters per day [L/day]). Loadings and concentrations are not necessarily related. For example, during the spring freshet or snowmelt period, there tends to be large quantities of runoff and streamflow and high concentrations of phosphorus. Later in the summer, during the growing season, there can still be storms that generate large quantities of streamflow, but concentrations of phosphorus can be much lower. It is this combination of seasonality, water volume and phosphorus concentration that differentially impact receiving waters that range from the pelagic or open water zone to the nearshore zone and coastal embayments.

The algae issues in Lake Erie – including free floating *Microcystis* in the western basin, and attached *Cladophora* at various locations along the shoreline – occur primarily due to high concentrations of dissolved phosphorus coming from tributary discharges. Deep water hypoxia in the central basin is strongly influenced by phosphorus loads delivered from the west basin. Therefore, reducing phosphorus impacts on the lake must focus on both high concentrations and high load inputs, which primarily come from a few key tributaries including the Maumee River in northwest Ohio. Reducing loads from low concentration sources like the Detroit River may have only a modest influence on algal blooms in the western basin of the lake, though circulation patterns may transfer the influence of load reduction elsewhere, such as the central basin.

2.2.2 Trends in Phosphorus Loading into Lake Erie

External Loading into Lake Erie

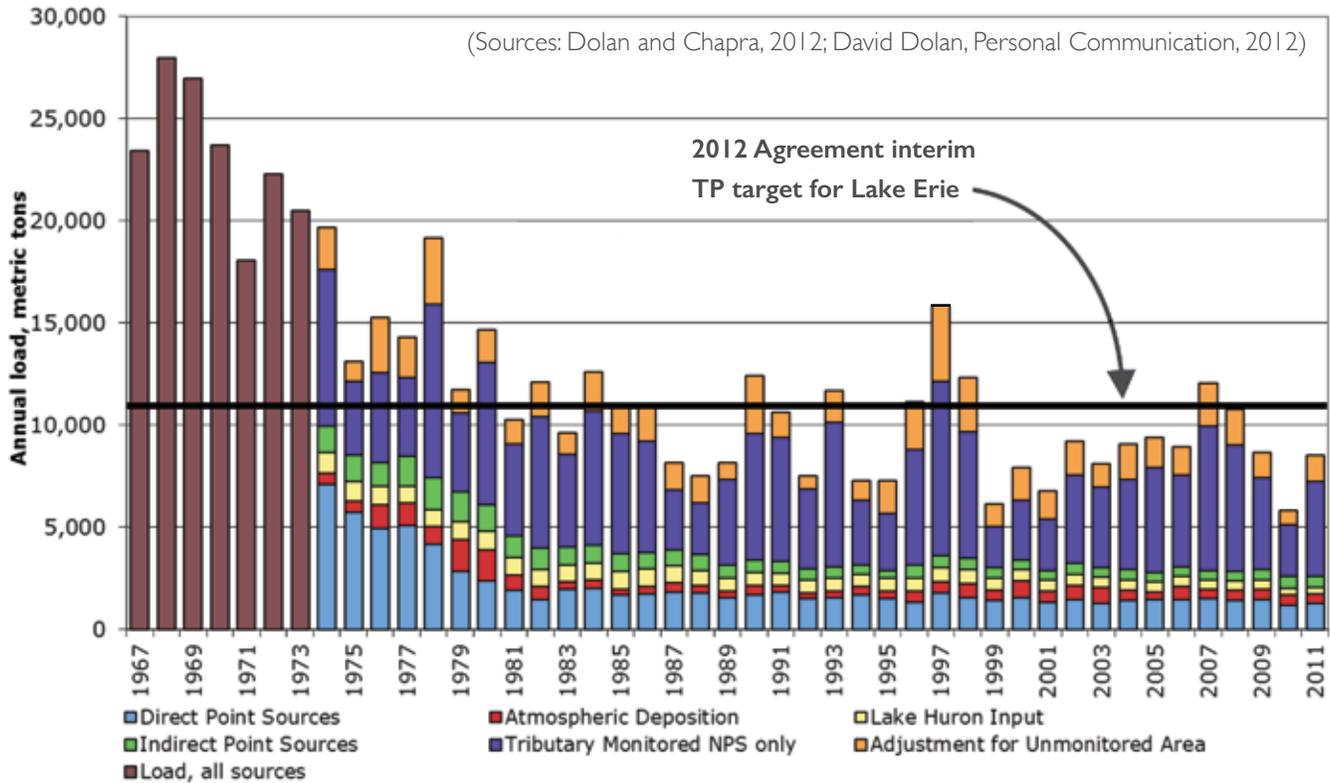
Researchers have updated TP loads for all of the Great Lakes, including from municipal and industrial point sources, monitored and estimated non-point sources, atmospheric deposition, and inter-lake transfers for 1994 to 2008 (Dolan and Chapra, 2012). LEEP updated these estimates for Lake Erie loads through 2011 using the same methods.

Figure 2-2 illustrates total external loadings of phosphorus into Lake Erie, from various sources, from

1967 to 2011. The study found that in most years, TP loadings into Lake Erie have been below the 11,000 metric tonnes (MT) a year target established under the Great Lakes Water Quality Agreement (the Agreement). Over the past 10 years, external loadings rose to a peak of nearly 12,000 MT a year in 2007, declined for three years and then again increased in 2011, to more than 8,500 MT.

The study concluded that the most dramatic reduction in loads into Lake Erie between the late 1960s and the early 1980s came from decreases in point sources of phosphorus, such that current loads are largely from non-point sources. Of the 2011 loadings, more than half came from tributaries into Lake Erie that are monitored, such as larger agricultural areas

Figure 2-2
Annual External Total Phosphorus Loads to Lake Erie (Metric Tonnes)



Note: This figure shows the annual external total phosphorus (TP) loads (in metric tonnes, MT) to Lake Erie for the years 1967 to 2011. Total loads were not differentiated for the period prior to 1974. The horizontal black line refers to the 2012 Great Lakes Water Quality Agreement interim annual TP load of 11,000 MT. NPS stands for non-point source.

and rural communities. Unmonitored areas (typically coastal communities and smaller agricultural areas adjacent to shorelines) and direct point sources each accounted for about 16%, while other sources each accounted for between 4 and 6% of external loadings. No long-term trends were identified over the period examined. Rather, annual variability in total external loading is driven largely by variability in loadings from the monitored tributaries.

Phosphorus loads to Lake Erie are not distributed equally across the basin. The western basin received 64% of the 2003-2011 average loads, while the central and eastern basins received 26 and 11%, respectively (Dolan and Chapra, 2012). Loads within each basin also vary among tributaries for both TP and DRP, with the largest contributions coming from the Maumee, Detroit, Sandusky, and Cuyahoga rivers.

In general, phosphorus concentrations in the open water decrease from west to east and from near-shore to offshore. The northern waters of the western basin are strongly influenced by flows from Lake Huron via the Detroit River, which tends to have comparatively low concentrations of phosphorus due to the large volume of water. Meanwhile, the lake's southern waters are influenced by the Maumee River and other Ohio watershed inputs, which have very high concentrations of phosphorus in a much smaller volume of water.

Differences in phosphorus loads across watersheds are affected by a wide variety of factors, including watershed size and drainage network topology, hydrological processes, surficial geology and soils, distribution and fragmentation of native vegetation,

settlement patterns and population density, industrial and agricultural activities, and the extent and effectiveness of nutrient management planning and water quality protection measures. Two of the largest watersheds that contribute nutrients to the western basin of Lake Erie are: the Maumee in the United States, which discharges directly into the western basin of Lake Erie; and, the Thames in Ontario, which discharges into Lake St. Clair, upstream of the Detroit River. Though their river lengths are similar (220 km [about 136 mi] for the Maumee and 275 km [about 167 mi] for the Thames), their watershed areas are different (16,500 km² [about 6,369 mi²] for the Maumee and 5,300 km² [about 2,046 mi²] for the Thames). The land use of both watersheds is dominated by agriculture. Both support livestock farming, particularly in their upper watersheds. However, the Maumee watershed is dominated by corn-soybean rotations, while the Thames is composed of corn-soybean rotations plus a broader array of commodities and cropping systems. Differences in land use zoning between the two jurisdictions, as well as differences in agricultural management, physiographic relief and soils, makes watershed-to-watershed comparisons of phosphorus concentrations and loads difficult to interpret.

Establishment of load targets for Lake Erie, or targets for any other aquatic system, is predicated on measurements of flow (or deposition) rates and nutrient concentrations from rivers throughout the watershed. Numerous water quality monitoring programs are in operation in the Lake Erie watershed, including Heidelberg University's National Center for Water Quality Research in Ohio, state agencies and the United States Geological Survey (USGS), the province of Ontario's Provincial Water Quality Monitoring Network, and Environment Canada's Great Lakes Nutrient Initiative, among others. These programs are focused on tributaries that discharge directly into Lake Erie, though it includes others that discharge into Lake St. Clair, such as the Thames and Sydenham rivers.

A critical influence on nutrient dynamics in Lake Erie is assumed to be the Detroit River. The river is thought to contribute 90% of the discharge and about 50% of the phosphorus to the western basin on a

mean annual basis. By the time the river discharges into the northwest corner of Lake Erie, it has integrated nutrient sources from the upper Great Lakes via the St. Clair River; tributaries of Lake St. Clair, including the Thames River in southwestern Ontario, and the cities of Windsor and Detroit (location of one of the largest wastewater treatment plants in North America). However, the only monitoring data available for the connecting river system between the upper Great Lakes and Lake Erie are from the northern section of the St. Clair River, just after water exits Lake Huron. At this point, the average annual (2005-2010) load of phosphorus is 326 MT (Dolan and Chapra, 2012). While no comparable monitoring data exist for the Detroit River outlet, research conducted in 2007 estimated that the annual phosphorus load from the river to Lake Erie was 3,500-4,300 MT, suggesting at least a 10-fold increase between Lake Huron and Lake Erie (Bruxer *et al.*, 2011). An important conclusion from this research is that future monitoring of the lower reaches of the Detroit River requires a series of monitoring stations to account for complexities associated with multiple channels and islands.

Agricultural Sources

Agricultural operations are the major source of non-point loadings of phosphorus into Lake Erie (Michalak *et al.*, 2013). These loadings can arise particularly from fertilizer application and manure. During spring snowmelt and heavy rainstorms, phosphorus is transported by runoff. Agricultural non-point sources of phosphorus have increased significantly in the last 15 years, especially the fraction of TP that is bioavailable (Baker, 2010).

Urban Sources

Phosphorus from urban areas is associated with discharges from wastewater treatment plants, construction activities, stormwater runoff, lawn and garden activities, leaves from deciduous trees and pet waste. Although urban non-point sources of phosphorus can be significant, discharges from urban areas often are closely associated with point sources. Over the last 40 years, discharges from most point sources have

declined significantly. However, wet weather overflows that bypass municipal wastewater treatment plants during and after heavy rainfall or snowmelt can discharge significant loadings of phosphorus.

Atmospheric Deposition

Atmospheric deposition to lakes contributed about 6% of the total external phosphorus load in 2011. Phosphorus can find its way from the airshed into lake ecosystems via inputs to the watershed from rain or snowfall (known as wet deposition) and wind transported particles (dry deposition) (Anderson

and Downing, 2006; Zhai *et al.*, 2009). Wet and dry nutrient loadings to aquatic ecosystems, particularly phosphorus, have increased over the years as a direct result of human activities (Herut *et al.*, 1999; Zhai *et al.*, 2009). Important potential sources of atmospheric deposition of phosphorus into Lake Erie include: microbial decomposition of sewage sludge, landfill and compost heaps; coal combustion; burning of biomass; dust from quarries, agricultural fields and unpaved roads; and automobile emissions.

Detroit Wastewater Treatment Plant

The Detroit wastewater treatment plant is one of the largest sewage plants in North America, serving more than three million people in 76 communities and treating an average of about 2.7 million m³ (710 million gallons U.S.) per day of wastewater. The plant discharges into the Rouge and Detroit rivers upstream of Lake Erie. Cleanup of the facility's discharges in the 1970s was one of the most important factors in the reversal of Lake Erie eutrophication.

In 1970, the facility began removing phosphorus from its effluent using pickle liquor and polymer to meet a 1 mg/L phosphorus standard for all major plants (about 3,800 m³ or 1 million gallons per day or greater). State policy changes affecting household laundry detergents also contributed to the cleanup. Michigan's 1977 phosphorus detergent rules restricted the phosphorus content of household laundry detergents to no greater than 0.5% by weight.

The combined result was a greater than 90% reduction in phosphorus concentration and loading from the treatment plant. Given the size of the Detroit plant, the improvement in the quality of Lake Erie's water was substantial.

Concerns about the current impact of the facility's discharge on western Lake Erie algal blooms were voiced by a number of parties at the IJC's LEEP public meetings in 2012. Similar concerns about phosphorus discharges from the plant and from combined sewage overflows (which result from major storms that force the bypass of untreated or partially treated sewage from the plant into the river) have resulted in more stringent pollution permit requirements. For example, the facility's most recent permit issued by the Michigan Department of Environmental Quality requires a reduction in monthly average TP concentrations in effluent from 1 mg/l to 0.7 mg/l beginning in January 2015.

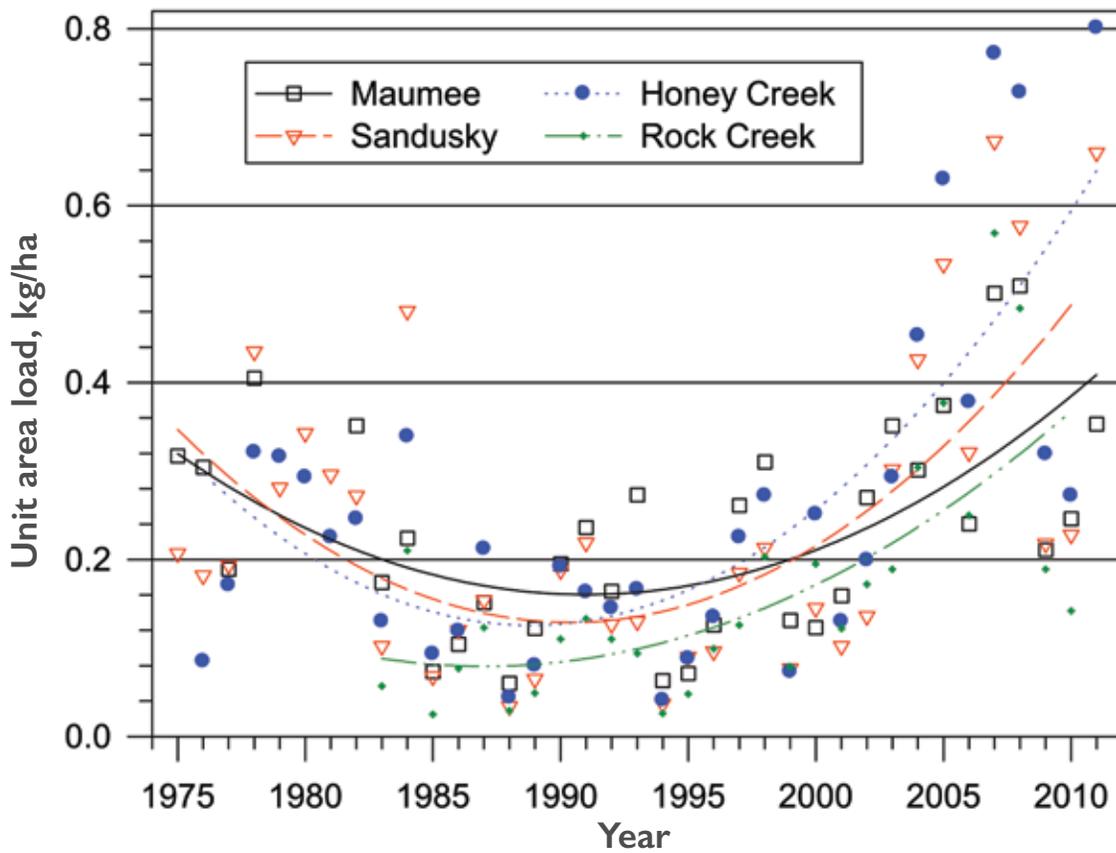
Work remains to further reduce phosphorus discharges from the Detroit plant. A capital improvement program started in 2000 included more than \$1 billion for controlling combined sewer overflows. However, in 2012, the plant still was responsible for the release of more than 29.4 million m³ (about 7.8 billion gallons) of untreated or partially treated sewage into the Detroit River. Moreover, uncertainty remains regarding future improvements, as Detroit's bankruptcy portends potential changes in the governance and funding structure for the Detroit Water and Sewerage Department. The outcome of negotiations between city and suburban leaders may affect planned capital improvements estimated at \$1.2 billion over the next four years.

Dissolved Reactive Phosphorus (DRP)

The Agreement originally focused on TP as the water quality parameter by which Lake Erie eutrophication was to be assessed and managed, and those load targets have generally been met since the 1980s. However, recent research has identified DRP, a form of phosphorus that is highly bioavailable, as a potential issue of concern (Vanderploeg *et al.*, 2009; Richards, 2006). Analysis conducted for the LEEP study of loads from several Lake Erie watersheds revealed that while DRP loads declined in the early 1990s, they have increased since the mid-1990s, in contrast to the relatively stable loads for TP and the fraction of TP known as particulate phosphorus, which is attached to suspended sediment and organic matter (Figure 2-3).

In addition, it was found that *average concentrations* of TP and DRP in the Detroit River are low compared to those measured in other major tributaries. In contrast, the phosphorus concentrations in the rivers draining the agricultural areas of the western basin, particularly the Maumee, are generally much higher and may have a more direct influence on the development of HABs. Nevertheless, the Detroit River represents the largest hydrological loading to Lake Erie and by virtue of its flow, contributes significantly to total phosphorus loading (estimated at 40 to 50%), which may be a significant factor in the annual development of hypoxic conditions in the central basin of the lake (see section 2.3.2).

Figure 2-3
Dissolved Reactive Phosphorus Loads at Four Lake Erie Watersheds



Note: This figure shows unit area loads (kg/ha) for dissolved reactive phosphorus (DRP) for four Lake Erie river systems for the years 1976 to 2011.

Source: NCWQR, Heidelberg University, unpublished data.

Regional-scale Modeling of Nutrients in the Great Lakes Basin

To help address eutrophication problems in the Great Lakes, including the sources of nutrients leading to harmful algal blooms, SPARROW (SPATIally Referenced Regression On Watershed attributes) models were recently developed to simulate phosphorus (P) and nitrogen (N) loading in streams throughout the Great Lakes and Upper Midwest of the United States (Robertson and Saad, 2011). Results from these SPARROW models were used to: estimate P and N loads to each Great Lake from U.S. drainages; rank all United States tributaries with drainage areas greater than 150 km² (57.9 mi²) based on total loads and relative yields; and, determine the relative magnitude of P and N inputs from major sources (atmospheric, point sources, fertilizers, manure, fixation, and forested and urban lands).

Led by the IJC, a binational modeling effort is now underway by the United States and Canada to develop SPARROW models for P and N for the entire Great Lakes Basin, including the complete Lake Erie watershed. These models are being developed using smaller catchments to enable improved spatial descriptions of where and from what sources the P and N originate and calibrated using more accurate loads, including more data from smaller watersheds, than used in previous models. This improved spatial resolution using harmonized hydrographic and geospatial datasets will facilitate comparisons of watershed attributes between the two countries and provide insight into why nutrient loads vary across the Lake Erie watershed. For example, loads from watersheds such as the Maumee and Sandusky rivers in the United States and the Grand and Thames rivers in Canada can be interpreted according to differences in land cover, agricultural practices and wastewater treatment facilities.

A new model that links SPARROW with outputs from water-quantity models, called HydroSPARROW, has been developed. The new model is being used to forecast changes in nutrient loads associated with various future climate and land-use change scenarios projected to occur by about 2050 and 2090.

For more information on the SPARROW model, visit the USGS homepage: water.usgs.gov/nawqa/sparrow/

Internal Loading in Lake Erie

Internal loading of phosphorus is the recycling of external loads that have accumulated and temporarily been stored in lake-bottom sediments in response to in-lake processes. As a result of this internal cycling, lakes can potentially exhibit a slow response to any reduced external loading (Sondergaard *et al.*, 2003). So while internal loading is not “new” phosphorus and cannot be controlled directly, it is important to understand and quantify recycling processes to better anticipate system response times. However, internal loads are not routinely measured and the role of sediment re-suspension from all basins within Lake Erie is not well understood.

There are three types of internal phosphorus cycling in Lake Erie:

- *inter-basin transfers*, involving a transfer of phosphorus entering the western basin (most of the Lake Erie load) to the lake’s central basin;
- *water column recycling*, involving a complex mixture of phosphorus uptake and excretion by algae, bacteria, zooplankton, fish, birds, macro benthos, and micro benthos, as well as death, decay, sedimentation; and,
- *release of phosphorus from sediment* through decomposition of sedimentary organic matter; (particularly under anaerobic conditions) from

iron-rich particulates, and re-suspension of sediment into the water column.

The role of internal loads in delaying responses to external load reductions has been considered, though primarily in small, shallow European lakes (Sondergaard *et al.*, 2003). In these lakes, most reached equilibrium following reduction of phosphorus loads in 10 to 15 years (Jeppesen *et al.*, 2007). It is unknown whether this range of response times can be transferred to Lake Erie, a much larger and more complex system. However, it is important to recognize that in response to the 1972 Agreement, reduced phosphorus loads into Lake Erie decreased western basin phosphorus concentrations from 40µg/L (micrograms per liter) to 20µg/L by the mid-1980s, despite internal recycling.

This information suggests that there could be a delay in the response of the Lake Erie ecosystem to external load reductions of at least several years and possibly longer, due to this internal load cycling. However, in relation to HABs in the west basin, more recent experience, particularly the much smaller spring phosphorus load and bloom in 2012 following the very large load and bloom in 2011, suggests a more rapid response for the blooms than for central basin hypoxia.

2.3 Trends in Effects on the Lake Erie Ecosystem

This section briefly summarizes trends in the effects of phosphorus loading on the Lake Erie ecosystem.

2.3.1 Harmful and Nuisance Algal Blooms

Planktonic Harmful Cyanobacterial Blooms

Beginning in the mid-1990s, increases in highly bio-available DRP loading to Lake Erie have coincided

with a resurgence of planktonic cyanobacterial HABs. Blooms of *Microcystis aeruginosa* and other cyanobacteria have formed annually in the western basin, and now are appearing elsewhere along the coast. In the last decade, the blooms have developed earlier and extended later than in the past. For example, the 2011 Lake Erie bloom was the worst on record (Michalak *et al.*, 2013), and was visible from satellites until mid-October.

Blooms of *Microcystis* have generally been reported from the western basin, but have recently been developing along the shorelines of the central and eastern basins. Potentially toxic species of *Planktothrix* and *Anabaena* have also been observed with increasing frequency (Davis *et al.*, 2012; Saxton *et al.*, 2012). While cyanobacteria are known to produce a number of toxins, microcystins are of particular concern.

Early detection of HAB formation is critical to formation of a proper response. Available detection methods, including remote-sensing, have greatly improved response times in recent years. Molecular methods have tracked historical existence of *Microcystis* dating to the 1970s in Lake Erie, and show that at specific sites the current population is genetically indistinguishable from the historical population (Rinta-Kanto *et al.*, 2009). **This finding suggests that environmental or anthropogenic influences have resulted in a surge in the *Microcystis* population in recent years, rather than an invasion of a distinct population.**

An understanding of the collective effects of these factors will lead to more accurate mathematical modeling and prediction of future HABs. In addition, climate models predict temperature increases that would favour cyanobacterial dominance in freshwaters and may contribute to an extension of annual bloom duration.

Nuisance Algal Blooms in Lake Erie: Benthic Algae

Over the past 10 to 15 years, study of benthic algae in Lake Erie has been largely limited to two species that form annual nuisance blooms: *Cladophora* in the eastern basin; and, more recently, *Lyngbya* in the western basin. These blooms foul recreational beaches, clog municipal and industrial water intakes, impair water quality, and pose potential microbial health risks to wildlife, household pets and humans.

Although the ecology of *Cladophora* is generally well documented in Lake Erie, far less information is available for *Lyngbya*. Recent applications of remote-sensing technology and mobile survey technology have successfully documented spatial patterns in the coverage and attached biomass of *Cladophora* and offer new approaches to expand the spatial scope of future research. Differences in substrate availability and light appear to be major determinants of *Lyngbya* and *Cladophora* abundance in Lake Erie. For example, in the more turbid western basin, *Lyngbya* is often found in turbid shallow water, associated with sand and crushed and live dreissenid mussels (small, freshwater mussels) over a limited depth range (1.5 to 3.5 m [4.9 to 11.5 ft]). *Cladophora*, meanwhile, is found in the more transparent eastern basin attached to dreissenids, rocks and other hard substrate at depths between 0.5 to 10 m (1.6 to 32.8 ft).

The arrival of zebra and quagga mussel populations in Lake Erie likely has contributed to nuisance blooms of *Cladophora* by improving water clarity, supplying nutrients, and providing substrate for filament attachment. This transformation of some stretches of the nearshore zone is consistent with the nearshore shunt hypothesis, which links the trapping of phytoplankton by dreissenid mussels to the proliferation of attached algae (Hecky *et al.*, 2004). The degree of influence of dreissenid mussels on *Lyngbya* is less clear and merits further exploration (Higgins and Vander Zanden, 2010).

The problem of nuisance algal blooms is particularly evident in the nearshore (shoreline and shallow waters adjacent to the shoreline). Nutrient-related problems in the nearshore are worsening, with increasing incidents of algal fouling in many of the Great Lakes including Erie (OMOE, 2013).

It is important to note that much of the information regarding nuisance benthic algal blooms in the Great Lakes in the past (and in more recent years) has been limited to site-specific assessments, supplemented by experimentation and simulation modeling. Researchers now know that there are several important factors influencing the dynamics of benthic algal blooms in nearshore waters of the Great Lakes. Hydrodynamics and circulation of water masses shape the interaction of lake water with land-based runoff and tributary discharges, and strongly influence the nutrient, light, temperature and disturbance regimes in the nearshore. In addition, more is known about the ability of filter-feeding organisms such as dreissenid mussels, to reduce or exacerbate conditions suitable for the growth of benthic algae.

Finally, climate change has the potential to greatly influence these interrelationships, as a result of changes in precipitation and temperature. Such changes likely will significantly alter seasonal growth patterns of algae.

A comprehensive understanding of how these various factors work together to create the conditions associated with nuisance blooms of *Cladophora* and *Lyngbya* is lacking. Addressing this knowledge gap can support the development of sound management activities.

2.3.2 Hypoxia

Hypoxia refers to a condition where the dissolved oxygen content of water is reduced to very low levels. This can occur during the summer months in deeper lake basins, such as the central basin of Lake Erie, where the water column stratifies in layers and the warmer oxygenated waters at the surface are separated from the colder, denser bottom water.

High external nutrient inputs stimulate the production of excessive organic material (algae and other organisms) in the sunlit surface layers, and the subsequent decay of this material in the bottom waters rapidly depletes the supply of oxygen, creating “dead zones,” where dissolved oxygen levels are so low that fish and other aquatic life cannot survive. Hypoxic conditions also lead to the release of phosphorus from sediments, known as internal loading, which may also contribute to the development of algal blooms.

Hypoxia, especially in the Lake Erie’s central basin, is an annual and natural event and one that probably preceded current urban and agricultural development (Delorme, 1982). In fact, the recurrence of seasonal hypoxic events in the central basin subsequent to the nutrient reductions set out in the Agreement suggests that these events are not due solely to human-induced eutrophication (Charlton *et al.*, 1993).

The dissolved oxygen depletion rate and areal extent of hypoxia, however, can be modified by human activities (Rosa and Burns, 1987; Bertram, 1993). For example, owing to excessive phosphorus inputs that stimulated algae production, dissolved oxygen depletion rates during summer increased during the mid-1900s, producing a hypoxic area as large as 11,000 km² (about 4,247 mi²) (Beeton, 1963). During the height of eutrophication, even the shallow western basin of Lake Erie could become hypoxic during windless periods in summer (Hartman, 1972). In fact, by 1963, even a five-day period of hot, calm weather could cause 50% of the western basin to become hypoxic (Hartman, 1972).

Phosphorus abatement programs initiated as part of the 1972 Agreement are credited with contributing to a decline in bottom hypoxia in both western and central Lake Erie through the early 1990s (Charlton *et al.*, 1993). However, since the late 1990s, the extent of bottom hypoxia has increased to levels on par with those observed during the previous era of eutrophication prior to the Agreement (Hawley *et al.*, 2006). The causal mechanisms for this increase are not fully understood, though the shift does coincide with altered precipitation patterns, warmer water

temperatures, increased non-point nutrient inputs and extensive algal blooms.

Climate Change and Hypoxia

Climate change is predicted to influence hypoxia formation in the Lake Erie ecosystem in several ways. Predictions made for other temperate freshwater ecosystems indicate that continued climate change likely will exacerbate the magnitude, duration and frequency of hypoxia (Kling *et al.*, 2003; Ficke *et al.*, 2007; Fang and Stefan, 2009; Jiang *et al.*, 2012). Most directly, warmer future conditions are expected to facilitate a longer stratified period during summer, with earlier establishment of thermal stratification and turnover occurring later in the year. Bottom dissolved oxygen depletion, therefore, will begin earlier and hypoxic conditions are likely to persist over an extended time period (Fang and Stefan, 2009). Reductions in water levels could further exacerbate bottom hypoxia.

While uncertainty surrounding future regional precipitation patterns is greater than the uncertainty about future regional temperatures, it is plausible that precipitation patterns will be characterized by less frequent, but more intense, precipitation events (Kling *et al.*, 2003; Kunkel *et al.*, 1999). Such intense events could lead to higher nutrient runoff from agricultural and urban lands, and, in the absence of dramatic changes in land use, lead to increased overall nutrient loads to Lake Erie. Depending on the timing of runoff, future nutrient loading, coupled with warmer water temperatures, could lead to greater overall phytoplankton production and ultimately exacerbate decomposition and oxygen depletion rates.

Potential changes to future wind patterns have not received the same amount of attention as temperature and precipitation (Kling *et al.*, 2003). By affecting thermal stratification, wind pattern changes also have the potential to alter hypoxia patterns. Specifically, intense wind events could contribute to mass movement of water, including seiches (caused by high sustained winds from one direction that push the water level

up at one end of the lake and make the level drop by a corresponding amount at the opposite end) and the potential influx of hypoxic bottom waters into nearshore zones. As well, strong wind events could facilitate vertical mixing and both delay stratification in the late spring and bring about earlier turnover in the fall, decreasing the period of oxygen depletion. In short, while future wind patterns likely will affect hypoxia patterns, the magnitude (and even direction) of such effects is unclear.

The effects of hypoxia on food webs (particularly invertebrate and fish communities), and how this may be influenced with climate change, are addressed below.

2.3.3 Effects on Fish

Lake Erie fisheries have important ecological, recreational and commercial value. Each species of fish has preferred food choices and temperature ranges, and all depend upon adequate oxygen. In general, the shallow, warm and productive western basin is currently dominated by species that are tolerant of high turbidity and warm temperatures. The eastern basin, the deepest, coldest and least productive, is dominated by deepwater fish, such as lake trout, that prefer cold temperatures, high dissolved oxygen and non-turbid waters. The central basin is dominated by cold water species, including yellow perch and walleye.

Algal blooms in Lake Erie indirectly reduce the integrity of native fish populations through loss of aquatic habitat. When algae die, the decomposition process uses much of the available oxygen dissolved in the water column. This effect is variable in combination with other factors, and is most pronounced in the deeper waters of the central basin where a hypoxic 'dead zone' forms. Additionally, decomposing algae on the lake bottom may play a role in the *Type E* botulism outbreaks that cause significant numbers of deaths of fish-eating birds (Lake Erie Committee, 2003).

As described above, warmer temperatures, lower lake levels and increased frequency of intense precipitation

events all have the potential to enhance phytoplankton blooms, reduce water clarity and exacerbate future hypoxia. Changes in lake temperature may dramatically alter the existing distribution of fish species, even to the loss of cold water species from the lake. Further, organisms that can readily avoid hypoxic regions (through vertical or horizontal migrations) may be forced to occupy inferior habitats, immediately constraining growth.

Such behavioral migrations may alter the overlap, efficiencies, and vulnerabilities of predators and prey, leading to long-term changes to food-web structure and energy flow. Coincident shifts in invertebrate/fish community composition would be expected.

In general, the interactive effects of climate change and nutrient loading are expected to promote a fish community not unlike that of the 1960s and 1970s, which was more tolerant of eutrophic conditions (that is, relatively high concentrations of nutrients). Visual feeding, cold-water and hypoxia-sensitive fish will decline, while species more tolerant to warm water will increase. However, the complex interactions between hypoxia, reduced water clarity, HABs and altered prey base have the potential to directly and indirectly mediate population patterns in ways not yet fully understood.

In addition, the impacts of climate change on lower trophic levels of Lake Erie likely will not be straightforward. Future climatic conditions will undoubtedly interact with nutrient loading and aquatic invasive species in structuring lower trophic level communities. These expected responses would favor eutrophic-tolerant invertebrate taxa. That is, zooplankton and benthic invertebrate taxa likely would increase in abundance if they are able to tolerate relatively warm temperatures, effectively consume cyanobacteria, feed under low light conditions, and utilize a low oxygen zone as a refuge from predation. On their own, expected climate change impacts could lead to invertebrate assemblages trending toward patterns observed during the 1950s and 1960s, at the height of eutrophication, when populations of desirable species sensitive to water quality conditions, such as burrowing may-

flies, were virtually eliminated and the overall diversity of benthos was lower.

2.4 Effects on Human Health and Socio-economic Conditions

Lack of data severely limited efforts to estimate the economic effects of Lake Erie algal blooms throughout the entire lake basin. For example, the LEEP study was unable to quantify impacts related to HABs on coastal property values, commercial fishing, boating, and the tourism industry. As a result, the study chose to limit its analysis of economic costs and benefits to the state of Ohio, which has more recent and available relevant information than other jurisdictions in the Lake Erie Basin. The Ohio data, therefore, can serve as a proxy, providing illustrative order-of-magnitude data on economic costs and benefits that could be expected at the broader regional level.

2.4.1 Human Health

The Agreement places considerable emphasis on preventing human health effects from use of waters of the Great Lakes. Of the five Great Lakes, only Lake Erie has an indicator status of 'fair to poor' for HABs (SOLEC, 2012).

Research on the effects of HABs on human health dates back to the 1930s (IJC, 2014). Cyanobacteria, more commonly known as blue-green algae, produce toxic cyanotoxins. Microcystis is the most common cyanobacteria in the western basin of Lake Erie, and produces the secondary metabolite microcystin. In addition to microcystin-LR (the most toxic of all the microcystin variants), other cyanotoxins found in Lake Erie are on the USEPA's Contaminant Candidate List 3, including *anatoxin-a* and *cylindrospermopsin*.

Individuals swimming, waterskiing, or boating in HABs can be exposed to microcystins. Although the likelihood of people being seriously affected by a *Microcystis* bloom is low, minor skin irritation can occur with contact. As well, gastrointestinal discomfort and,

in very rare but severe cases, acute liver failure can occur if water from a bloom is ingested.

A recent assessment of human health effects from HABs completed for the IJC's Health Professionals Advisory Board (HPAB) found that exposures to cyanotoxins have led to acute animal and human toxicity and acute lethal poisonings in domestic animals and wildlife in many Great Lakes states and Ontario (IJC, 2014). In the Great Lakes basin, only Lake Erie has had documented cases of human illness and animal (dog) deaths.

In cases where HABs appear, municipal water treatment facilities drawing water supplies from Lake Erie may need to carry out additional treatment before the water is safe for human consumption. A 2009 survey of 15 public water systems in Ohio using lake water found that 10 reported having used additional treatments in response to algal bloom events that year (OEPA, 2010). These treatments included the application of powdered activated carbon, chlorine dioxide, and potassium permanganate. Additional control costs totaled \$417,200 for the 10 water utilities, ranging from individual plant costs of \$400 to \$240,000. It is important to note that algal bloom events of 2009 were less severe than in 2011, and as such, these costs can be seen as a conservative estimate.

Public concerns about the impact of HABs on drinking water in Lake Erie were heightened in the summer of 2013. Residents in Carroll Township, OH, were advised not to drink water from their local treatment plant due to high levels of microcystin – the first time a toxin associated with algae led to a plant shutdown in the state. About the same time, water treatment plant operators in Toledo announced they required an additional \$1 million to properly treat microcystin in Lake Erie water supplies. Other water treatment plant operators are incurring additional costs, as well. These events coincided with the IJC's public open houses on the draft LEEP report, and a number of residents raised the issue of HABs and drinking water during the consultations.

Despite the human health threat posed by HABs, there is little guidance provided to drinking water treatment plant operators. In the United States, there are no USEPA standards or mandatory monitoring requirements, and though at least five states have routine state-wide or watershed-based monitoring programs and another four have developed guidance documents to support monitoring at the local level, none of those states are in the Great Lakes basin (IJC, 2014). Health Canada has established a guideline for drinking water of 1.5 parts per billion of microcystin, though there are no routine monitoring requirements in Ontario. The World Health Organization recommends that treated drinking water not exceed more than 1 part per billion of microcystin.

The IJC plans to develop a more complete understanding of Lake Erie HABs and drinking water quality, including an analysis of numeric criteria and monitoring for microcystin in drinking water.

2.4.2 Socio-economic Conditions

Property Values

HABs are known to diminish aesthetic qualities of shoreline and nearshore properties. While there are examples from the literature about how changes in water quality can impact property values, the magnitude of impacts of these blooms on nearby property values is not clear.

However, the LEEP study estimated that between 24,000 and 210,000 properties could be affected by HABs if effects to properties extend between 1.6 and 16 km (1 to 10 mi) inland from the Lake Erie coastline. This estimate, coupled with previous findings from study sites including lakes in Maine, the headwaters of the Mississippi River, and Ontario's Hamilton harborfront, suggests that future research to examine changes in housing values along Lake Erie that can be attributable to the presence of HABs is warranted. Increased property values could represent a large share of the benefits of future efforts to reduce these harmful blooms.

Regional Tourism

The presence of HABs can have immediate economic impacts on a region's tourism industry. Blooms can detract from enjoyment of water-based or near-water activities by spoiling aesthetics or producing unpleasant odors. Public health advisories or site closures issued due to the presence of the blooms can keep visitors from participating in activities and keep prospective visitors from making trips. Foregone or shortened trips translate into losses in tourist spending in the region, which in turn have implications on incomes, employment, and tax revenues.

However, the LEEP study concluded that despite the historically severe algal event in the summer of 2011, Ohio's tourism industry statewide and in the Lake Erie region experienced growth over recent years. This finding suggests that a wide range of factors affects annual tourism expenditures, including employment and general economic conditions and summer weather.

Although available data do not point to an immediate economic impact to the tourism industry caused by HABs, there may still be longer-term or delayed impacts in the future. Tourism supports a substantial amount of regional and statewide employment, as well as contributing to local, state, and federal tax revenues. Therefore, it will be important to continue efforts to better understand the potential effects of such blooms on the tourism industry.

Beach Recreation

Ohio's Lake Erie shoreline provides vast and varied beach recreation choices, with 62 public beaches along its approximately 502 km (312 m) coast (Ohio Department of Health, 2010 and 2011). During the serious outbreak of HABs in 2011, the Ohio Department of Health issued advisories at four beaches in Lake Erie's western basin. The advisories, which recommended against swimming and wading, were issued in late August and extended into October.

Combining an estimate of the per trip benefit of reducing one beach advisory obtained from a previous economic study of Lake Erie beaches (\$3.65), the number of beach trips taken to Maumee Bay State Park (178,500), and the assumed equivalence factor between the HAB-related advisory and a typical advisory, the LEEP study estimated the economic value of damages to beach recreation caused by HABs in 2011 to be approximately \$1.3 million for Maumee Bay State Park.

Recreational Fishing

Lake Erie is considered to have world-class walleye and smallmouth bass fisheries, attracting anglers from across Canada and the United States. In 2011, anglers in Ohio took more than 550,000 fishing trips on Lake Erie by private or charter boat, spending on average more than five hours a trip. Recreational anglers on Lake Erie also support a substantial charter boat industry, which totaled an estimated \$9.9 million in revenue in the state in 2010 (Lucente *et al.*, 2012).

HABs pose a threat to the health of the fishery of Lake Erie in several ways. If these effects on Lake Erie's fishery continue to the extent that fish populations decrease, then sport fishing also could decline, contributing to economic losses across the recreational fishing sector. In addition, if algal toxins affect the safety of consuming fish or if taste and odor issues arise frequently enough among sport-caught fish intended for consumption, then recreational anglers may react by taking fewer trips or by taking trips to sites other than Lake Erie.

Applying an accepted economic value per recreational fishing trip, the LEEP study estimated the economic value of impacts to recreational fishing from the severe 2011 HAB event on Lake Erie at approximately \$2.4 million in Ohio.

Commercial Fishing

The LEEP study did not identify any decline in the value of commercial fishing as a result of the 2011 HABs. Rather, the weight and value of the 2011 harvest were above typical values, particularly compared to harvests in the early 2000s. Any economic impacts to the commercial fishery as a result of the linkages among HABs, hypoxia and fish kills may become evident only over a number of years.







Yellow Perch swimming in Lake Erie.

Chapter 3 Improving the Health of the Lake Erie Ecosystem

The core objective of the **Lake Erie Ecosystem Priority** (LEEP) undertaken by the International Joint Commission (IJC) is to provide advice to federal, state, provincial and local governments in their development of policy and management approaches to help restore the lake's ecosystem by reducing nutrient loads and resulting algal blooms.

Chapter 3 reviews existing and potential initiatives to address the impacts on the Lake Erie ecosystem from phosphorus loading. The chapter:

- describes modeling efforts to identify new phosphorus loading targets that could be established to reduce the loadings into Lake Erie;
- describes the role that best management practices (BMPs) in urban areas and agricultural operations can play in reducing phosphorus loading; and,
- identifies important gaps in monitoring and research.

The chapter also highlights examples of efforts underway by various governments and organizations to address phosphorus loads in Lake Erie.

3.1 Establishing New Loading Targets

Response curves show relationships between variables and were developed to predict levels of harmful algal blooms (HABs) and hypoxia as a function of phosphorus loading. These load-response curves, in turn, can guide the establishment of new loading targets, as part of a comprehensive management plan to restore the ecological integrity of Lake Erie. Due to the bathymetry of the lake, the outlet of the Detroit River and the relative importance of different watersheds as sources of phosphorus, **the western basin is prone to HABs and the central basin is prone to hypoxia.**

3.1.1 Harmful Algal Blooms in the Western Basin

Recent advances in satellite imagery have been used to quantify the extent and severity of HABs in Lake Erie. Stumpf *et al.* (2012) developed a Cyanobacterial Index (CI) for the years 2002 to 2011 and related it to phosphorus loads. CI and area are linearly related, with a CI of 1.0 being approximately equivalent to 300 km² (116 mi²) of bloom. The CI-TP loading model was calibrated using phosphorus data from Heidelberg University and discharge data from the USGS. Stumpf *et al.* (2012) found that spring discharge and

TP loads from the Maumee River during the March-June period were strongly correlated with the CI.

Spring phosphorus loading from the Maumee River is considered a primary driver of HABs in western Lake Erie as the watershed is the dominant source of non-point nutrient loading to the western basin. It contributes about 5% of the discharge to the western basin, but nearly 50% of the phosphorus loading, making the Maumee River a good surrogate for all western basin non-point sources. The other major source of loading to the western basin is the Detroit River, which also contributes almost 50% of the phosphorus load, but more than 90% of the discharge. Detroit River concentrations are considered too low to make a significant contribution to major cyanobacterial blooms in the western basin of Lake Erie, though loadings from the Detroit River may have a larger influence on central basin hypoxia and the overall trophic status of the lake.

The relationship between the March-June TP load and the CI is exponential (Figure 3-1). Uncertainty around predictions of bloom severity tends to increase with higher loads. Rather than use this statistical model to calculate specific numerical CI values or annual forecasts, bloom categories were devised to capture the variability in observed blooms from 2002 to 2011 (Ohio EPA, 2013a). CI categories are: None/Mild (absence of a bloom or a bloom extent considered acceptable); Moderate; Severe; and Extreme (a category observed in Lake Erie in 2011) (Table 3-1).

Using these categories, severe or extreme blooms have been recorded in four of the 12 years and during another two years, borderline moderate/severe blooms have been recorded. Of the remaining six years, two fall into the moderate category and four fall into the None/Mild category.

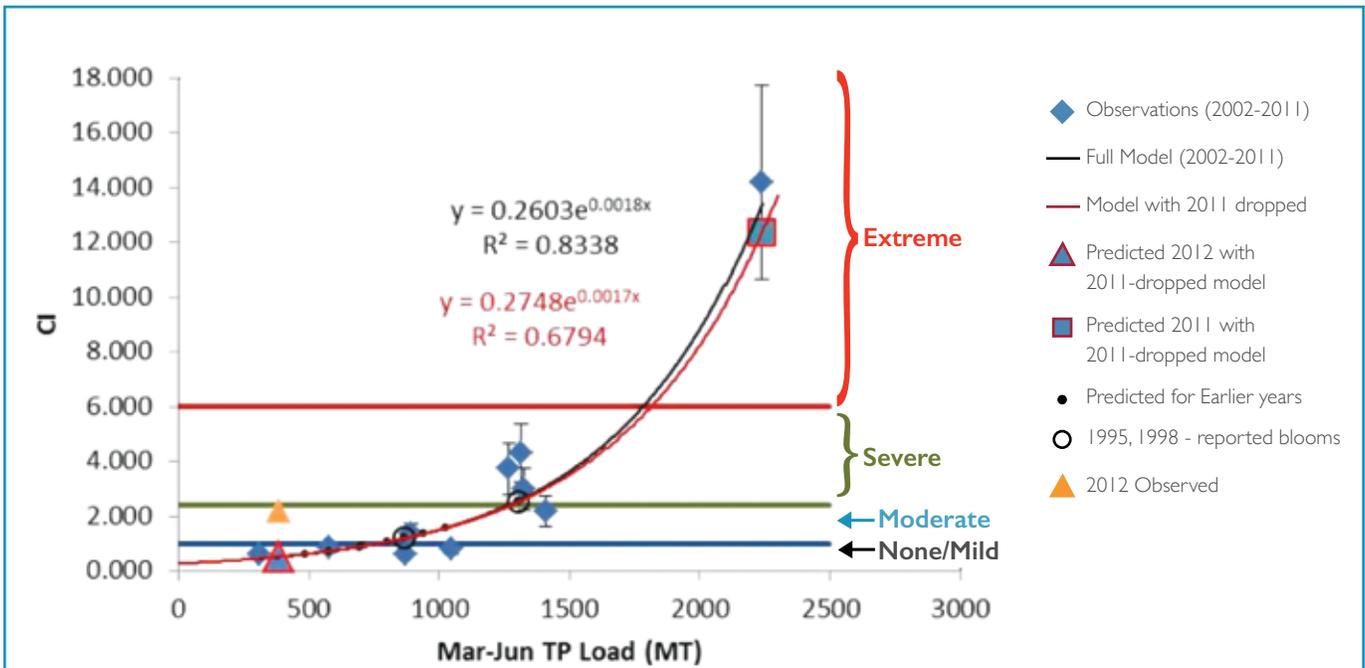


Figure 3-1
Observed and Modeled Response Curve Relationship between Total Phosphorus Load and the Cyanobacterial Index (CI) for the Maumee River

Note: This plot shows the distribution of observed harmful algal blooms in the western basin of Lake Erie, expressed as the Cyanobacterial Index (CI), against total phosphorus (TP) load for the March to June period of each year. CI categories overlay the relationship to show the distribution of blooms observed over the past decade. The diamond and square near the top-right corner of the plot correspond to the year 2011.

Source: modified from Stumpf *et al.* (2012)

To achieve an average annual bloom of None/Mild for western Lake Erie, the provisional TP load target for the Maumee River for the spring (March-June) period is 800 MT (Table 3-1). DRP is considered the most bioavailable fraction of TP and the fraction that triggers and sustains algal blooms. Under the assumption that DRP comprises approximately 20% of TP in western Lake Erie tributaries (Baker 2010; Ohio EPA, 2013a), a provisional DRP target for the spring period can be set at 150 MT. In addition, annual (12-month) load targets for the Maumee River can be estimated with the following conversion factor: Approximately 50% of the annual TP load from the Maumee River enters the western basin during the spring, meaning the provisional annual TP load target for the Maumee River can be estimated at 1,600 MT.

The Maumee River watershed covers about 50% of the western Lake Erie Basin, not including contributing upper Great Lakes watersheds upstream of the outlet of the Detroit River. Other important watersheds that drain into or immediately adjacent to the western basin include the Sandusky, Raisin, Huron, Ottawa-Stony, and Cedar-Portage, among other smaller watersheds. All have approximately the same level of agricultural land use (Han *et al.*, 2012). Therefore, the provisional TP load target for the western basin for the spring period is 1,600 MT and for the entire year is 3,200 MT. The provisional DRP load target for the spring period is 300 MT.

Table 3-1
Proposed Total Phosphorus and Dissolved Reactive Phosphorus Load Targets for the Maumee River Watershed and the Western Lake Erie Basin

Cyano Index (CI)	Bloom Category	Year(s)	Mar-Jun TP load (MT)	Mar-Jun DRP load (MT)	Annual TP load (MT)
Maumee River					
<1	None/Mild	2002, 2005, 2006, 2007, 2012	<800	<150	<1600
1-2.4	Moderate	2003, 2004	800-1,250	150-225	1,600-2,500
2.4-6	Severe	2008, 2009, 2010	1,250-1,750	225-315	2,500-3,500
>6	Extreme	2011	>1,750	>315	>3,500
Western Lake Erie					
<1	None/Mild	2002, 2005, 2006, 2007, 2012	<1,600	<300	<3,200
1-2.4	Moderate	2003, 2004	1,600-2,500	300-450	3,200-5,000
2.4-6	Severe	2008, 2009, 2010	2,500-3,500	450-630	5,000-7,000
>6	Extreme	2011	>3,500	>630	>7,000

Note: Targets are for the March to June period and annually; harmful algal bloom extent is expressed as the Cyanobacterial Index, CI.

Source: Based on Stumpf *et al.*, 2012

For the 2005 to 2011 period of record, the average March-June TP load from the Maumee River was 1,160 MT, the average March-June DRP load was 240 MT, and the average annual TP load was 2,580 MT (Heidelberg University, National Centre for Water Quality Research [NCWQR], Ohio EPA, 2013a). To achieve their respective targets, the March-June TP load reduction factor is 31%, the March-June DRP load reduction factor is 37%, and the annual TP load reduction factor is 38%.

Selection of a baseline period of record for calculation of average annual loads can have a direct influence on load reduction factors. If the 2007 to 2012 period of record from the same Heidelberg University NCWQR database is used to calculate annual loads, the average March-June TP load for the Maumee River is 1,275 MT. Against the same target of 800 MT, the load reduction factor increases to 37%. For the average March-June DRP load (255 MT), the load reduction factor increases to 41% and, for the average annual TP load (2630 MT), the load reduction factor increases marginally to 39%.

In comparing observed average loads against target loads, three additional factors should be taken into consideration. First, the recent trend toward more frequent and larger algal blooms in western Lake Erie means that more recent periods of record yield relatively higher phosphorus load reduction factors than longer periods of record that stretch back into the 1990s. Secondly, if the current trend of DRP displacing particulate phosphorus in TP loads continues, then load reduction factors for DRP will increase. Third, given the scale of the HAB and hypoxia issues in Lake Erie and the degree of nutrient control measures considered necessary to meet these targets, lag times should be anticipated before changes in phosphorus levels and ecological conditions are observed.

Further, the 2012 Agreement includes an interim TP load target for Lake Erie as a whole of 11,000 MT per year. Most of the phosphorus entering Lake Erie does so into the western basin. The response curve relationships reported in Figure 3-1 suggest that the 2012 Agreement's interim target should be revised; on average, annual phosphorus loads of 11,000 MT

will not have the net benefit of reducing the size and severity of HABs in western Lake Erie.

3.1.2 Central Basin Hypoxia

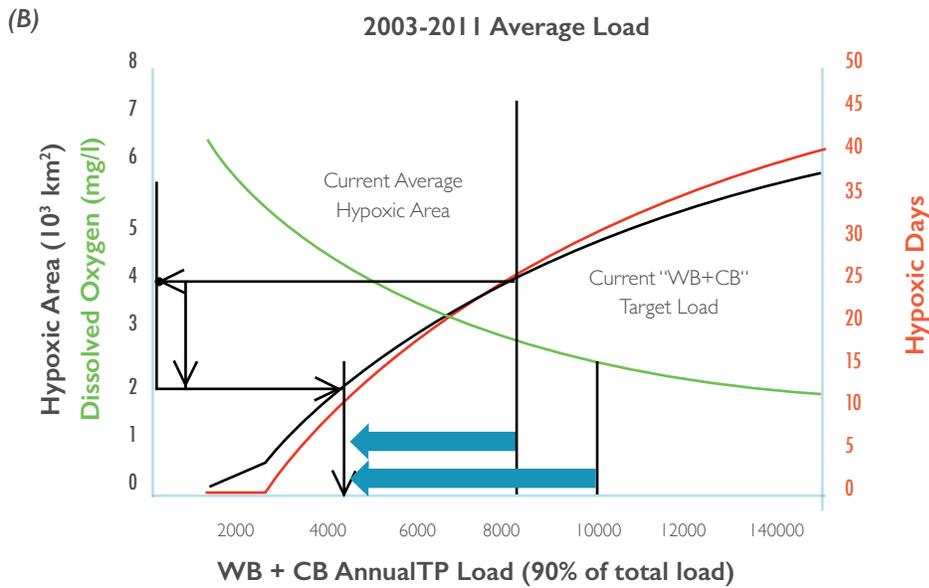
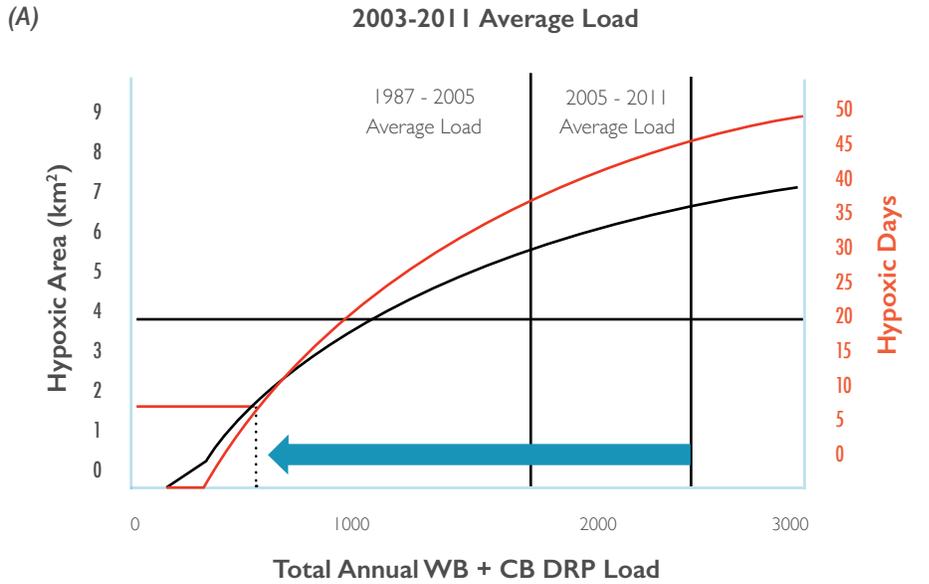
Response curves relating hypoxia to phosphorus loads were developed for the central basin of Lake Erie through application of hydrodynamic and eutrophication models (Rucinski *et al.*, 2010, Rucinski *et al.*, 2014) and geostatistical relationships observed between hypoxic area or hypoxic days and bottom-water dissolved oxygen concentrations (Zhou *et al.*, 2013). In general, higher phosphorus loads are inversely related to dissolved oxygen levels, which, in turn, result in larger hypoxic areas and a greater number of hypoxic days.

Though the Agreement states that an objective for the Great Lakes is to minimize the extent of hypoxic zones associated with excessive phosphorus loading, with particular emphasis on Lake Erie, no targets are specified. Prior to the return of algal blooms in the past decade, the mid-1990s represented a period of time when the extent of hypoxia was considered reasonable, as it coincided with the recovery of several recreational and commercial fisheries (Ludsin *et al.*, 2001). During that period, the hypoxic area was estimated at about 2,000 km² (772 mi²).

For the years 2003 to 2011, the average TP load to the western and central basins of Lake Erie was about 8,000 MT (Figure 3-2). This translates into an average hypoxic area of 4,000 km² (1,544 mi²) and 25 hypoxic days. To decrease the hypoxic area by one-half to 2,000 km² (772 mi²) and to about 10 hypoxic days a year, the target TP load for the western and central basins is 4,300 MT, a 46% reduction from the 2003-2011 observed average load and 56% below the current target.

When expressed as annual DRP load, the target for achieving the same hypoxic area (2,000 km²) and number of hypoxic days (10) is 600 MT. This value is slightly lower than the average estimated for the early 1990s. However, as there has been a significant increase in DRP load over the past two decades, this new level represents a 78% reduction from the 2005-2011 average DRP load.

Figure 3-2
Response Curve Relationships between Phosphorus Loads in the Western Basin (WB) and Central Basin (CB) and Hypoxic Area and Hypoxic Days



Note: (A) Relationship between annual total phosphorus (TP) loads and hypoxic area and the number of hypoxic days; the inverse relationship between TP and dissolved oxygen is also shown. The blue arrows show the amount of TP that needs to be reduced to achieve a desirable level of hypoxia in the CB, relative to the current target load and average observed load for the years 2003 to 2011.

(B) Relationship between annual DRP loads and hypoxic area and the number of hypoxic days. The blue arrow shows how the amount of DRP that needs to be reduced to achieve a desirable level of hypoxia in the CB has increased from the 1987 to 2005 period to 2005 to 2011 period.

Source: Modified from Rucinski et al., 2010

When the ecological issues of HABs and hypoxia are considered together, comparisons can be made between recommended targets between the two sets of response curves. For the long-term elimination of HABs, the March-June TP target recommended by the IJC for the Maumee River is 800 MT, a 31% reduction from 2005-2011 period of record or a 37% reduction from the 2007-2012 period of record. If all western and central basin non-point sources were reduced by the same percentage and applied across the full year, then the resulting annual TP load would be reduced from 8,000 MT to 6,275 MT, which clearly exceeds that estimated for achievement of an average hypoxic area of 2,000 km² (772 mi²), 4,300 MT. Therefore, in setting future targets, it is critical that HAB and hypoxia endpoints are developed separately.

3.1.3 Whole-lake Phosphorus Targets for Lake Erie

Establishment of new phosphorus load and concentration targets is the responsibility of the two national governments. The 2012 Agreement specifies an interim total phosphorus load target for Lake Erie of 11,000 MT per year. It does not specify targets according to the western, central and eastern basins of the lake. However, it does for open water phosphorus concentrations (15 µg/l for the western basin and 10 µg/l for the central and eastern basins). The Agreement indicates that the stated loading targets will stand until updated by the governments of Canada and the United States and that new loading targets for Lake Erie are expected in 2016. Annual time-series data over the past decade show that, coincident with the reoccurrence of HABs, total and particulate phosphorus loads from key United States tributaries have been either levelling off or decreasing, while DRP loads have been increasing. **This suggests that the interim load target for Lake Erie may be obsolete and not reflective of the importance of particular forms of phosphorus.**

Total Maximum Daily Load Process

As noted in the IJC's 16th Biennial Report (Appendix 2), most pollution reduction under the United States Clean Water Act has been accomplished through pollution discharge limits imposed via permits for individual facilities or point sources such as wastewater treatment plants and industrial plants. While effective in reducing a significant proportion of pollution to Great Lakes tributaries and open lakes, a different approach is needed to address most non-point sources, such as pollution runoff from agricultural and other land-based human activities.

In the United States, the Clean Water Act provides a mechanism for addressing both point and non-point sources of pollution for a given water body that does not meet water quality standards for a particular pollutant. These water bodies are deemed "impaired waters." The total maximum daily load (TMDL) process entails calculation of the maximum amount of loading of pollutant(s) of concern that the impaired waterbody can receive and still meet water quality standards for that particular pollutant. The TMDL allocates the load to both point and non-point sources. Following development of a TMDL, implementation should proceed in a way that meets water quality standards and restores impaired waterbodies. States are required to develop TMDLs and may use available regulatory authority in their implementation.

In the case of Chesapeake Bay, a plan with firm pollutant reductions and timelines is taking shape under circumstances not unlike those found in the western Lake Erie Basin. State and federal efforts to remediate the Chesapeake Bay's impaired status date back more than 30 years. The bay is degraded by pollution from both point and non-point sources but, as in the case of Lake Erie's western basin, reduction in polluted runoff from non-point sources has been more difficult to achieve. A number of voluntary cooperative agreements among the six basin states, Washington, DC and the USEPA have not led to progress toward attainment of water quality standards for phosphorus, nitrogen and sediments in the bay. In 2009, President

Obama issued an executive order that, among other things, supported the USEPA's efforts to develop a multi-jurisdictional TMDL for the three pollutants. The agency's authority to do so – and to take action regarding water quality standards and establishment of TMDLs if the states' efforts fall short – was affirmed by the recent ruling of a U.S. District Court. Issued in 2010, USEPA's Chesapeake Bay TMDL establishes waste load allocations of nitrogen representing a 25% reduction from current levels, a 24% reduction of phosphorus, and a 20% reduction of sediments among the Bay jurisdictions. The TMDL sets forth allocations for sectors including non-point sources such as agriculture, on-site septic, and urban sources, and provides target loads for each state and the District of Columbia. States and the District are required to submit watershed implementation plans with specific measures proposed so as to achieve their target loads. Reflecting a 2007 agreement among the jurisdictions, the TMDL requires that all pollution control measures be fully implemented by 2025, with at least 60% of the actions taken by 2017.

An important step in the TMDL process is a state listing of waters as impaired. To date, neither Michigan nor Ohio has listed the open waters of western Lake Erie as impaired by nutrients, despite nutrient-caused algal blooms. The USEPA could call for the states to do so. A related problem is that neither of the two states has developed numeric phosphorus ambient water quality criteria, though Ohio is in the process of developing such statewide criteria. The USEPA could call on Michigan to move forward in developing similar statewide criteria.

3.1.4 Phosphorus Targets in the Context of Adaptive Management

Adaptive management is a planning process that provides a structured, iterative approach for improving actions through long-term monitoring, modeling and assessment. It allows decisions to be reviewed, adjusted and revised as new information and knowledge become available and/or as conditions change. The IJC has embraced adaptive management as an approach for addressing transboundary water issues,

as stated in the Agreement, including extreme water levels in the Great Lakes (International Great Lakes-St. Lawrence River Adaptive Management Task Team, 2013).

The approach also can be applied to the issues of HABs and hypoxia in Lake Erie. Where the Great Lakes-St. Lawrence River adaptive management plan focuses on uncertainty surrounding water level fluctuations as a function of climate change, a Lake Erie adaptive management plan would focus on uncertainty surrounding recommended measures for reducing nutrient loads to the lake and its tributaries. For the issue of HABs in the western basin, the IJC suggests phasing in TP and DRP targets over a nine-year period (2014-2022) by setting transitional targets on a three-year basis to coincide with the triennial cycle and assessment of progress outlined in the 2012 Agreement (Figure 3-3).

3.2 Implementing Best Management Practices (BMPs)⁸

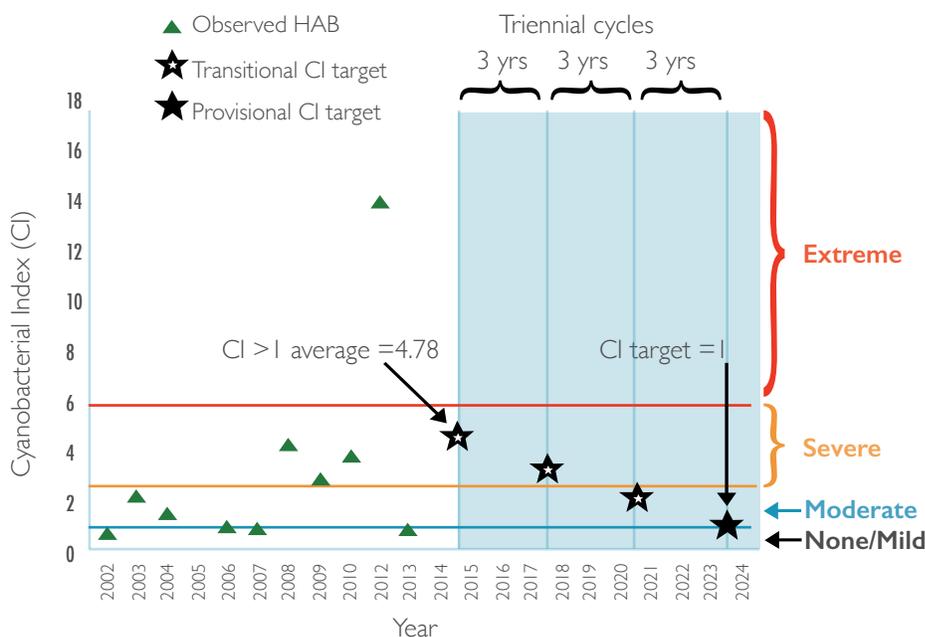
This section presents an overview of BMPs in both agricultural and urban settings that should be considered for implementation within the Lake Erie Basin to reduce phosphorus loads.

BMP is a term used in the United States and Canada to describe a range of practical methods, techniques and other actions that allow individuals or organizations to prevent or reduce the risks of water pollution resulting from activities on the land. BMPs typically evolve over time, as new approaches (for example, based on new information or new technology) are introduced, proven to be effective and adopted.

LEEP undertook a comprehensive review of more than 240 primary sources on the implementation and effectiveness of BMPs in Canada and the United States (McElmurray *et al.*, 2013). The review focused on BMPs that have been evaluated using scientific methods for phosphorus reduction. A secondary focus was to highlight BMPs that have been implemented within the Lake Erie watershed, or more generally, in the Great Lakes region.

⁸ BMPs typically are referred to as beneficial management practices in Canada.

Figure 3-3
Harmful Algal Blooms, Western Lake Erie, as Represented by the Cyanobacterial Index (CI) in an Adaptive Management Context.



Note: Harmful algal blooms (HABs) as represented by the Cyanobacterial Index (CI) are plotted over time from 2002 until 2012 (green triangles). Horizontal lines across the plot correspond to break-points between CI categories that correspond to None/Mild (or acceptable), Moderate, Severe or Extreme blooms. The period from 2014 to 2022 covers the next three triennial cycles of the 2012 Great Lakes Water Quality Agreement, which can serve as three-year transitional targets (open stars) for evaluation of progress between the observed mean annual CI of 4.78 (Severe blooms) and the final CI provisional target (solid star) of 1 (None/Mild blooms).

Source: Observed data from Stumpf et al., (2012) and Ohio EPA (2013a).

3.2.1 BMPs in Agricultural Operations⁹

Agricultural systems have evolved from being net phosphorus sinks, where crop production is phosphorus-limited, to being phosphorus sources, where there is net phosphorus export from most farms (McElmurray et al., 2013). As a result, as noted in Chapter 2, agriculture is the major source of non-point inputs of phosphorus in the Lake Erie Basin.

The basin receives 44% of the TP entering the Great Lakes from agricultural activities, more than any other Great Lake. Commercial fertilizers account for the majority of agriculturally-applied phosphorus in most locations. In Ohio, for example, 84% of phosphorus applied to agricultural land in the Lake Erie Basin is from commercial fertilizers, and 16% is from manure (Ohio EPA, 2013a).

⁹The Ohio Lake Erie Phosphorus Task Force II Final Report (Ohio EPA, 2013a) provides an excellent review and analysis of agricultural practices, nutrient management and phosphorus mitigation. Readers are referred to that document for a thorough review of the issues related to TP and DRP, and policy and management recommendations to achieve phosphorus reduction from agricultural landscapes. Although focused on Ohio, the report has application to other, comparable parts of the Lake Erie Basin.

Livestock production in the basin and elsewhere has trended in recent decades toward a smaller number of larger feedlot operations. Concentrated (or confined) animal feeding operations (CAFOs) are livestock facilities that raise a large number of animals in production barns or confinement pens. These large and concentrated operations generate a large amount of manure, which may runoff to nearby watercourses if not managed properly. It has been estimated that CAFOs account for 60% of the waste from animal feeding operations (Mikalonis, 2013). A review undertaken as part of the LEEP study found that CAFOs are regulated in both Canada and the United States, though in slightly different ways. In Ontario, all CAFOs are regulated under the *Nutrient Management Act*, while in the United States, the operations fall under the *Clean Water Act* (Dupre, 2013).

The control of agricultural phosphorus losses should be directed toward the long-term goal of increasing the efficiency of phosphorus use on farms and therefore, farm profitability. This goal can be achieved through practices that balance inputs and outputs of phosphorus within a watershed and improve the management of soil, manure, and commercial fertilizer at the farm, watershed, or regional scales, while preserving or improving crop and livestock yields.

BMPs in agricultural operations can be grouped according to *source* and *transport*:

- *source* BMPs minimize the potential of phosphorus as pollution at the origin, before it is transported from the soil by water movement; and,
- *transport* BMPs are mostly structures and methods that reduce the transport of phosphorus.

Phosphorus Source BMPs

Table 3-2 summarizes the major BMPs associated with addressing the sources of phosphorus in agricultural operations. Key activities associated with source BMPs include nutrient management, which includes fertilizer and manure management, and animal feed management.

Nutrient management is designed to:

- budget, supply, and conserve nutrients for plant production;
- minimize agricultural non-point source pollution of surface and groundwater resources;
- properly utilize manure or organic by-products as a plant nutrient source;
- protect air quality by reducing odors, nitrogen emissions (ammonia, oxides of nitrogen), and the formation of atmospheric particulates; and,
- maintain or improve the physical, chemical, and biological condition of soil (USDA-NRCS, 2012).

The LEEP study found that nutrient management and related practices in crop-based agriculture (for example, soil and plant tissue testing, fertilizer rates calculation, variable rate application, precision agriculture) were primarily geared toward efficient agronomic output but not necessarily environmental quality. Concern with the latter seems to be more prevalent in animal-based agricultural production and is not well-studied in purely crop-based production agriculture. The effect of fertilizer application rate on phosphorus loss at a farm scale is directly related to application method, the hydrologic soil group, and crop type, among other factors. Nutrient management in combination with tillage and erosion practices may reduce TP loads by more than 80%, but in some cases may increase the loads (Cestti et al., 2003). The efficacy of BMPs improves when multiple BMPs are implemented, rather than a single BMP (Bosch et al., 2013). BMP effectiveness also will vary depending on site conditions.

Manure export from the farm generally is not a viable management option because of hauling costs and off-farm land application options generally are restricted to the nearest neighbors (Sharpley et al., 2006). As a result, in most areas, waste storage, composting, and land applications are the most viable options for manure management.

Table 3-2
BMPs Associated with Phosphorus (P) Sources in Agricultural Operations

- Balance P inputs with outputs at farm or watershed scale
- Minimize P in livestock feed
- Test soil and manure to maximize P management
- Physically treat manure to separate solids from liquid
- Chemically treat manure to reduce P solubility (i.e., alum, fly ash, and water treatment residuals)
- Biologically treat manure (i.e., microbial enhancement)
- Calibrate fertilizer and manure spreaders
- Apply proper application rates of P
- Use proper method for P application (i.e., broadcast, plowed in, injected, subsurface placement, or banding)
- Carefully time P application to avoid imminent heavy rainfalls
- Implement remedial management of excess P areas (spray fields and disposal sites)
- Compost or pelletize manures and waste products to provide alternate use
- “Mine” P from high-P soils with certain crops and grasses

(Source: Sharpley *et al.*, 2006)

Reducing Phosphorus Discharges from Greenhouse Operations

In addition to the widespread impacts to water quality associated with fertilizer and manure application to agricultural lands, other agricultural activities can influence Lake Erie water quality. For example, Essex County in southwestern Ontario has the highest concentration of vegetable greenhouses in Canada. When recycled greenhouse irrigation water is no longer useful for growing plants, it must be treated before being discharged to waterways.

In 2011, an Ontario Ministry of Environment study concluded that many Essex County greenhouses discharged wastewater containing high levels of phosphorus to nearby creeks, which in turn discharged to Lake Erie. The province now is working with greenhouse growers to inspect and assess their operations, and ensure measures are taken to reduce phosphorus in their discharges.

Canada –Ontario Environmental Farm Plan (EFP)

The Environmental Farm Plan (EFP) program, begun in Ontario in 1993, is internationally recognized for its success in assisting Ontario farmers to implement more environmentally sustainable practices. To date, more than 35,000 Ontario farmers have participated in the program.

An EFP is a voluntary assessment prepared by farmers to increase their environmental awareness in up to 23 different areas related to their farming operation. Through EFP local workshops, farmers and experts work together to identify each farm's unique environmental strengths and areas of concern. The farmers then set realistic action plans to address the areas of concern, as well as appropriate time tables to improve environmental conditions. Cost-share programs are available to help implement projects and improve environmental weaknesses. Farms with EFPs in Ontario can easily be identified by the '*our farm has an environmental farm plan*' signage.

Source: www.omafra.gov.on.ca/english/environment/efp/efp.htm

Michigan Agriculture Environmental Assurance Program (MAEAP)

All U.S. states offer some form of agricultural outreach and extension services. In Michigan, MAEAP was created in 1998 with the input of a coalition of agricultural, environmental, and conservation groups, who had a common goal: the prevention of agricultural pollution. The program is innovative, proactive, and voluntary to help all farmers in the state of Michigan prevent or minimize the risk of agricultural pollution while keeping their farming operations sustainable. MAEAP is a three-stage process designed to reduce farmers' legal and environmental risks. The program teaches effective land stewardship practices that meet both state and federal regulations, while allowing farmers to identify and prevent agricultural pollution risks from their farming operations. After the requirements are met, the farmer becomes certified and can display MAEAP signage.

To date, 1,400 MAEAP verifications have been completed, more than 10,000 Michigan farmers have started the process, and, an average of 5,000 Michigan farmers attend an educational session each year. MAEAP is credited with reducing soil erosion by more than 272,000 MT (300,000 tons) and phosphorus by more than 227 MT (500,000 pounds) annually. In addition, nearly 4,050 ha (10,000 acres) have been taken out of agricultural production and restored in the form of filter strips and almost 1,900 gullies have been stabilized to protect water quality.

Sources: www.michigan.gov/mdrd/0,4610,7-125-1599-12819--,00.htm osceolalakecd.org/maeap/

The “4R” stewardship framework is a major initiative in nutrient stewardship, jointly promoted by the Fertilizer Institute, the International Plant Nutrition Institute, the International Fertilizer Industry Association, and the Canadian Fertilizer Institute (see text box).

In animal-based agriculture, feed mass balance has become an evolving and important BMP. Animal

farms have decreased in numbers but their capacity has increased in terms of herd size and farm densities. As a result, net nutrient influxes and net nutrient excess occur in most of these farms (Sims et al., 2005). Decreasing phosphorus in feeds is the best method to mitigate phosphorus loss from manure. Manure TP reductions with feed management range from 16 to 33%.

4R Stewardship Framework – Right Source, Right Rate, Right Time and Right Place

Originally developed by the fertilizer industry to increase public confidence in the industry's ability to manage nutrients responsibly, the 4R Stewardship Framework aims to match nutrient supply with crop requirements and minimize nutrient losses from fields (IPNI, 2007). The philosophy of the 4R approach is to base nutrient recommendations and application on scientific principles, including site-specific considerations and adaptive management, with the goal of improved sustainability. The approach provides a framework to achieve cropping system goals that include increased crop yields and therefore farm profitability, and enhanced environmental protection (Ohio EPA, 2013b).

The 4R Stewardship Framework is based on:

1. **Right Fertilizer Source:** matching appropriate fertilizer source and product with soil properties and crop needs. Nutrient interactions should be accounted for and nutrients should be balanced according to crop needs and soil tests. Balanced fertilization is one of the keys to increasing nutrient use efficiency, and therefore reducing excess nutrient loss from the field.
2. **Right Rate:** matching application rates with crop requirements. Excessive fertilizer application may lead to nutrient loss to the environment with no additional gain in crop yield and quality. Soil testing is essential for determining the right application rate, while other BMPs, such as variable rate application and applicator calibration, also can be important.
3. **Right Time:** making the nutrient available when the crops need them. Nutrients are used most efficiently when their availability is synchronized with crop demand. BMPs that influence the timing of nutrient availability include pre-plant or split application timing, controlled release technologies, stabilizers, and inhibitors.
4. **Right Place:** placing and keeping nutrients where the crop can efficiently use them. The method of fertilizer application is critical, and the most appropriate placement method is determined by the crop, cropping systems, and soil properties. Injection or incorporation are most effective at keeping nutrients in place and increasing their uptake by plants, but soil disturbance needs to be balanced with erosion-control BMPs such as conservation tillage, buffer strips, cover crops, and irrigation management. Proper fertilizer placement revolves around applying phosphorus in a manner that maximizes contact, binding, and/or retention of phosphorus with soil to minimize off-site movement.

More information on 4R Nutrient Stewardship can be accessed online, including at www.ipni.net/4R and www.nutrientstewardship.com.

Phosphorus Transport BMPs

Transport BMPs are aimed at erosion control and TP reduction.

Residue and Tillage Management (Conservation Tillage)

Conservation tillage involves management practices that leave at least 30% of the soil surface covered with crop residue following tillage and planting to reduce soil erosion (Galloway *et al.*, 1981). In general, conservation tillage reduces TP loads by as much as 60 to 80% when undertaken in conjunction with other nutrient management practices (Cestti, 2003). However, several studies have evaluated DRP reduction and found a wide range of removal efficiencies (McElmurray *et al.*, 2013). Soil stratification can lead to accumulation of phosphorus at the top of the soil profile, and soil macropores frequently result in the preferential flow of DRP to drain tiles, and then to the receiving environment.

Conservation Cropping

This BMP includes crop rotation, conservation cover and strip cropping. Bosch *et al.* (2009) observed that post-BMP loading of DRP decreased by 74% and nitrate by 73% to 88%.

Conservation Buffers

Conservation buffers are designed to create or improve habitat, and reduce sediment, organic material, nutrients and pesticides in surface runoff and shallow ground water flow. These buffers include contour buffer strips (narrow strips of permanent, herbaceous vegetative cover around landscape contours), riparian forest buffers (areas dominated by trees or shrubs adjacent to and up-slope of watercourses or water bodies) and filter strips or areas of herbaceous vegetation.

However, these features may have limited effectiveness in reducing phosphorus export in the western

basin's agricultural watersheds because buffer effectiveness relies on sheet flow through the feature, whereas in practice buffers often are bypassed by field furrows and concentrated flow outlets. In addition, subsurface drain tiles are common in the west basin's relatively flat, agricultural watersheds with clay soils, and tiles discharge directly to waterways without passing through the buffer (Ohio EPA, 2013b). Forested riparian buffers have been shown to be more effective where they incorporate a wetland function for discharges received from agricultural uplands.

Wetlands Protection and Restoration

Addressing the twin problems of coastal wetland loss and hardened shorelines has potential to benefit water quality in western Lake Erie.

Coastal wetlands and coastal terrestrial systems are important components of Lake Erie ecosystem biodiversity. They also provide ecosystem services such as filtration of polluted non-point source runoff. Both of these systems are highly threatened by coastal development and shoreline alterations, due to the resulting physical alteration of the land-water interface (SOLEC, 2009).

Lake Erie has lost more than 80% of its pre-settlement coastal wetlands, significantly affecting water quality as well as habitat. The 2006 Lake Erie Lake-wide Management Plan observed: “[P]hosphorus can be strictly managed, but unless natural land or habitat is protected and restored, only marginal response will be seen by many components of the ecosystem. It was determined that changes in land use that represent a return towards more natural landforms or that mitigate the impacts of urban, industrial and agricultural land use, are the most significant actions that can be taken to restore the Lake Erie ecosystem.” (LAMP, 2006)

In a study of lakes in the Pacific Northwest, Scheuerell and Schindler (2004) found a negative relationship between TP concentrations and fish aggregations, suggesting that as the number of coastal houses per unit of lake area increases, TP also increases and fish aggregations decrease.

A restorable wetlands assessment for the United States portion of western Lake Erie (not including the Detroit River) prepared for The Nature Conservancy suggests a potential restorable wetland area of 63,841 ha (157,755 acres) – a figure that likely underestimates the true potential, as it does not include any areas currently inundated by the lake (Saarinen *et al.*, unpublished).

Based on data developed by the Great Lakes Coastal Wetland Consortium, there are now about 10,455 ha (25,835 acres) of coastal wetlands in the western basin (including the Detroit River and Ontario). The Nature Conservancy's Lake Erie Basin Conservation Strategy (LEBCS) goal to increase wetland area by 10% suggests a need for 1,046 ha (2,584 acres) of new coastal wetlands in this area by 2030. Given the recent pace of wetland conservation and restoration and the commitment by agencies and organizations at all levels and on both sides of the lake, this goal is feasible, contingent on funding. The cost of achieving this goal in the United States alone is likely to approach \$19 million. However, wetlands provide substantial economic benefits, including, for example, improving water quality by filtering pollutants, storing floodwaters, and serving as fisheries habitat.

Restoring natural land cover and softening shorelines also are key initiatives. Based on an analysis of land cover data from the National Oceanic and Atmospheric Administration Coastal Change Analysis Program and the Ontario Ministry of Natural Resources Land Information Ontario Program, the entire Lake Erie coastal area (within 2 km [1.2 mi] of the lake) falls short of The Nature Conservancy's goal of 40% natural land cover (Pearsall *et al.*, 2012). The western basin is particularly deficient, generally falling well below 30%. The western basin also leads the lake in the amount of artificial shoreline.

Drainage Water Management

Agricultural drainage practices throughout most of the Lake Erie Basin are designed to remove water quickly from the landscape through an elaborate network of subsurface and surface drains. This BMP

manages the discharge water from surface and/or subsurface agricultural drainage systems to avoid impacts on downstream receiving waters. Typically, drainage water management involves the installation of adjustable retention devices to interrupt runoff and drain tile discharges. Drainage and water table management practices address both crop productivity needs, as well as environmental objectives.

A review conducted for the LEEP study found that previous studies have focused only on nitrogen reduction from drain tiles. It noted that this focus reflects conventional wisdom in the past that the majority of phosphorus losses occur as particulate phosphorus attached to sediments transported by surface runoff (McElmurray *et al.*, 2013). The same review found a number of studies that confirmed drain tiles are a source of phosphorus to streams. Additional research on the efficacy of drainage water management in mitigating phosphorus export is needed.

Current and Emerging Technologies

LEEP identified several current and emerging technologies for the reduction of phosphorus loadings from agricultural areas that have received recent research attention and deserve further investigation. These technologies include two-stage ditches (Powell *et al.*, 2007), controlled drainage (Kroger *et al.*, 2011; Nistor and Lowenberg-DeBoer, 2007), hydrologic attenuation, and treatment of tile outlet discharge with, for example, bioreactors and filters (McDowell *et al.*, 2008).

To conclude, LEEP found that measurements of the efficacy of agricultural BMPs are variable and evolving – and that they vary between locations and site conditions. Therefore, additional research is required. However, the need for additional research should not delay the implementation of the numerous BMPs that have been shown to be consistently effective for reducing phosphorus in both its particulate and dissolved forms, including cover crops and residue management (conservation tillage).

Encouraging BMPs on Ohio Farms: Ohio's Healthy Lake Erie Fund

Less than a year after it was implemented, the \$3 million Healthy Lake Erie Fund has enabled farmers to apply agricultural nutrient reduction practices on more than 14,000 ha (35,000 acres) of farmland in the western Lake Erie Basin watershed.

The Healthy Lake Erie Fund is administered by the Ohio Department of Natural Resources (ODNR) in cooperation with local soil and water conservation districts through the Ohio Clean Lakes Initiative. The main goal of the Ohio Clean Lakes Initiative is to reduce HABs in the western Lake Erie Basin by implementing and installing BMPs to reduce nutrient runoff into the lake.

Under the Healthy Lake Erie Fund, farmers have adopted a range of agronomic practices, including cover crops, variable rate fertilizer applications, nutrient incorporation and controlled drainage structures. Participating farmers are required to conduct soil tests to determine the nutrient levels and follow recommendations to determine the appropriate amount of fertilizer to apply to their fields. The ODNR plans to designate some of these farmers as “ambassadors” so they can share their experiences and help expand the adoption of additional practices by other farmers throughout the western Lake Erie Basin and the rest of Ohio.

Source: www2.ohiodnr.com/cleanlakes/healthy-lake-erie-fund

Agricultural Practices and DRP

As noted in Chapter 2, the management of DRP has become an increasingly important issue, due to the large fraction of DRP that is bioavailable. How to best manage DRP is of particular importance in considering BMPs for agricultural practices.

The recurrence of severe algal blooms in Lake Erie since the mid-1990s coincided with an increase in DRP loads. A combination of several factors may have caused the increase in DRP export from agricultural lands (Ohio NRCS, 2012):

- conservation practices (for example, reduced- and no-till cropping systems) implemented since the early 1990s across the basin focused on reducing sediment and TP, but these practices are less useful for controlling DRP;
- farming equipment has become larger and producers now typically broadcast fertilizer onto the

soil surface, rather than banding, where fertilizer is placed adjacent to the crop;

- large-equipment traffic may have caused soil compaction, resulting in decreased infiltration and increased runoff;
- increasingly, fertilizer is applied in the fall instead of spring;
- the application of two years' worth of fertilizer in one year for a corn-corn or corn-soybean crop sequence saves money, time, and labor for the producers but results in higher rates and amounts of fertilizer available for export out of the cropland into the streams; and,
- the maximization of crop yields through fertilizer application and the use of conservation tillage also may have increased soil phosphorus levels, particularly at the soil surface (soil stratification) over a long period of time.

Finally, it is important to note that the effectiveness of BMPs in agricultural operations is likely to be chal-

lenged by a changing climate. For example, recent data indicate that large phosphorus loads – including DRP – are exported into Lake Erie during major storms. Under future climate conditions, such storms likely will become more frequent and more intense. However, current BMPs are targeted primarily to reducing particulate phosphorus, not DRP. Therefore, there will need to be a shift in focus for BMPs in agricultural operations to take into account this climate change effect.

Rural Residential Areas and On-Site Septic Systems

On-site septic systems likely are contributing to phosphorus loadings in the Lake Erie watershed. Maintenance of such systems and replacement of failing systems by homeowners is an element of proper stewardship.

In rural areas and small communities, municipal sewers typically are not available. Instead, homes often discharge wastewater to on-site household sewage systems (commonly known as on-site septic systems) rather than publicly owned sewage treatment plants. Household sewage systems are used in approximately 20% of all homes in the United States and are also widely used in Ontario.

A septic system is comprised of an underground tank, a network of pipes and microscopic organisms to process waste. Waste leaves the septic tank and is discharged into a drainfield for soil treatment. When properly maintained and operated, septic systems remove viruses, bacteria and organic materials from wastewater.

A malfunctioning septic system, by contrast, can result in contaminants leaching into adjacent drains, watercourses and lakes, posing a risk to the environment and human health. If the drainfield is overloaded with too much liquid, it will flood, causing sewage to flow to the surface or create backups in plumbing fixtures and prevent treatment of all wastewater. This generally happens with older or poorly maintained systems. Systems installed in insufficiently porous soils also may fail. Pollutants released to groundwater or surface water from these systems include phosphorus.

Local health districts in the Lake Erie Basin watershed of Ohio that responded to a 2013 information request reported 252,617 septic systems. An estimated 96,339 of these systems were failing, a failure rate of 38.14%. Leading causes of failure included age (53%) and soil limitations (41%). In Ontario, approximately 1 million households rely on septic systems, most of them in the Great Lakes basin. Investigators estimate that 30% of those systems are failing to adequately protect the environment (Ontario Soil and Crop Improvement Association, 1999).

Recognizing the potential significance of this source of phosphorus to Lake Erie, the Ohio Phosphorus Task Force estimated in its 2010 report that septic systems in the Lake Erie Basin watershed of Ohio contributed 88 MT of phosphorus per year to local waterways – a level comparable to the estimated 90.4 MT a year in phosphorus loads from combined sewer overflows in the state (see section 3.2.2).

The task force recommended establishment of statewide minimum standards and rules to provide program continuity across all 88 counties in Ohio. In its November 2013 report, the Ohio Phosphorus Task Force II observed that this recommendation has essentially been adopted through the promulgation of rules.

In Ontario, standards for design, installation and proper maintenance of a septic system are set out in the Ontario Building Code. Under the code, an evaluation is required on every site where a new or replacement septic system is installed. Additionally, to protect drinking water sources, the Ontario Building Code was amended to include the implementation of a mandatory septic system maintenance re-inspection program in designated areas. A “designated area” is where a septic system is, or could be, a significant threat to drinking water based on the vulnerability of wellhead protection areas and intake protection zones.

Following the death of several Ontarians due to the contamination of a municipal drinking water supply with livestock runoff, the Report of the Walkerton Inquiry (Ontario Ministry of Attorney General, 2002)

issued a series of recommendations, including that septic systems should be inspected as a condition for the transfer of a deed. That recommendation has not been enacted to date.

In Michigan, which lacks a statewide sanitary code, local health departments oversee the installation of on-site septic sewage systems. Approvals for wastewater systems serving single- and two-family dwellings fall under the jurisdiction of the sanitary codes of these local health departments. These codes vary considerably in their requirements.

3.2.2 Urban BMPs

Given the significant loading of phosphorus into Lake Erie from urban areas, there is a clear need to evaluate the effectiveness of urban-focused BMPs. Moreover, because there are many diffuse sources of phosphorus within urban areas, the relevant BMPs will need to be highly varied as well, and targeted for implementation in a wide range of urban activities.

Non-Point Source BMPs

The LEEP study reviewed two types of non-point source BMPs in the urban setting:

- alternative behavior/management BMPs (known as non-structural BMPs); and
- structural (or engineered) BMPs.

Alternative Behavior Management BMPs

Educational campaigns focused on changing behavior of urban residents typically result in only modest changes, with some BMPs adopted more readily than others. A common non-structural BMP often considered by communities facing phosphorus related problems in surface waters is reducing phosphorus loads from lawn fertilizers. Loadings are reduced considerably if fertilization is based on soil tests rather than routine practice (Erickson *et al.*, 2005).

Scotts Phosphorus-Free Lawn Fertilizers

In 2006, recognizing the link between nutrient runoff and algal blooms, the Scotts Miracle-Gro Company made a commitment to the Chesapeake Bay area that phosphorus in its lawn foods would be reduced by 50%. In 2011, Scotts expanded this commitment and pledged to remove phosphorus entirely from their Turf-Builder lawn food maintenance products across the United States. In May 2013, Scotts announced that this goal has been achieved for both the United States and Canada. All Scotts lawn maintenance products are now phosphorus-free; this will reduce the amount of nutrient runoff that is able to enter waterways and promote the growth of potentially harmful algae.

Alternatively, composted manure used as a source of slow-release phosphorus reduces TP loadings to urban streams compared to conventional commercial turf-grass sod imported and maintained with inorganic phosphorus fertilizer (Richards *et al.*, 2008). In Ann Arbor, MI, significant reductions in TP and a trend of DRP reduction followed a municipal ordinance limiting the application of lawn fertilizers containing phosphorus (Lehman *et al.*, 2008). In the same city, Dietz *et al.* (2004) found 82% of residents began to leave lawn clippings in place, while only 11% applied fertilizer after soil tests. However, these latter changes were not found to result in a significant change in phosphorus loadings.

Other non-structural changes include better management of leaves and pet waste, street sweeping, and the use of native plants. One study found that nearly three times more phosphorus was released when leaves were cut (for example, when mulched) (Cowen and Lee, 1973).

In another study, pet waste accounted for 84% of phosphorus inputs on a sample of 360 single-family, detached, owner-occupied homes in the Minneapolis-Saint Paul, MN metropolitan area, where state law restricts the use of phosphorus fertilizer (Fissore et al., 2012). In northern Virginia, regular street sweeping was reported to result in 40 to 70% removal of TP (NVPDC and ESI, 1992). Finally, the use of low maintenance plants that are indigenous to the eco-region are expected to reduce the transport of phosphorus through stormwater runoff (Hipp et al., 1993).

Non-Point Source Structural BMPs

Urban structural BMPs consist of a wide spectrum of approaches – ranging from filtration systems to detention, and designed as artificial systems or applied to natural processes.

Traditionally, stormwater infrastructure was designed to mitigate flooding and move water as rapidly as possible to nearby water bodies. More recently, new infrastructure has been designed and some existing infrastructure has been modified to reduce peak flows, sediment loads and turbidity during runoff events. However, both of these objectives ignore other factors such as nutrient loads that play a significant role in water quality impairments (USEPA, 2009). As a result, BMPs are evolving to be more holistic and sustainable with the aim of reducing pollutant loads (Batroney et al., 2010). The following BMPs appear to be promising structural BMPs in urban settings:

- **porous pavements:** TP removal rates of 60 to 71% have been reported through the use of porous pavements, though one study found no evidence of removal (McElmurray et al., 2013);
- **media filters:** subsurface sand filters are reported to remove 43 to 82% TP (Maniquiz et al., 2010; Leisenring et al., 2010);
- **filter strips/bio-swales:** level-spreader-grassed filter strips along highways appear to result in significant reductions (48%) in phosphorus loadings in stormwater runoff (Horner et al., 1994; McElmurray et al., 2013);
- **green roofs:** these can reduce the peak flow generated from urban roof tops; however, they

may contribute more P than they absorb as a result of leaching from material used to construct the green roof. Limited data indicate differences in performance in the short- versus long-term, suggesting a need for more rigorous long-term study and monitoring (Berndtsson, 2010);

- **bio-retention basins:** include rain gardens, filter boxes and all other vegetative basins designed to increase infiltration and evapotranspiration. Removal efficiencies of phosphorus by bio-retention basins are reported to be as high as 97%, depending on the composition of soils used (Carpenter and Hallam, 2010);
- **detention and retention basins:** treatment efficiencies vary considerably, ranging from 20 to 90% removal, depending on their design (City of Austin, 1995);
- **constructed wetlands:** removal efficiencies of constructed wetlands vary widely, ranging from 30 to 70% of TP loads, with some evidence of reduced DRP loads, as well. However, removal in both subsurface flow and open surface wetlands is hampered by low oxygen conditions that can result in the release of previously sequestered phosphorus (Van de Moortel et al., 2009); and,
- **commercial devices:** oil and grit separators have been found to be relatively ineffective (less than 10% removal efficiency) in reducing TP loads. Another type of commercial device, a subterranean concrete detention basin designed to remove settled solids, similar to septic systems, was found to remove approximately 50% (Zhang et al., 2010).

In reviewing the treatment efficiency of these various structural BMPs, the LEEP study reviewed more than 6,000 records from the International Stormwater BMP Database (www.bmpdatabase.org). Based on this review, the study concluded that:

- only 43% of the samples demonstrated phosphorus removal; and,
- bio-retention ponds and wetland basins were the most effective urban BMPs, with about 82% and 75%, respectively, showing some removal.

Milwaukee Leading the Green Infrastructure¹⁰ Movement

The City of Milwaukee, WI, like many cities in the Midwest, lacked the capacity to contain high-flow water events and discharged pollutants directly into its rivers and Lake Michigan. Milwaukee's greatest problem was outdated infrastructure, which combined stormwater with sewage in the sewer systems. The Milwaukee Metropolitan Sewerage District (MMSD) decided to take the initiative to begin investing in infrastructure solutions and urban BMPs. To solve the issues of high-flow events and the combined sewers, a deep tunnel project was undertaken. The Deep Tunnel project is a 31.2 km (19.4 mi) inline stormwater storage system that has reduced the likelihood of overflow events from more than 50 to less than three times per year.

The MMSD also has implemented a number of urban BMPs to help reduce the amount of runoff entering the sewage system. A commitment to reduce runoff by 15% is being achieved through green infrastructure, native plantings, and low-tech devices. The efforts made by the city are consistent with the Leadership in Energy and Environmental Design (LEED) initiative. Milwaukee now is considering making LEED a requirement for all city-funded development projects. A stormwater fee, based on the percentage of on-site impervious surface area, also has been implemented city-wide. The fee can be challenged by the owner if one or more urban BMPs are implemented on the owner's property. The City of Milwaukee now is a leader in green infrastructure. The city's initiative represents a useful case study of the effectiveness of urban BMPs and provides valuable insights into the implementation of these initiatives.

Note: Green infrastructure refers to the use of vegetation, soils, and natural processes to manage water and create healthier urban environments. At the scale of a city or county, green infrastructure typically refers to the patchwork of natural areas that provides habitat, flood protection, cleaner air, and cleaner water. At the scale of a neighborhood or site, green infrastructure typically refers to stormwater management systems that mimic nature by soaking up and storing water.

(source: USEPA website: water.epa.gov/infrastructure/greeninfrastructure/gi_what.cfm)

The review of treatment efficiency also highlighted the importance of understanding the different forms of phosphorus – total and DRP. For example, detention basins, bio-filters and wetland channels were all found to have clearly different removal efficiencies for total versus dissolved phosphorus.

There are limited reliable data available on the cost of structural urban BMPs. In general, the LEEP study found that engineered infiltration basins are the most expensive, while detention basins and infiltration trenches are among the cheapest. However, these cost estimates are based on a small sample size and a diversity of specific BMPs included within broad categories. Moreover, the estimates do not account for size of watersheds and facilities.

Urban Point Sources

Lake Erie receives the largest municipal load of phosphorus of the Great Lakes, though large-scale wastewater treatment plants in the basin have been nearly 100% compliant with their discharge permits since the 1990s.

However, combined sewer overflows allowed under U.S. permits, in which treatment is bypassed during intense rain or snowmelt, deliver about 90.4 MT a year in TP to the lake from Ohio alone (Ohio EPA, 2010). Nineteen combined sewer overflows discharge untreated sewage directly into Lake Erie and 107 others discharge to receiving waters that empty into Lake Erie, including Mill Creek, the Cuyahoga River, Rocky River, and Big Creek in Ohio (Gomberg, 2007).

Partnerships are Critically Important to Protecting Lake Erie

Many organizations and agencies on both sides of the border play an active role in working to protect and improve the health of Lake Erie. Partnerships both across the border and between public and private groups are critical to achieving the goals of reducing phosphorus loads and HABs.

Lake Erie Lakewide Action and Management Plan (LAMP): The LAMP's Binational Nutrient Management Strategy was a strategic response from Canada and the United States that outlines nutrient management actions to reduce excessive phosphorus loading and the eutrophication of Lake Erie. The report establishes nutrient targets for Lake Erie and its basins and provides goals for nutrient management, research and monitoring. The report also provides recommendations for how governments, academia, conservation authorities, non-governmental organizations, community groups, industry, and the general public can help reduce nutrient runoff to Lake Erie.

Lake Erie Waterkeeper: The Lake Erie Waterkeeper acts as an advocate for the health of Lake Erie and its tributaries like the Maumee and Cuyahoga Rivers. The Lake Erie Waterkeeper website provides the opportunity for members of the public to report pollution and algal blooms. It also provides recommendations for simple measures that people can take to reduce the phosphorus runoff from their homes and neighborhoods as well as ideas for urging government officials to improve wastewater management and best management practices.

Conservation Ontario: Conservation Ontario has been a key player in the *Source Water Protection Program* that aims to protect water quality by reducing runoff and erosion. This program helps farmers and landowners recognize when runoff and erosion may be occurring on their land, and provides recommendations for eliminating those problems. Recommendations include riparian area management, such as the establishment of buffer zones and restoring native plant ranges, and nutrient management measures, such as improving manure storage and handling or treating manure.

National Wildlife Federation: The NWF released a report in April 2013, *Taken by Storm: How Heavy Rain is Worsening Algal Blooms in Lake Erie*. This report examines the link between spring rainfall and Lake Erie algal blooms and notes that heavy rains flush farm fertilizers and manure into local waters, which in turn drain into Lake Erie. This causes a build-up of phosphorus in the lake and, ultimately, toxic algal blooms. The report focuses on the Maumee River and provides a number of solutions to: help implement strong conservation practices; restore the natural landscape and wetlands to reduce runoff; and, reduce carbon pollution that causes global warming.

Ecojustice: In its 2013 *Great Lakes Sewage Report Card*, Ecojustice analyzes 12 Ontario municipalities and ranks each one based on how it deals with sewage treatment. This report was then provided to mayors and city councilors in each of the 12 municipalities, along with Ecojustice's recommendations for improving sewage management. These recommendations include prioritizing sewage infrastructure investment, investing in green infrastructure, and reporting whenever inadequately treated sewage is released.

Ducks Unlimited Canada (DUC) and Ducks Unlimited U.S. (DU): DUC and DU work with public and private landowners to restore and retain wetlands. Natural wetlands play a critical role in the filtering out of nutrients like phosphorus before they reach rivers and lakes. By ensuring that wetlands are restored to health and by protecting currently healthy wetlands, DUC and DU hope to reduce the amount of nutrient runoff that reaches Lake Erie, thereby reducing the size and severity of nuisance algal blooms.

Measuring the Performance of Urban BMPs

The LEEP study's analysis indicated that BMP performance can vary dramatically depending on the metric used (Lenhart and Hunt, 2011). Evaluating BMPs based on concentrations alone can be misleading, because performance varies during and between stormwater runoff events. Particularly problematic is the simple percentage removal metric, because it is dependent on the initial concentration of a pollutant (Zhang *et al.*, 2010) and does not account for background water quality, eco-region differentiation, and background, or "irreducible," concentrations. Additionally, it inherently assumes an association between influent (incoming) and effluent pollutant concentrations (McNett *et al.*, 2011).

Regardless of the type of BMP, three main mechanisms are responsible for phosphorus removal in stormwater: bio-uptake; sorption; and precipitation. Ultimately, phosphorus is retained through physical processes, either by attaching to material within BMPs (for example, sorption to wetland plants) or by settling out directly as a precipitate or indirectly while associated with biological material or suspended solids. Of these mechanisms, sorption reactions are the most common mechanism employed by most BMPs. However, because phosphorus partitioning between particulate and dissolved forms can vary widely depending on the amount and type of solids present and can convert rapidly, improving BMP performance "will also likely need to address dissolved P in order to achieve high and/or consistent pollutant removal" (Leisenring *et al.*, 2010). This need for more advanced analysis of phosphorus is a common theme throughout urban and agricultural BMPs.

3.3 Data and Knowledge Gaps

The LEEP study undertook an extensive review of the data and knowledge gaps in the areas of monitoring and research for addressing lake-wide challenges in Lake Erie.

3.3.1 Monitoring

An appropriate targeted monitoring program is an important element of an effective and coordinated management plan for addressing declining water quality, increasing frequency and severity of algal blooms and associated ecosystem impacts. Monitoring data can provide input for the models used to establish new target loads and feedback on the results of management actions.

Status

The LEEP study conducted an inventory of federal, provincial and state government sampling programs in Lake Erie, as well as programs conducted by academic institutions. The analysis identified a wide variety of monitoring efforts, depending on the purpose of the monitoring.

Sampling programs aimed at the open waters of Lake Erie, such as the USEPA Great Lakes National Program Office's monitoring and Environment Canada's Great Lakes Surveillance Program are undertaken on an annual or bi-annual basis. Other programs, including the Lake Erie Index Station Monitoring (near shore tributaries and open water), the United States National Coastal Assessment (nearshore and open water), the Ontario Broad Scale Monitoring Program (inland lakes), and the New York Lake Classification and Inventory Program (inland lakes), operate on a rotational basis every three to five years. These programs are focused on detecting long-term trends. By contrast, the majority of tributary monitoring programs aim to detect nutrient samples on a monthly basis during the ice-free season.

While the long-term annual or monthly monitoring efforts may give a reasonable picture of the status of nutrients in tributaries and Lake Erie over time, they may not fully capture the complexities of nutrient loading, such as those that occur during wet weather events. This limitation may make it more difficult to calculate nutrient loadings in the long run. The LEEP study found that only a few monitoring programs

sample more frequently, on either a bi-weekly, weekly or daily basis. These programs can capture the effects of wet weather events and can be used to calculate nutrient loading more accurately. Heidelberg University, in Tiffin, OH, has a sampling program that samples on a daily basis and three times daily during wet weather events. The USGS recently installed automated tributary monitoring gauges that monitor on a daily basis and include special sampling during storm events. The Great Lakes Intakes Program (Ontario Ministry of Environment) and the Great Lakes Nutrient Initiative (Environment Canada) both sample tributaries and the nearshore on a weekly basis.

These findings highlight the importance of seasonality, frequency and coordination of programs to meet the different needs of program managers, whether they are focused on loading analysis, modeling, long-term trends or unique wet weather events that can cause a rapid influx of nutrients.

In general, there are frequent sampling programs for DRP and TP in all of the major tributaries to Lake Erie. However, many of the monthly programs do not perform specific sampling during wet weather. There are also consistent efforts to assess the nutrient concentrations in Lake Erie on a less frequent basis. However, many smaller tributaries are not monitored on a regular basis.

Most programs monitor for TP as well as DRP, among a wide variety of other water quality parameters, though several programs have indicated that they do not have the capacity to monitor for DRP. Most but not all of the major water quality sampling programs collect flow data or have nearby gauges that collect flow data. Several programs do not have flow gauges directly associated with the phosphorus water quality monitoring.

Key Gaps in Monitoring

Based on the review of current monitoring in Lake Erie, the LEEP study identified a number of important gaps with respect to monitoring. In general, there are limited detailed data on seasonal in-lake ecosystem

dynamics, including nearshore-offshore connections, and on higher spatial-resolution watershed monitoring, with an emphasis on dissolved and particulate forms of phosphorus. Specific gaps include the following:

Detroit River near the Outlet to Lake Erie

Lack of accurate measurements of Detroit River phosphorus loading creates a sizable uncertainty in the phosphorus budget for Lake Erie. Without current information on the hydrology and chemistry of the Detroit River, it is difficult to estimate flow and phosphorus loads to Lake Erie, disentangle upstream sources of phosphorus, and modernize load targets for Lake Erie as a whole and for its western, central and eastern basins. The IJC notes that the deployment of monitoring instruments in the autumn of 2013 in the lower Detroit River by Environment Canada, through consultations with USGS and others, will be helpful in advancing understandings of phosphorus loadings from the river.

Tributary Monitoring and Loading Measurements

There is limited high-frequency monitoring of phosphorus loading to Lake Erie from key sub-basins, other than that carried out by Heidelberg University's National Centre for Water Quality Research. To track changes over targeted timeframes, including during the critical snowmelt period and rainfall events and develop, refine, and calibrate watershed models, it is important to establish robust monitoring networks. For example, loads quantified for reaches of the Maumee and Sandusky rivers can be used to track seasonal variation and changes in the ratio of particulate phosphorus to DRP, and can be interpreted according to watershed attributes, such as agricultural systems and practices. Monitoring initiated through the Great Lakes Nutrient Initiative along the north shore of Lake Erie and in the Thames River will complement existing, more intensive, monitoring efforts in Ontario's Grand River. This kind of information can enable evaluation of the effectiveness of BMPs and facilitate transfers and scaling of edge-of-field results to other basins and at larger spatial scales.

Lake Erie Charter Boat Association and the Ohio EPA Nearshore Monitoring Partnership

In 2011, the Ohio Environmental Protection Agency gained a partner in its water monitoring program in Lake Erie. With the help of the Lake Erie Charter Boat Association, an increased amount of nearshore data is being collected in the western basin of Lake Erie. Prior to this partnership, Ohio EPA staff monitored 13 nearshore water stations monthly, from March through October. The new partnership enables charter boat captains to help monitor water quality related to HABs between Toledo and Sandusky. The cooperative agreement provides researchers with more data on water quality, the effects of improved watershed management practices, and nutrient loading information in the western basin of Lake Erie from tributary streams.

Source: www.epa.state.oh.us/newsbycategory/tabid/5980/vw/11/itemid/19/ohio-epa,-lake-erie-charter-boat-association-partner-to-monitor-lake-erie.aspx

Wet Weather Monitoring

There is a need to obtain nutrient loading data during wet weather events at a wider range of seasons in all major tributaries. This need will only increase as a changing climate brings the likelihood of more frequent and intense storm events.

Nearshore Monitoring

Current monitoring efforts in Lake Erie's nearshore are limited, particularly at higher resolution time and space scales. This gap inhibits a better understanding of nutrient dynamics in the ecologically important nearshore, and the exchange of water and nutrients between nearshore and offshore areas.

3.3.2 Research

LEEP identified several key gaps in current understanding of critical relationships in the Lake Erie ecosystem. The IJC acknowledges the important role of the binational LAMPs and Coordinated Science and Monitoring Initiative in establishing and accomplishing research priorities, and the facilitation role of the Lake Erie Millennium Network.

Harmful Algal Blooms

To date, most of the research on HABs has addressed single model organisms. There are gaps in understanding the dynamics of entire bloom communities, including the interactions of the different physical, chemical and biological factors that influence freshwater blooms. This broader view could provide a more comprehensive picture of harmful bloom dynamics, and thus support better modeling efforts and lead to innovative management practices in the field.

One important example of the limited understanding of HABs is the potential impacts of the disposal of dredge spoils in the open waters of Lake Erie. The Toledo Navigational Port, located in the shallowest portion of Lake Erie, is dredged on an annual basis to maintain a clear navigational route, with the spoils relocated for disposal farther out in the lake. However, open-lake disposal may contribute to the occurrence of HABs through re-suspension of nutrient-rich sediments that support algal growth. In 2009, the Ohio EPA estimated that sediment dredged from the Toledo navigational channel contained about 1,096 MT (about 1,209 tons) of phosphorus.

Citing, among other factors, the possible link between open-lake disposal and exacerbation of HABs, the Ohio EPA in 2010 declared, “open lake disposal of these huge quantities of dredged sediment in the Western Basin of Lake Erie is not environmentally acceptable to the State of Ohio and needs to be discontinued.” (Ohio EPA, 2010).

In 2013, the United States Army Corps of Engineers, which is responsible for dredging in the basin, undertook a field assessment to help scientists assess the relative contribution of dredged material disposal to algal blooms in the basin. Data are expected to be available by the summer of 2014.

Nuisance Algal Blooms

Much of the information regarding nuisance blooms in the Great Lakes in the past has been limited to site-specific assessments, sometimes supplemented with experimentation and simulation modeling. Lacking is a comprehensive understanding of how various factors, such as the interaction of lake water with land-based runoff and tributary discharges, can be used to predict the conditions associated with nuisance blooms.

Fish and Fisheries

As noted in Chapter 2, HABs, in combination with greater storm intensities and warmer water temperatures in the summer as a result of climate change, can affect Lake Erie fishes both directly (for example, by altering fish reproduction) and indirectly (for example, by altering food web interactions and the use of particular habitats). It will be critically important to better understand how the rich and diverse fish communities of the lake could respond under the warming trends and altered precipitation patterns associated with continued climate change.

BMPs

There are substantial gaps in the understanding of the effectiveness of current and emerging BMPs designed to prevent or reduce the risks of phosphorus loads to the Lake Erie ecosystem. For example, few studies have quantified phosphorus load reductions by urban or agricultural BMPs within the Lake Erie watershed. Reports of BMP effectiveness are variable and often contradictory.

Model Development

There is an important gap with respect to the development of models that can support the development of future target loads for Lake Erie. For example, the response curves in the LEEP study’s assessment of target loads were based on a limited set of models related to algal blooms and a single set of models related to hypoxia. As was the case when the original target loads were established for Lake Erie under the Agreement, it is important to develop, test, and deploy a suite of models to decrease the uncertainty in the forecasts.

Watershed-based models are useful for quantifying sources of phosphorus from Lake Erie watersheds, evaluating BMPs, and forecasting the influence of climate change on phosphorus loads to stream and river networks.

Environment Canada's Great Lakes Nutrient Initiative

Focusing on Lake Erie, Environment Canada's \$16 million Great Lakes Nutrient Initiative is helping address the complex problems of recurrent toxic and nuisance algae, nearshore water quality and ecosystem health in the Great Lakes. The Initiative targets five priority areas:

- establishing current nutrient loadings from selected Canadian tributaries;
- enhancing knowledge of the factors that impact tributary and nearshore water quality, ecosystem health, and algae growth;
- establishing binational lake ecosystem objectives, phosphorus objectives, and phosphorus load reduction targets;
- developing policy options and strategies to meet phosphorus reduction targets; and,
- developing a binational nearshore assessment and management framework.

The Initiative will help Canada to deliver on key commitments under the Canada–United States Great Lakes Water Quality Agreement.

Source: Environment Canada website: www.ec.gc.ca

United States Great Lakes Restoration Initiative

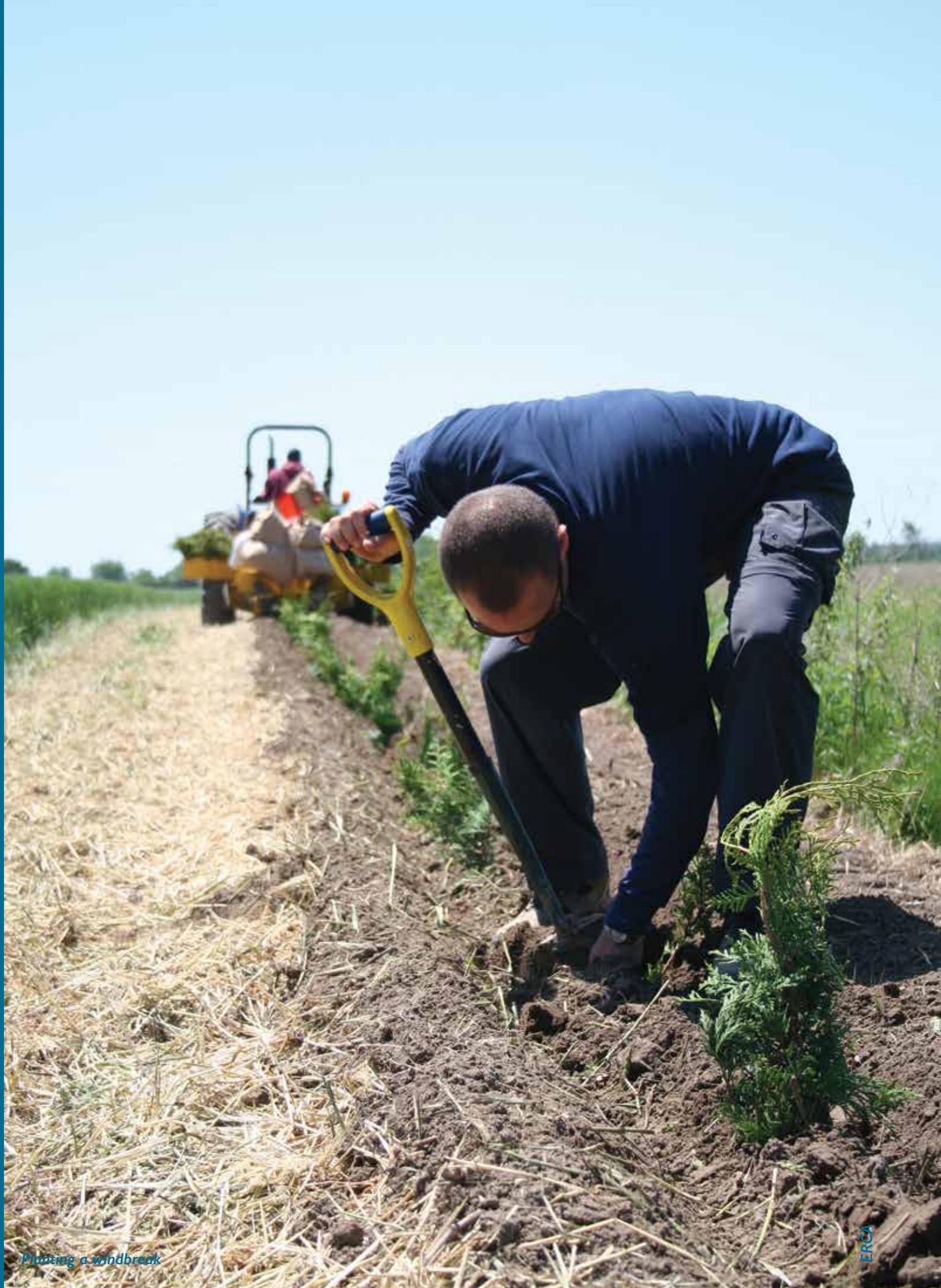
The U.S. government's Great Lakes Restoration Initiative was funded at approximately \$285 million in 2013, bringing the total investment since 2010 to \$1.3 billion. Led by the USEPA, the Initiative has funded numerous projects to restore and protect Lake Erie. One of the Initiative's objectives is to promote nearshore health by protecting watersheds from polluted runoff. Examples of projects designed to reduce nutrient runoff into Lake Erie and tributaries include:

- a \$194,000 project to increase nutrient management plan expertise in the Blanchard River watershed;
- a \$497,000 grant to promote best management practices in the Maumee River Basin; and,
- a \$527,000 grant to promote nutrient reduction in Powell Creek.

(Source: Great Lakes Restoration Initiative website greatlakesrestoration.us/)



Dead Fish, Lake Erie 2011, Western Basin



Planting a windbreak



Green Innovation Great Lakes Program

Example of a green roof at the Village of Medina (NY) wastewater treatment plant.

Chapter 4 Lake Erie Ecosystem Priority: Recommendations

The International Joint Commission (IJC) fully appreciates the formidable challenges ahead in restoring the health of Lake Erie. Harmful algal blooms (HABs) and an expanded hypoxic area developed over a 10- to 15-year period, and remedying these problems will take a comparable amount of time.

History shows, however, that the degradation of Lake Erie by human activities can be reversed by human effort. Fifty years ago, some declared Lake Erie “dead” and suggested that it was beyond remedy. Instead, with the collaboration of governments at all levels, an informed and active citizenry, and strong science underpinning, ambitious goals for Lake Erie’s recovery were established and attained.

The IJC commends the governments of Canada and the United States for renewing their commitment to restore Lake Erie in the 2012 Great Lakes Water Quality Agreement (the Agreement) and for investing in new initiatives that hold promise in furthering understanding and cleanup of the lake. This report is intended to support and inform this work. The IJC is confident that the same government, public and scientific collaboration that reversed the degradation of Lake Erie in the 1970s and 1980s will do so again in the years immediately ahead.

4.1 The Challenge

The **Lake Erie Ecosystem Priority** (LEEP) was initiated by the IJC in 2012 in response to a growing challenge: lake-wide changes in Lake Erie related to problems of nutrient enrichment, compounded by the influence of climate change and aquatic invasive species. As a result of these changes, Lake Erie has experienced a decline in water quality over the past decade, with impacts on ecosystem health, drinking water supplies, recreation and tourism, and property values.

In support of this objective, the IJC has spent much of the past two years developing a better scientific understanding of the causes and controls of phosphorus loading into Lake Erie. This report has presented the major findings of the study in terms of:

- the key factors contributing to changes in the Lake Erie ecosystem, and the important effects of these changes on the Lake Erie ecosystem, human health and socio-economic conditions (Chapter 2); and,
- existing and possible initiatives to address the impacts on the Lake Erie ecosystem from phosphorus loading (Chapter 3).

4.2 Recommendations¹⁰

Responsibility for the development and implementation of plans, programs, policies and related activities to address Lake Erie water quality rests with the governments of the United States and Canada and Ontario and the Lake Erie Basin states (Ohio, Michigan, Indiana, Pennsylvania and New York). The IJC serves in an advisory role to the governments, and offers its recommendations in a spirit of cooperation.

The participation of the province of Ontario and Lake Erie Basin states is essential to realizing improved Lake Erie health. Due to their location around the lake and land use, some states have deeper phosphorus reductions to make than others. For example, while Lake Erie's western and central basins require urgent targeted phosphorus reductions, the states of Pennsylvania and New York State contribute phosphorus loads only to the eastern basin. Efforts to reduce phosphorous inputs into the eastern basin will have little impact on algal bloom and hypoxic conditions occurring upstream. However, reduced phosphorous inputs into the eastern basin will benefit the local environment as well as Lake Ontario, which receives 80% of its flow from Lake Erie.

The IJC's recommendations are grouped into four major categories:

- setting phosphorus reduction targets for Lake Erie;
- reducing phosphorus loading into Lake Erie from agricultural sources and septic systems;
- reducing phosphorus loading into Lake Erie from urban sources; and,
- strengthening monitoring and research in the Lake Erie Basin.

4.2.1 Setting Phosphorus Reduction Targets

New Loading Targets

The 2012 Agreement provides an interim TP concentration substance objective for western Lake Erie of 15 parts per billion, and an interim phosphorus load target for the entire lake of 11,000 MT annually. The governments of Canada and the United States have agreed to develop revised phosphorus concentration objective targets and phosphorus loading targets for Lake Erie within three years of the Agreement's entry into force in 2013. The response curve relationships developed for this report suggest that the interim target of 11,000 MT should be revised; on average, phosphorus loads at this level will not have the net benefit of reducing the size and severity of HABs in western Lake Erie.

The IJC believes that sufficient science exists to propose loading targets for TP and DRP for Lake Erie that will reduce HABs in the western basin and reduce the hypoxic area in the central basin by half. In addition, the IJC believes that phased targets for reduction also should be set for three-year intervals, leading to attainment of the targets within nine years. Such an approach can be established within an adaptive management framework whereby nutrient management policies and practices can be evaluated and prioritized.

Therefore, the IJC recommends that:

- I. **The Governments of the United States and Canada should adopt new targets for maximum acceptable phosphorus loadings in Lake Erie:**
 - to reduce the frequency and severity of harmful algal blooms in the western Lake Erie Basin to an acceptable level (None/Mild blooms), the total phosphorus load target for the Maumee River for the spring (March-June) period should be

¹⁰ Note: Appendix 2 provides an overview of related recommendations on improving Lake Erie water quality from previous reports by the IJC.

established as 800 MT, a 37% reduction from the 2007-2012 average; for dissolved reactive phosphorus, the target for the spring period should be 150 MT, a 41% decrease from the 2007-2012 average; extended over the course of a full year, the total phosphorus target should be 1,600 MT, a 39% decrease from the 2007-2012 average;

- when the rest of the watersheds in the western Lake Erie Basin are included, the total phosphorus load target for the spring should be 1,600 MT and the dissolved reactive phosphorus target should be 300 MT; extended over the course of a full year, the total phosphorus target should be 3,200 MT;
- to decrease the central Lake Erie Basin hypoxic area by 50% to about 2,000 km² (772 mi²) and 10 hypoxic days a year, the target total phosphorus load for the western basin and central basin should be 4,300 MT, a 46% reduction from the 2003-2011 observed average load and 56% below the current target;
- when expressed as annual dissolved reactive phosphorus load, the target for achieving the same hypoxic area (2,000 km²) and number of hypoxic days (10) in the central Lake Erie Basin should be 550 MT. This new level represents a 78% reduction from the 2005-2011 average dissolved reactive phosphorus load; and,
- total phosphorus and dissolved reactive phosphorus targets should be phased in over a nine-year period (2014-2022) by setting transitional targets on a three-year basis to coincide with the triennial cycle and assessment of progress outlined in the 2012 Agreement.

Intergovernmental Cooperation on Targets

The application of the total maximum daily load (TMDL) process under the United States *Clean Air Act* to establish reduction targets in Chesapeake Bay was noted in section 3.1.3. However, Lake Erie presents a key difference, in that Ontario cannot be part of a TMDL process. Without consideration of the On-

tario sources of Lake Erie's phosphorus pollution, a complete picture of the problem and appropriate reduction targets cannot be developed. Therefore, there is a need for cooperation between the two countries on jointly establishing new phosphorus reduction targets.

The governments of Canada, the United States, Ontario and the states that share a common boundary on Lake Erie could apply a public trust framework, a set of important common law legal principles shared by the states, provinces, and both countries. Under these principles – known as the public trust doctrine in the United States and the public right to navigation, fishing, and boating in Canada – the governments could hold Lake Erie as a public trust for their citizens. The public trust framework would provide the governments with an affirmative obligation to assure that the rights of the public with respect to navigation, fishing, swimming, and the water and ecosystem on which these uses depend are protected and not significantly impaired. A public trust framework and principles shared by the common heritage of both countries would be an added measure of protection of the water quality and public uses of Lake Erie and complement the principles and approaches of accountability, anti-degradation, precaution and prevention outlined in Article 2(4) of the 2012 Agreement.

To help attain the IJC's proposed targets, the USEPA could work with the governments of Michigan, Ohio and Indiana to develop a tri-state phosphorus TMDL for the western Lake Erie Basin. The measure would take into account all significant sources of phosphorus loadings, allocate specific reductions of phosphorus according to relative contributions from point and non-point sources, require the submission of state watershed implementation plans to the USEPA, and set timelines for action.

Annex 4 of the 2012 Agreement commits the USEPA and Environment Canada to develop Substance Objectives for Lake Erie phosphorus concentrations and phosphorus loading targets by February 2016, and phosphorus reduction strategies and domestic action plans by February 2018. The IJC recommends that

these processes proceed with greater concurrency so that phosphorus reduction strategies and domestic action plans are completed within six months of confirmation of the Substance Objectives.

Therefore, the IJC recommends that:

2. To establish and implement new targets of phosphorus loadings:

- the governments of the United States and Canada should develop domestic action plans including both regulatory and non-regulatory measures to reduce nutrient pollution of Lake Erie sooner than the 2018 goal set in the 2012 Agreement;
- the governments of Michigan, New York, Ohio, Pennsylvania and Ontario should apply a public trust framework consisting of a set of important common law legal principles shared by both countries, as an added measure of protection for Lake Erie water quality; governments should apply this framework as an added decision-making tool in policies, permitting and other proceedings; and,
- the governments of Michigan and Ohio should, under the United States *Clean Water Act*, list the waters of the western basin of Lake Erie as impaired because of nutrient pollution; this would trigger the development of a tri-state phosphorus total maximum daily load (TMDL) involving those states and Indiana, with U.S. Environmental Protection Agency oversight.

4.2.2 Reducing Phosphorus Loading into Lake Erie from Agricultural Sources and Septic Systems

The IJC concludes that the major sources of phosphorus to Lake Erie now are from non-point sources, especially agricultural operations. Reducing non-point source loads into Lake Erie poses a special challenge. There are many such sources across the area, mostly small in scale and widely distributed. Furthermore, reducing nutrient runoff from these sources requires

changes in practices that until now typically have been voluntary and incentive-based, and may now in some cases need to be enforceable through statute and/or regulation. Even if such practices are adopted, the results might appear only after a number of years and thus it can be difficult to measure their success in the short term.

The IJC also concludes that although TP loads have remained fairly constant since the late 1990s, the dissolved fraction of the total load has increased significantly. There is increasingly clear scientific consensus based on available research and prevailing expert opinion that reducing eutrophication problems in Lake Erie will require significant reductions in phosphorus loadings from agricultural operations.

Federal, state and provincial governments, with sometimes considerable involvement from local agencies and agricultural organizations, have developed a very complex suite of agri-environmental programming in the Great Lakes basin. The governments should accelerate their pursuit of a blend of activities to reduce nutrient loadings to Lake Erie by fully incorporating the following initiatives.

Dissolved Reactive Phosphorus

The LEEP study found that DRP is primarily responsible for driving the problem of HABs in Lake Erie. Yet traditional agricultural BMPs typically are targeted toward particulate phosphorus, which has relatively low bioavailability, though those BMPs have been credited with basin-wide reductions in soil erosion and associated environmental benefits.

As a further complication, the LEEP study confirms that the effectiveness of various BMPs at reducing DRP is poorly understood, though studies currently underway will be instructive. Further, the LEEP study found that the influence of subsurface drainage (i.e., agricultural tiles) is poorly understood and poorly managed in comparison to surface runoff, as is the role of drains in assimilating nutrients from surrounding farmland.

Therefore, the IJC recommends that:

3. The Governments of the United States, Canada, Ontario, Michigan, Indiana, Ohio, Pennsylvania and New York should immediately expand the focus of existing and planned incentive-based agri-environmental programs beyond particulate phosphorus to include an emphasis on best management practices that are most likely to reduce dissolved reactive phosphorus, such as reducing the amount of phosphorus applied to fields, slowing the movement of water to the field drainage system, and detaining flows at field drainage outlets.

Project Targeting

It has long been understood that different locations in the Great Lakes basin have different potential for phosphorus contributions to the lakes based on soil types, climate, gradients, prevailing agricultural practices, and other factors. Research and monitoring have identified the tributaries, and in some cases individual sub-watersheds, that release a disproportionate share of the total amount of DRP entering Lake Erie. The Maumee River in Ohio contributes about 5% of discharge, but nearly 50% of phosphorus loading to the western basin, and should be the primary focus of phosphorus reduction efforts from non-point sources in the Lake Erie Basin. Although project targeting in priority areas is underway – for example, the United States Great Lakes Restoration Initiative Action Plan (USEPA, 2010) and Ohio's Nutrient Reduction Strategy (Ohio EPA, 2013b) identify priority watersheds, as do efforts in Ontario to target the Lake Simcoe watershed – greater emphasis on priority watersheds and sub-watersheds throughout the Lake Erie Basin is required. The need to target phosphorus reduction also responds to the reality that there probably will always be limited resources available to address the sources of agricultural non-point source runoff.

Research conducted in the Maumee River watershed confirms that the spring load (March 1 to June 30) of

phosphorus is highly predictive of subsequent HAB size. Thus, management actions that target the timing of delivery of phosphorus to the lake are also critically important.

Therefore, the IJC recommends that:

4. Future phosphorus management efforts of the Governments of the United States, Canada, Ontario, Michigan, Indiana, Ohio, Pennsylvania and New York should focus on:
 - avoiding agricultural applications of phosphorus in autumn;
 - reducing the load delivered during the spring period (March 1 to June 30); and,
 - those sub-watersheds that are delivering the most phosphorus into the lake, including the Maumee River.

Incentive-based programs

The IJC found that all Lake Erie jurisdictions offer some form of agricultural outreach and extension services, including technical advice and financial assistance for completing agricultural BMPs. As noted above, the effectiveness of BMPs in reducing the impact of phosphorus on Lake Erie would be improved by targeting management actions to the spring runoff period, high delivery potential sub-watersheds, and selecting BMPs that are effective at reducing the dissolved fraction of TP.

Despite the widespread implementation of BMPs, the LEEP study found that the overall proportion of TP loadings to the lake attributable to non-point sources has been increasing, especially from agriculture. Modeling has confirmed that while agricultural BMPs are having some effect in reducing the export of TP from watersheds to the lake, BMPs need to be much more widely implemented to substantially reduce nutrient yields.

Education and awareness-building are essential tools to promote greater adoption of BMPs. Research

suggests that initiatives using a one-on-one interaction and on-farm visits are the most successful at encouraging adoption of specific nutrient management practices. Several jurisdictions have developed special stewardship outreach programs with these features. There is now an opportunity to build on the success of these initiatives throughout the Lake Erie Basin.

Therefore, the IJC recommends that:

- 5. The Governments of the United States, Canada, Ontario, Michigan, Indiana, Ohio, Pennsylvania, New York and local agencies should increase the scale and intensity of agricultural best management practices programs that have been shown to reduce phosphorus runoff.**

Lake Erie has lost more than 80% of its pre-settlement coastal wetlands, significantly affecting water quality as well as habitat. These wetlands not only support biodiversity, but also filter pollutants. Opportunities exist for substantial restoration of wetlands in the western Lake Erie Basin and should be pursued as part of a comprehensive plan to reduce algal blooms.

Therefore, the IJC recommends that:

- 6. The Governments of the United States, Canada, Ontario, Michigan and Ohio should:**
 - commit to the goal of a 10% increase by 2030 beyond current levels of coastal wetland areas in the western basin of Lake Erie to reduce nutrient pollution and promote biodiversity (an increase of about 1,053 ha or 2,600 acres);
 - allocate adequate funding to support this significant first step in coastal wetland restoration, in concert with non-governmental funders; and,
 - set a science-based goal for protection and restoration of wetlands inland from the Lake Erie coastal zone and develop appropriate strategies to meet the goal.

Regulatory Programs

The IJC’s analysis confirms that for most agricultural operations, the management of nutrients relies primarily on incentive-based programs and influence-based models. The LEEP study found that several decades of this approach have not reduced agricultural non-point sources of nutrients to Lake Erie – TP loads have not declined appreciably in many watercourses draining agricultural areas, and the highly bioavailable dissolved fraction of total loads (DRP) has been steadily increasing. The IJC also found that some regulatory controls are used to supplement traditional incentive- and education-based programming.

Therefore, the IJC recommends that:

- 7. The Governments of the United States, Canada, Ontario, Michigan, Indiana, Ohio, Pennsylvania and New York should strengthen and increase the use of regulatory mechanisms of conservation farm planning to reduce nutrient loadings.**

The 4Rs program -- the right fertilizer source, right rate, right time and right place – provides a useful framework for guiding fertilizer application in the Lake Erie Basin and beyond. The 4Rs can be effective in reducing nutrient export from fields, while meeting plant nutrition needs and therefore maximizing crop yields.

The IJC’s analysis determined that there are some good examples of voluntary 4R nutrient stewardship in the Lake Erie watershed. Almost all of the jurisdictions in the Lake Erie watershed have voluntary certification programs, the *4R Nutrient Stewardship Certification Standard* in Indiana, Michigan and Ohio for Lake Erie’s western basin – a voluntary program expected to be launched early in 2014 – noteworthy among them.

However, a review of ongoing efforts to reduce nutrient loadings to Lake Erie revealed that more progress is required to characterize fertilizer use. For example,

Ohio EPA's Ohio Nutrient Reduction Strategy (Ohio EPA, 2013b) describes how current procedures by fertilizer retailers and applicators do not allow for farm-specific tracking of applications. Reporting procedures in other Lake Erie jurisdictions also make tracking fertilizer application difficult. It is also generally accepted throughout the agricultural community that while most farmers routinely sample soil fertility, only a smaller proportion apply fertilizer at variable rates within a field based on those results. Further, agricultural fertilizer application rates are increasing in some locations – for example, trends in the Sandusky River watershed, a predominantly agricultural watershed in Ohio draining to the west basin of Lake Erie, show higher fertilizer application rates in the 1970s and after a reduction in the 1990s, an increase during the past decade (Daloglu *et al.*, 2012). Thus, nutrients frequently are applied at rates that do not reflect site-specific soil fertility needs and exceed the agronomic need of the crops being grown (Carpenter, 2005).

Through a mandatory process that requires training for fertilizer industry actors, well-considered and science-based prescriptions for nutrient amendments at the field level, application practices that minimize runoff, and appropriate record keeping and reporting, nutrient loading to receiving waters can be minimized without compromising crop yields.

Therefore, the IJC recommends that:

- 8. The Governments of the United States, Canada, Ontario, Michigan, Indiana, Ohio, Pennsylvania, and New York should accelerate 4Rs (right source, right rate, right time and right place) outreach/extension programs, and phase in mandatory certification standards for agrology advisors, retailers and applicators to ensure fertilizer is applied based on the 4Rs.**

Regulatory controls should include those that link agricultural program benefits to environmental performance. In both the United States and Canada, crop insurance (also known as production insurance) is a key risk management program available to most pro-

ducers. Crop insurance subsidies are an increasingly large share of U.S. federal agriculture spending, costing approximately \$14 billion in 2012. In Ontario, approximately 2.025 million ha (5 million acres) of farmland are insured through production insurance each year. Both United States and Canadian programs are taxpayer-supported – for example, in Ontario, producers pay 40% of the premium cost while the federal and provincial governments pay the balance of the premium cost and all of the administration costs. The insurance guarantees farmers a certain price for more than 100 crops, including those commonly grown in the Lake Erie Basin. The security provided to farmers by crop insurance is valuable, but there is no linkage between the insurance and environmental stewardship. Without conservation compliance incentives, increased pressure from the marketplace puts marginal areas at risk, resulting, among other things, in tiling and draining of marginal lands, as has happened in the Lake Erie watershed.

Therefore, the IJC recommends that:

- 9. United States and Canadian federal policies should link the cost and availability of crop insurance purchases or premiums to farm conservation planning and implementation of nutrient management practices.**

Regulatory controls include legislated requirements related to the handling and application of nutrients at a national or state/provincial level. Indiana prohibits manure application on frozen ground except in emergencies, while Ontario, New York State, Michigan, Ohio and Pennsylvania allow it under certain conditions. Liquid or semi-liquid manure, which contains phosphorus, cannot easily permeate frozen ground and is much more likely to run off into nearby water bodies, particularly if the region also has snow cover that melts during the winter. The LEEP analysis showed different jurisdictional regulatory responses to application of other sources of phosphorus, including the application of biosolids and fertilizers containing phosphorus on frozen ground and restrictions on manure application rates. It is likely that other areas of difference exist that were not considered as part of the analysis.

Therefore, the IJC recommends that:

10. The Governments of Ontario, Michigan, Indiana, Ohio, Pennsylvania and New York should ban the application of manure, biosolids and commercial fertilizers containing phosphorus from agricultural operations on frozen ground or ground covered by snow for lands that drain to Lake Erie.

The IJC's analysis determined that inadequately maintained and failing on-site septic systems in rural residential areas are contributing to phosphorus loadings in the Lake Erie watershed. Ensuring the maintenance of such systems and the replacement of failing systems by rural homeowners should be an important element of nutrient management. While voluntary efforts of various jurisdictions may prove helpful in reducing the failure rate of household sewage systems, legal requirements to ensure proper maintenance of the systems would provide an added level of protection. For example, some Ontario municipalities have enacted bylaws that require a septic inspection and replacement/upgrade, if necessary, as a condition of land severance. Several local health departments in Michigan have done the same. A requirement that such systems be inspected at regular intervals – for example, every five years – and subject to required maintenance or replacement would further reduce phosphorus loadings to Lake Erie.

Therefore, the IJC recommends that:**11. The Governments of Ontario and Michigan should:**

- enact legislation requiring inspection of septic systems at regular intervals, and at the time of property sale or land severance, to identify and assure upgrade/replacement of failing and potentially failing systems; and,
- expand state/provincial and community education initiatives promoting homeowner awareness of the need for septic system maintenance, including regular pumpout, and upgrade/replacement.

4.2.3 Reducing Phosphorus Loading into Lake Erie from Urban Sources

The LEEP study concluded that there are immediate opportunities to reduce nutrient runoff into Lake Erie from point and non-point sources in urban areas.

Urban Stormwater Management

Urban stormwater can be an important source of nutrients, especially as urbanization increases in the Lake Erie Basin. Construction projects in urban areas can cause significant soil disturbance. Eliminating sod cover and forested areas to make way for development removes water filtration and soil stabilization systems that contribute to the removal of nutrients from stormwater. Stormwater accumulates nutrients from a variety of sources including lawn fertilizers, cleaning agents and other urban residues. Impervious surfaces in urban areas, such as pavement and roofs, are responsible for increases in the volume of stormwater and the distance that it travels to the nearest water-body. Green infrastructure – including green walls, filter strips, rain gardens, bio-swales, engineered wetlands and stormwater ponds, among other measures – can help reduce nutrient runoff in urban stormwater, often at lower cost than traditional “gray infrastructure.” Increased federal, state and provincial incentives, including financial and technical assistance, are needed to support municipalities in the adoption of green infrastructure in the Lake Erie Basin. As an alternative to requirements for more expensive conventional stormwater controls, the Lake Erie Basin states and Ontario also can authorize green infrastructure as a condition of permits or environmental compliance approvals.

Therefore, the IJC recommends that:

12. The Governments of the United States, Canada, Ontario, Indiana, Michigan, New York, Ohio and Pennsylvania should work with municipalities to promote and accelerate the use of green infrastructure (such as filter strips, rain gardens,

bio-swales, and engineered wetlands) in urban stormwater management in the Lake Erie Basin by:

- providing funding, regulatory direction and technical support to municipalities and, where feasible and appropriate as an alternative to more expensive stormwater controls, authorize green infrastructure in United States municipal water discharge permits and Ontario environmental compliance approvals; and,
- encouraging the adoption of local ordinances/by-laws promoting green infrastructure.

Phosphorus Fertilizers for Lawn Care

The application of fertilizer containing phosphorus to turf or gardens in urban areas can contribute to eutrophication, as fertilizer often runs off directly into surface water bodies or into storm sewers that may discharge into the environment without treatment. At the same time, sufficient phosphorus is present in most turf to support healthy lawns without phosphorus fertilizer. In the Great Lakes Basin, Illinois, Indiana, Michigan, Minnesota, New York and Wisconsin have implemented limitations on the use of phosphorus fertilizer and require phosphorus-free fertilizer for most residential lawns. The Minnesota Department of Agriculture reports that since the implementation of lawn fertilizer restrictions in the state, there has been no difficulty for homeowners in finding phosphorus-free fertilizers. The law has substantially reduced phosphorus lawn fertilizer use without increasing consumer costs (Minnesota Department of Agriculture, 2007). Implementing this type of regulation has reduced the amount of phosphorus found in nearby rivers in some cases. This may be significant because similar reductions were not observed in nearby areas that did not have a similar regulation in place (Lehman et al., 2009). Ontario and Quebec do not have province-wide laws that restrict the use of phosphorus for lawn care, though municipalities may pass bylaws that restrict the use of fertilizers in urban settings.

Therefore, the IJC recommends that:

13. The Governments of Ontario, Ohio and Pennsylvania should prohibit the sale and use of phosphorus fertilizers for lawn care, with the exception of the establishment of new lawns during the first growing season or in cases where soil testing indicates a need for phosphorus.

4.2.4 Strengthening Monitoring and Research in the Lake Erie Basin

The LEEP study concluded that an improved understanding of critical relationships in the Lake Erie ecosystem and the ability to model them are core tasks for addressing the complex challenges of nutrient enrichment and the associated environmental and socio-economic impacts. Strengthened monitoring and research are needed to support management initiatives, evaluate the effectiveness of BMPs, and develop models used in establishing new target loads for phosphorus and other nutrients.

Therefore, the IJC recommends that:

14. The Governments of the United States and Canada should commit sustained funding to enhance and maintain monitoring networks in the Lake Erie Basin, focusing on:
 - tributaries throughout the Lake Erie Basin, including key sub-basins and wet weather events to capture seasonal differences from a wider range of basin tributaries;
 - dissolved reactive phosphorus which, in addition to total phosphorus and other parameters, will need to be regularly monitored at all appropriate sites;
 - establishment of water quality monitoring stations to quantify the nutrient dynamics of Lake Huron, the St. Clair River and Lake St. Clair;
 - establishment of a continuous, long-term water quality monitoring system at the outlet of the

Detroit River that measures critical nutrient parameters; and

- an evaluation of the cumulative effectiveness of urban and rural best management practices.

15. The Governments of the United States and Canada should support research to strengthen understanding of:

- the dynamics of harmful algal blooms through a comprehensive limnological approach to studying entire bloom communities;
- how open-lake disposal of dredged sediments from the Toledo navigational channel affects phosphorus loadings in Lake Erie;
- environmentally sustainable methods of sediment disposal;
- how various factors, such as the interaction of lake water with land-based runoff and tributary discharges, can be used to predict the conditions associated with nuisance blooms under current and future climate change scenarios;
- how Lake Erie's diverse and productive fish communities could respond under the warming trends and altered precipitation patterns associated with continued climate change; and,
- the economic effects of Lake Erie algal blooms throughout the entire lake basin.

16. The Governments of the United States and Canada and organizations involved in lake management should improve data management through greater coordination and sharing.

4.3 Next Steps

Through the analyses undertaken during the preparation of the LEEP report and input received through public consultations, several important issues arose that could not be adequately addressed in this report. As a result, the following issues will be further investigated during the remainder of the IJC's Triennial Cycle (2012-2015), and may be the subject of future reports and/or advice to the governments of Canada and the United States:

- developing a more complete understanding of:
 - the economic impacts of Lake Erie eutrophication and the economic benefits of addressing the nutrient threat, building on the LEEP's preliminary economic analysis; and,
 - the costs and benefits to agriculture of nutrient pollution reduction initiatives;
- strengthening the application of water quality models in addressing excessive nutrient loading in Lake Erie and its watershed to support the development of water resource and nutrient management strategies; and,
- developing a more complete understanding of Lake Erie HABs and drinking water quality, including an examination of numeric criteria and monitoring for cyanotoxins in drinking water; building on the Health Professionals Advisory Board (HPAB) report on human health and HABs (IJC, 2014).



APPENDICES

1. Acknowledgements

The International Joint Commission (IJC) acknowledges and expresses its sincere appreciation for the contributions of the many individuals in Canada and the United States who contributed to the planning, research, analysis and report preparation of the **Lake Erie Ecosystem Priority** (LEEP). Dozens of scientists, engineers, planners and technical experts drawn from a wide range of disciplines and from governments and academia have worked together in a true spirit of cooperation to address the critical challenges facing Lake Erie's ecosystem.

The IJC also acknowledges and thanks the many members of the public who participated in the LEEP public outreach events in 2012 and 2013 and who provided valuable comments on Lake Erie's challenges and possible actions to address those challenges.

The following is a list of the individuals who directed participated in the LEEP.

LEEP Leadership and Management

The IJC gratefully acknowledges the work of the LEEP project team, which was responsible for the overall planning and management of the research, analysis and report preparation:

- Raj Bejankiwar, Great Lakes Regional Office, Windsor, ON (Lead);
- Glenn Benoy, Canadian Section, Ottawa, ON;
- Matthew Child, Great Lakes Regional Office, Windsor, ON;
- Dave Dempsey, United States Section, Washington, DC; and,
- John Nevin, Great Lakes Regional Office, Windsor, ON.

Advisory Boards and Technical Work Groups

The LEEP research and report greatly benefited from the advice provided by the members of the following boards and work groups:

- the Great Lakes Science Advisory Board, co-chaired by: William Bowerman, University of Maryland; and William Taylor, University of Waterloo;
- the Great Lakes Water Quality Board, co-chaired by Susan Hedman (U.S. Environmental Protection Agency) and Michael Goffin (Environment Canada); and,
- the Council of Great Lakes Research Managers, co-chaired by Norm Granneman (U.S. Geological Survey) and John Lawrence (Environment Canada).

Taking Action on Lake Erie (TAcLE)

The IJC expresses its sincere appreciation for the work of the Great Lakes Science Advisory Board's *Taking Action on Lake Erie* (TAcLE) work group, which undertook extensive research and analysis of the key research questions and prepared papers summarizing findings and conclusions. The group was composed of board members and experts drawn from governments and academia.

Members of the work group were:

- George Arhonditsis, University of Toronto*
- Nate Bosch, Grace College
- Greg Boyer, University of New York*
- David Carpenter, University of Albany*
- John Casselman, Queen's University*
- Murray Charlton, Environment Canada, Retired Scientist
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- Sue Watson, Environment Canada*
- Steve Wilhelm, University of Tennessee
- Weitao Zhang, University of Toronto.

* Denotes that the individual also was a participant in the 2013 LEEP Science Synthesis Workshop, below.

Lake Erie Ecosystem Priority (LEEP) Science Synthesis Workshop

The IJC also thanks the researchers who attended the LEEP Science Synthesis Workshop in Windsor, ON, in February 2013. The scientific work that was presented and the lively debate and discussion that followed ensured that this report reflected a diversity of views from a variety of disciplines.

Workshop participants (in addition to IJC staff who attended) were:

- Elin Betanzo, Northeast-Midwest Institute
- William Bowerman, University of Maryland
- George Bullerjahn, Bowling Green State University
- Hunter Carrick, Central Michigan University
- Jan Ciborowski, University of Windsor
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Report Production

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- Vic Serveiss of the IJC, who reviewed drafts of this report and offered valuable comments and suggestions;
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- *Technical Editor/Writer*: Tom Shillington, Ottawa, ON; and,
- *Report Design and Production*: Paul Santos, Provisional RGD, Leamington, ON.

2. Related Recommendations from Previous Reports by the International Joint Commission

Under the terms of the previous Great Lakes Water Quality Agreement, the International Joint Commission (IJC) issued biennial reports between 1987 and 2013 assessing the progress of the Parties in achieving the general and specific objectives of the Agreement. Moving forward, the IJC will be issuing triennial assessments of progress, as called for in the 2012 Agreement.

The last two biennial reports included consideration of issues related to LEEP – the *15th Biennial Report* (IJC, 2011) included a section on eutrophication, while the *16th Biennial Report* (IJC, 2013) included a section on phosphorus loadings.

In the *15th Biennial Report*, the IJC recommended that the Parties:

- develop new or improved models to improve estimates of phosphorus loadings to the Great Lakes from tributaries and other sources and use the results to establish phosphorus concentration targets for nearshore and offshore waters of the Great Lakes;
- issue a reference to the IJC for a binational scientific investigation into the causes of the resurgence of nuisance and harmful algal growths in the Great Lakes from land use activities and to test causal hypotheses of the linkages between land use and algal problems and associated ecosystem changes in the Great Lakes;
- institute “no regrets” actions – measures that would be justified under all plausible future scenarios –using adaptive management to better retain nutrients and sediment on the land, especially in watersheds with high phosphorus loadings; and,
- promote the implementation of successful “no regrets” management actions by developing, maintaining, and sharing an inventory of effective techniques and programs.

In the *16th Biennial Report*, the IJC recommended that:

- federal, state, and provincial governments should continue to develop and implement best or beneficial management practices to reduce DRP runoff from agricultural lands and to develop and enforce measures to decrease loadings in high-risk watersheds;
- governments should support and encourage farmers to be aware of recommended phosphorus levels for the crops they are growing, to test soil regularly, and to apply fertilizer or manure to soil only when phosphorus is needed;
- governments should support and encourage development and use of related technologies such as using manure digesters and transporting manure to areas needing fertilizer;
- governments should develop improved models to more accurately estimate phosphorus loadings to western Lake Erie and to other basins experiencing problems associated with excess phosphorus;
- governments should collaborate to develop, maintain and share an inventory of effective management actions that are used to better retain nutrients and sediments on the land, especially in watersheds yielding high phosphorus loadings; examples of such management actions include: nutrient-use planning for croplands and livestock operations; implementing outreach to waterfront residents on better construction and maintenance of septic systems; and, establishing requirements that septic systems be inspected at time of house sale and upgraded when necessary; and,
- the states of Ohio, Michigan and Wisconsin should work with the USEPA to complete phosphorus TMDLs for the respective water bodies of western Lake Erie, Saginaw Bay and Green Bay.

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4. Glossary

ADAPTIVE MANAGEMENT -- A planning process that can provide a structured, iterative approach for improving actions through long-term monitoring, modeling and assessment. Through adaptive management, decisions can be reviewed, adjusted and revised as new information and knowledge becomes available or as conditions change.

ALGAE – Aquatic organisms that survive through photosynthesis; they can range in size from microscopic organisms to large seaweed and giant kelp.

ALGAL BLOOMS – An excessive and relatively rapid growth of algae on or near the surface of water. It can occur naturally as the result of a change in water temperature and current or as a result of an excess of nutrients in the water.

BASIN – All land and water within the confines of a drainage basin.

BEST MANAGEMENT PRACTICES (BMP) – A term used to describe a range of practical methods, techniques and other actions that allow individuals or organizations to prevent or reduce the risks of water pollution resulting from their activities. Best practices typically evolve over time, as new approaches are introduced, proven to be effective and adopted. Also known as beneficial management practices.

BOUNDARY WATERS TREATY OF 1909 – The agreement between the United States and Canada that established principles and mechanisms for the resolution of disputes related to boundary waters shared by the two countries. The International Joint Commission was created as a result of this treaty.

CLIMATE CHANGE – A change of climate that is attributed directly or indirectly to human activity, that alters the composition of the global atmosphere, and which is in addition to natural climate variability observed over comparable time periods.

DISSOLVED REACTIVE PHOSPHORUS (DRP) – The fraction of phosphorus that is dissolved in the water column and generally available to support algal growth.

EUTROPHICATION – The process by which a body of water becomes rich in dissolved nutrients, such as phosphorus, thereby encouraging the growth and decomposition of oxygen-depleting plant life and resulting in harm to other organisms; also known as nutrient enrichment.

EXTERNAL LOADING – Runoff of a pollutant from various point sources and non-point sources in the watershed, from upstream lakes and rivers, and from the atmosphere.

GREAT LAKES WATER QUALITY AGREEMENT (THE AGREEMENT) – First signed in 1972, the Agreement expresses the commitment of Canada and the United States to restore and maintain the chemical, physical and biological integrity of the Great Lakes basin ecosystem.

GREEN INFRASTRUCTURE – Green infrastructure refers to the use of vegetation, soils, and natural processes to manage water and create healthier urban environments. At the scale of a city or county, green infrastructure typically refers to the patchwork of natural areas that provides habitat, flood protection, cleaner air, and cleaner water. At the

scale of a neighborhood or site, green infrastructure typically refers to stormwater management systems that mimic nature by soaking up and storing water.

HARMFUL ALGAL BLOOM (HAB) – Harmful algal blooms (HABs) result from the proliferation of blue-green algae (including cyanobacteria) in environmentally stressed systems, where conditions favor opportunistic growth of one or more noxious species, which displace more benign ones. The blooms are considered harmful because excessive growth can harm ecosystems and produce poisons (or toxins) that can cause illness in humans, domestic pets and wildlife.

“HOT SPOT” – Locations within a lake’s watershed that contribute a disproportionate share of the total amount of DRP entering the lake.

HYPOXIA – A condition where excessive nutrients contribute to algal growth and subsequently high oxygen consumption during decomposition of the algae. This process creates “dead zones”, typically near the lake bottom, where dissolved oxygen levels are so low that fish and other aquatic life cannot survive.

INTERNAL LOADING – Transport of a pollutant from sources within the lake, such as from bottom sediments.

INTERNATIONAL JOINT COMMISSION (IJC) – International independent agency formed in 1909 by the United States and Canada under the Boundary Waters Treaty to prevent and resolve boundary waters disputes between the two countries. The IJC makes decisions on applications for projects such as dams in boundary waters, issues Orders of Approval and regulates the operations of many of those projects. It also has a permanent reference under the Great Lakes Water Quality Agreement to help the two national governments restore and maintain the chemical, physical, and biological integrity of those waters.

LOADING – Entry of a pollutant, such as phosphorus, into a water body.

NEARSHORE – The Lake Erie LAMP divides the nearshore into two areas; coastal margin and nearshore open-water. Coastal margin is defined as the shoreline, water column and substrate in embayments with water depths of 3 meters or less. The nearshore open-water is defined as the water column and substrate with water depths between 3 and 15 meters. Thus, the nearshore is the zone where water depth is less than 15 meters.

NON-POINT SOURCES – Sources of pollutants associated with many diffuse locations and origins, typically transported by rainfall and snowmelt runoff over land; for example, excess fertilizers, herbicides and insecticides from agricultural lands and residential areas.

NUTRIENT – A food, or any nourishing substance assimilated by an organism, and required for growth, repair, and normal metabolism. For example, phosphorus and nitrogen are nutrients for algae.

PARTICULATE PHOSPHORUS (PP) -- The fraction of phosphorus that is attached to suspended sediment and organic matter.

PHOSPHORUS – An element used in a wide range of agricultural, industrial and domestic products; the key nutrient limiting the amount of phytoplankton and attached algae in Lake Erie.

POINT SOURCES – Sources of pollutants, such as phosphorus, associated with a specific location; for example, an industrial or sewage treatment plant.

TOTAL PHOSPHORUS (TP) – Refers to all forms of phosphorus in a given volume of water, including particulate and dissolved forms.

5. Metric System – United States Customary System Units

(with abbreviations)

Length

1 meter (m) = 3.2808 feet (ft)

1 ft = 0.3048 m

1 kilometer (km) = 0.6214 mile (mi)

1 mi = 1.6093 km

Area

1 square kilometer (km²) = 0.3861 square mile (mi²)

1 mi² = 2.59 km²

1 hectare (ha) = 2.47 acres

1 acre = 0.405 ha

Weight

1 metric tonne (MT) = 1.1 short tons (2,200 pounds)



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Rationale for Control of Anthropogenic Nitrogen and Phosphorus to Reduce Eutrophication of Inland Waters

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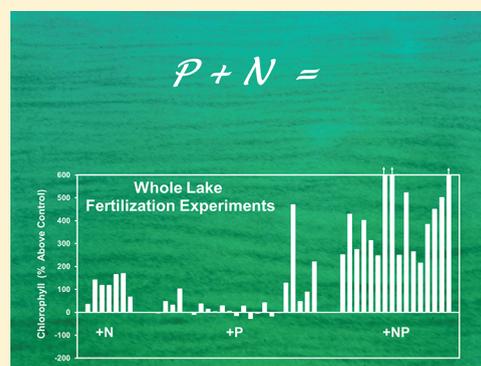
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ABSTRACT: Concentrations of phosphorus and nitrogen in surface waters are being regulated in the United States and European Union. Human activity has raised the concentrations of these nutrients, leading to eutrophication of inland waters, which causes nuisance growth of algae and other aquatic plants. Control of phosphorus often has had the highest priority because of its presumed leading role in limiting development of aquatic plant biomass. Experimental evidence shows, however, that nitrogen is equally likely to limit growth of algae and aquatic plants in inland waters, and that additions of both nutrients cause substantially more algal growth than either added alone. A dual control strategy for N and P will reduce transport of anthropogenic nitrogen through drainage networks to aquatic ecosystems that may be nitrogen limited. Control of total phosphorus in effluents is feasible and is increasingly being required by regulations. The control strategy for nitrogen in effluents is more difficult, but could be made more feasible by recognition that a substantial portion of dissolved organic nitrogen is not bioavailable; regulation should focus on bioavailable N (nitrate, ammonium, and some dissolved organic nitrogen) rather than total N. Regulation of both N and P also is essential for nonpoint sources.



INTRODUCTION

The United States and European Union are simultaneously moving toward nutrient regulation for inland waters with the goal of controlling eutrophication. The primary symptom of eutrophication is excessive growth of aquatic autotrophs, including suspended algae (phytoplankton), attached algae (periphyton), and aquatic vascular plants (macrophytes). Secondary symptoms include deep water anoxia in lakes, increased risk of harmful algal blooms, impairment of water treatment (taste and odor, filtration problems), and changes in the composition of aquatic communities.¹ Nutrient pollution has raised global algal biomass and photosynthesis in lakes by approximately 60% over background conditions;² streams and rivers are similarly affected. Within populated or agriculturally productive regions aquatic primary production and biomass often are many times greater than background.³

Two elements, phosphorus (P) and nitrogen (N), explain most of the experimentally diagnosed nutrient limitation of algal growth in inland waters under natural or human-modified conditions. Some research also suggests the potential for deficiencies

of other elements such as iron in inland waters,^{4,5} but this type of limitation is likely confined to special situations.

Although the scientific basis of nutrient regulation seemingly was settled in the 1970s with emphasis on phosphorus control, strong controversy now has emerged about the alternative possibilities for controlling one nutrient preferentially (P) or two nutrients with equal emphasis (P, N). We provide here a perspective on nutrient control as it applies to algae, first for lakes and then for flowing waters.

Regulation of total P concentrations is a well established practice.^{6,7} Regulation of nitrogen for control of eutrophication has been a lower priority, but has developed in a few places by control of total nitrogen concentrations (e.g., New Zealand⁸). National and international organizations (U.S. Environmental Protection Agency, Organisation for Economic Co-operation and Development)

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recognize the significance of both elements, but current regulatory practice emphasizes phosphorus control. We describe lines of evidence showing that nutrient control based on both P and N offers a broader range of strategies and reduces the potential for corollary damage caused by anthropogenic mobilization of N.

■ COMPARISONS OF PHOSPHORUS AND NITROGEN AS LIMITING NUTRIENTS IN LAKES

The limiting nutrient concept (Liebig's Law of the Minimum^{9,10}) holds that nutrient deficiency at any given time in a photosynthetic organism can be traced to a single element, which is the element available in the least amount relative to the needs of the organism. Therefore, in controlling excessive algal growth, it is important to know which element limits the expansion of algal populations when their growth stops because of nutrient depletion.

The limiting nutrient concept is more complex for an entire community or ecosystem than it is for a single organism. For example, species may differ, even among organisms of similar type (e.g., algae), in their optimal internal N:P ratios^{11–13} and their ability to store critical nutrients or to take up a nutrient at low concentrations.^{14,15} Thus, it is possible in a mixed community of algae for some species to be limited by phosphorus and others to be limited by nitrogen. In addition, it is possible for an environment to be very near the nutrient limitation thresholds for N and P simultaneously. Thus, a slight enrichment with one element could cause the other element to become limiting (e.g., refs 16–18). A third possibility is that seasonal or spatially heterogeneous changes may occur in the relative availability of potentially limiting nutrients (19). All of these circumstances have been documented experimentally and in nature.²⁰

Much more attention has been given to P limitation than to N limitation in inland waters for three reasons:²⁰ (1) phosphorus is more easily removed from anthropogenic sources than nitrogen, (2) N₂ fixation by cyanobacteria (also known as blue-green algae) has been assumed to make N control ineffective, and (3) the correlation between chlorophyll (an index of algal abundance) and total P among lakes is stronger than the correlation between chlorophyll and total N.³

A high proportion of total phosphorus can be removed (to concentrations as low as 30 µg/L) from waste streams by flocculation and sedimentation.²¹ Thus, phosphorus limitation can be induced even in a lake that is nitrogen limited by restricting the phosphorus supply to such an extent that phosphorus limitation overtakes nitrogen limitation.^{22,23} This is an effective strategy when the main source of phosphorus is wastewater effluent, which can be readily treated. It is less feasible where diffuse (non-point) sources are important, and may be entirely infeasible where background phosphorus concentrations are high.^{24–27}

Nutrient enrichment experiments (bottle bioassays, mesocosms, whole lakes) for lakes from all parts of the world now show that **nitrogen limitation is globally as common as phosphorus limitation** (Figure 1, refs 28,18, and 20). The occurrence of nitrogen limitation in lakes globally raises questions about the presumption that nitrogen limitation is self-correcting through the growth of N₂-fixing cyanobacteria.²⁹ Studies of the nitrogen fixation rates for cyanobacteria show that they are unable to compensate fully for nitrogen limitation in lakes,^{30,31} most likely because the process of N₂ fixation can be influenced by factors other than nitrogen and phosphorus, including turbulence coupled

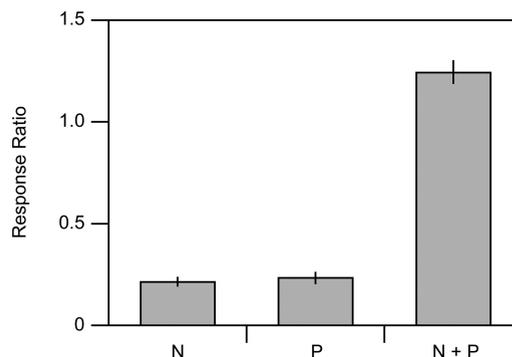


Figure 1. Growth response ratios (natural log of ratio of treatment to control, with standard error) of freshwater phytoplankton for worldwide bioassay studies (redrawn from ref 18; $n > 500$ for each treatment).

with low transparency, trace metal or iron deficiency, or organic matter availability.³² Eutrophic lakes that are nitrogen limited may even be dominated by cyanobacterial taxa that cannot fix N₂.³³ Another important factor that works against N accumulation in lakes is microbial denitrification that converts nitrate, which is bioavailable, to N₂ or N₂O which are not. Denitrification is stimulated by nitrate enrichment of lakes.³⁴ Thus, nitrogen fixation and nitrogen limitation can coexist in lakes, and suppression of N availability may suppress total algal biomass even when cyanobacterial N₂ fixers are present.

N₂ fixers may become a larger portion of the algal community if nitrogen availability is suppressed sufficiently to cause N limitation, even if total biomass is reduced.³⁵ The risk of inducing a shift in community composition favoring N₂ fixers is a possible undesirable byproduct of induced nitrogen limitation. Presence of N fixers at moderate abundances is common over a wide trophic range,³⁶ however, and is not exclusively a symptom of impairment.

The correlation between phosphorus and mean or peak chlorophyll among lakes has been erroneously interpreted as showing cause and effect. In fact, the correlation reveals little about nutrient limitation because phosphorus is a mandatory component of algal biomass, as is chlorophyll.²⁰ Therefore, chlorophyll and phosphorus will always be present together (as will all other biomass components), whether phosphorus is limiting or not (Figure 2). **Nutrient limitation cannot be inferred from such correlations.**

Algae excrete phosphatases at the cell surface and into the surrounding water that allow them to assimilate phosphorus derived from cleavage of phosphorus from organic matter.³⁶ Algae also can take up 10 or more times the minimum amount of P needed for synthesis of protoplasm³⁷ and store the excess P as polyphosphate. Thus, toward the end of the growing season, most of the phosphorus in the upper water column of lakes is incorporated into algal biomass, except in lakes that are so strongly polluted with P as to exceed algal capacity for P uptake.³⁴

For nitrogen, a significant portion of the dissolved fraction is refractory (not bioavailable, e.g., ref 39). Dissolved inorganic N (DIN, Table 1) typically is the main N source for algal growth in inland waters, but both unpolluted and polluted inland waters also contain substantial amounts of dissolved organic N (DON). Because DON persists even when phytoplankton show nitrogen stress, as indicated by very low concentrations of DIN, DON had until recently been considered entirely refractory, but experimental evidence now has shown that a significant portion of DON is

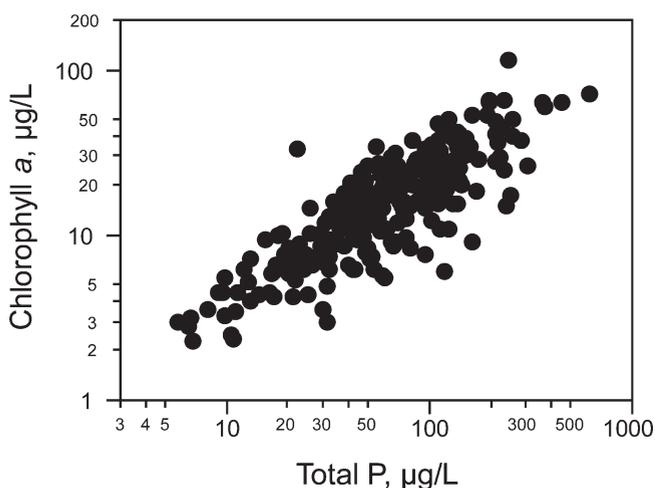


Figure 2. Simulation of the relationship between P and phytoplankton chlorophyll *a* among a hypothetical population of lakes (seasonal averages) for which P is not limiting ($r^2 = 0.70$, from ref 20).

available to algal cells,^{38–40} including not only DON from natural sources but also anthropogenic DON such as urea, which is widely used in agriculture.⁴¹ Some algal taxa have exoenzymes (amino acid oxidases, proteolytic enzymes) at the cell surface or excreted from the surface so that ammonium or small organic molecules can be released from large organic molecules and enter the cell; some taxa also are able to take up organic nitrogen by pinocytosis or phagocytosis.⁴² In addition, some components of DON are converted to DIN by photodegradation, but other components of DON resist photodegradation.⁴⁰ Thus, the persistence of DON in the absence of DIN indicates fractional turnover of the DON pool rather than complete unavailability of DON over time scales ranging from days to months during a growing season.

Natural waters vary greatly in amount of refractory nitrogen in the DON pool. A study of rivers in the eastern U.S. showed two rivers with no detectable bioavailability and seven rivers with a mean of $23\% \pm 4\%$ bioavailability as determined by change in DON concentrations in six-day incubations; an accompanying literature survey for 18 sites on rivers in Europe and the U.S. showed a mean of $30\% \pm 4\%$ for the labile fraction as judged mostly by 14 day incubations.⁴³ Thus, DON of natural waters must be viewed as potentially important nutritionally to algae under nitrogen stress, yet includes a significant refractory component.

Fractions of N and P differ in their potential to predict experimentally diagnosed nutrient limitation in lakes. For phosphorus, total P and total soluble P are equally accurate indicators. For nitrogen, dissolved inorganic nitrogen (almost entirely composed of nitrate plus ammonium) is an indicator superior to total nitrogen or total dissolved nitrogen.⁴⁴ This is not surprising, given the unavailability of a substantial portion of DON to algae.

■ CONTROL OF N, P, OR BOTH

Sole focus on phosphorus as a means of controlling algal biomass may seem advantageous because it is much less expensive than control of both N and P.⁴⁵ Some researchers also continue to argue that nitrogen control does not work because N_2 fixation can provide algae with labile nitrogen.⁴⁶ According to this argument, lakes that are N deficient will accumulate N over time, thus eventually reaching P limitation. Lake 227 of the Canadian Experimental Lake Area, which offers the longest record of whole

Table 1. Concentrations of Total N and P ($\mu\text{g/L}$) in a Representative Municipal Effluent with Secondary Treatment Plus 50% Nitrification and in Representative Unpolluted US Streams and Rivers^{68–71}

nutrient	effluent	unpolluted streams ^a
range total P, $\mu\text{g/L}$		
fractionation, %	2000–4000	10–30
total P	100	100
total dissolved P	96	63
dissolved inorganic P	88	30
dissolved organic P	8	33
particulate P	4	37
range total N, $\mu\text{g/L}$		
fractionation, %	10 000–15,000	100–500
total N	100	100
total dissolved N	96	79
dissolved inorganic N	77	29
NO ₃ ⁻ -N	61	23
NH ₄ ⁺ -N	16	6
dissolved organic N	19	50
particulate N	4	21

^a Unpolluted lakes will show lower DIP, DIN, PP.

lake manipulation, is cited as an example of evolving N sufficiency under P enrichment,⁴⁶ but a contrary interpretation of the data has been proposed.³¹ Multiyear whole lake enrichment experiments with P only document persistence of N limitation in lakes with substantial P and populations of N_2 fixers. For example, whole lake fertilization of several Swedish lakes with P only (multiple years), yielded no higher biomass or only slightly higher biomass than was found before fertilization.⁴⁷ The same lakes developed biomass 15–60 times higher with P + N fertilization (refs 47 and 41 give other examples).

Focus on phosphorus control presumes that phosphorus loading of a lake can be reduced sufficiently to induce and sustain phosphorus control of algae. Where nonpoint phosphorus or background phosphorus sources are strong enough to sustain eutrophic conditions, phosphorus control measures may not provide enough phosphorus recovery to reduce algal biomass. In addition, allowing the balance between nitrogen and phosphorus to be strongly distorted over entire regions by selective control of phosphorus may change the species composition or diversity of aquatic communities,^{13,48} which often reflect a close balance between nitrogen and phosphorus availability.^{18,49} Finally, because nitrogen limitation is quite common in fresh waters and even more common in coastal waters and saline lakes,^{50–52} allowing nitrogen to be released indiscriminately from one water body to another through the drainage network could cause widespread stimulation of algal growth by providing nitrogen to algal communities downstream that otherwise would be nitrogen limited.^{53,54} Thus, dual nutrient control has multiple advantages.

■ STRATEGIES FOR LIMITING PHOSPHORUS AND NITROGEN IN THE ENVIRONMENT

Use of total P as an index of P availability in lakes is defensible for lakes because most of the phosphorus in the growth zone of lakes is available to algae; it consists of total dissolved P (TDP)

with its two components, dissolved inorganic P (DIP, often designated soluble reactive P, SRP) and dissolved organic P (DOP) plus particulate P (PP), which consists mostly of phytoplankton with their internal phosphorus stores. In lakes the particulate fraction of N also consists mainly of phytoplankton, and can be counted as bioavailable, as can DIN and some DON. Thus, the concept of bioavailability suggests that water quality standards for P in lakes can be based on total P, but for N they should be based on total N minus refractory DON. Regulating total N without adjusting for unavailable DON would be equally effective, but would lower the feasibility and raise the cost of N control. For nutrient control we focus here on effluents as nutrient sources because regulation of effluents is feasible through established permitting processes and because the technological basis for regulation nonpoint of sources, which may be dominant nutrient sources in some cases,³⁴ is weak.

EFFLUENT REGULATION THAT IS CONSISTENT WITH STANDARDS BASED ON BIOAVAILABILITY

Point source effluents, which are the main target for discharge permitting, are rich in bioavailable total dissolved P (Table 1). For the dominant treatment technologies (i.e., with the exception of oxidation ponds or ditches), particulate P is not a major concern because of the efficiency of particle removal during treatment. Thus, permits written on the basis of total phosphorus in effluent typically will translate well into a limitation on bioavailable phosphorus in lakes.

For nitrogen, the presence of dissolved organic N in effluent is a complicating factor. DON in municipal effluent is derived partly from the influent waste stream and partly from microbial metabolism that occurs during treatment.⁵⁵ Effluents appear to be similar to inland waters and nearshore marine waters in having both refractory and labile components. One study of a domestic treatment effluent from a treatment facility with low nitrogen output attained by combined nitrification and denitrification showed a median labile component near 40% (range, 18–61%) based on 14-day bioassays.⁵⁵ Other studies have shown a similar range for bioavailable N in municipal effluent.^{56,57}

If the total N limits are strict enough to be fully effective in protecting lakes from enrichment with labile N, wastewater treatment facilities will find that the limiting factor in their ability to produce low nitrogen effluent is DON, which is more difficult to remove than DIN. In fact, the ultimate baseline for DON concentration, as estimated by time course bioassays for a wastewater facility operating at low nitrogen output, may approach 1 mg/L.⁵³ To regulate the refractory component of DON with stringency equal to that of DIN or labile DON overlooks the very different potential effects of the refractory and labile fractions of total dissolved nitrogen.

A regulatory system that takes into account the relative abundance of refractory DON in setting effluent limits for nitrogen would require a standardized analysis of refractory DON. Bioassays could be used for this purpose according to a rationale very similar to the long accepted CBOD₅ (5 day) and CBOD_u (ultimate) analyses for organic carbon.⁵⁵ For both nitrogen and carbon, improved technology also offers new possibilities through the use of fluorescence spectroscopy^{58–60} which, if calibrated with bioassay, might allow rapid analysis of large numbers of samples for both DOC and DON.

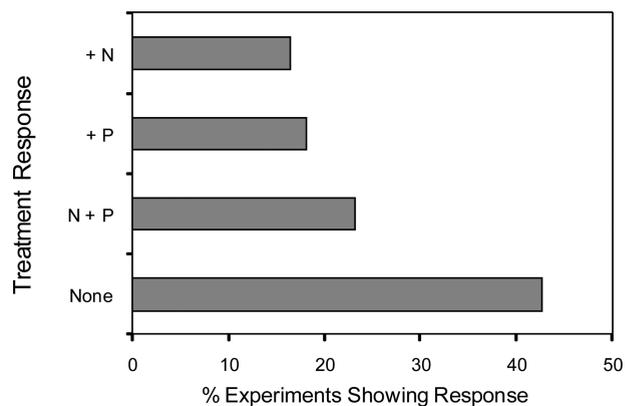


Figure 3. Response of attached algae in streams to experimental enrichments with N, P, or N+P ($n = 237$; redrawn from ref 63).

Table 2. Summary of Three Possible Effluent and TMDL-Related Regulatory Strategies for Nutrients

basis of regulation	feasibility	cost	comments
total P	high	moderate	allows N pollution
total P, Total N	low	high	may require removal of refractory N
total P ^a , total N – refractory N	high	high	focuses on bioavailable nutrients

^aTDP may be a better option for stream monitoring and lake loading limits where PP is mostly adsorbed onto mineral particles.

STREAMS

Although rivers and slowly flowing streams may produce phytoplankton populations comparable to those of lakes, periphyton (attached algae) also are important and may be dominant, especially in streams of small to intermediate size. Excessive growth of periphyton can be a byproduct of nutrient enrichment in streams or rivers. As in the case of lakes, extensive study at many sites has shown that phosphorus and nitrogen are about equally likely to be limiting to the growth of periphyton (Figure 3; refs 61–63). For stream periphyton, unlike lake phytoplankton, as much as half of experimentally tested locations show no nutrient limitation. As in the case of lakes, however the strongest responses to nutrient addition typically are for addition of both N and P. The stimulation threshold for nitrogen and phosphorus enrichment response in streams appears to be higher than in lakes.^{64–67} Thus, protective nutrient standard concentrations may justifiably be higher for streams than for lakes, but will differ among distinct categories of streams.

The arguments regarding fractions of phosphorus and nitrogen in lakes as given above are likely applicable to flowing waters as well. One exception is the consistently greater proportion of mineral particulate phosphorus (there is no significant mineral fraction for N) that is carried in suspension by flowing waters (Table 1). It may be preferable to use total soluble phosphorus rather than total phosphorus as a basis for regulation of P in flowing waters and for development of loading restrictions on lakes, given that mineral phosphorus is much less available to algae.

Assessment of eutrophication in streams and rivers has lagged behind that of lakes. Additional research will be necessary to

identify protective standards for them. Nevertheless, many of the issues surrounding nitrogen in streams and rivers are the same as for lakes. Regulation of eutrophication in flowing waters should be based on N and P controls and recognition of refractory DON as a regulatory consideration.

CONCLUSION

Restriction of the anthropogenic release of both N and P to inland waters is a means of controlling excessive algal growth. P regulation should be based on total P (for lakes) or total dissolved P (preferred for flowing waters). **N regulation should be based on bioavailable N** rather than total N; regulation of total N will likely be infeasible or will require unrealistically high standards (Table 2).

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Review Paper

Control of Lacustrine Phytoplankton by Nutrients: Erosion of the Phosphorus Paradigm

key words: algae, dissolved organic nutrients, eutrophication, lake ecosystems, lake management, nitrogen

Abstract

Control of lacustrine phytoplankton biomass by phosphorus is one of the oldest and most stable paradigms in modern limnology. Even so, evidence from bioassays conducted by multiple investigators at numerous sites over the last three decades shows that **N is at least as likely as P to be limiting to phytoplankton growth**. A number of important flaws in the evidence supporting the phosphorus paradigm have contributed to an **unrealistic degree of focus on phosphorus** as a controlling element. These include insufficient skepticism in interpretation of: 1) the phosphorus:chlorophyll correlation in lakes, 2) the results of whole-lake fertilization experiments, and 3) stoichiometric arguments based on total N:total P ratios for inland waters. A new paradigm based on parity between N and P control of phytoplankton biomass in lakes seems more viable than the P paradigm. The new paradigm renews interest in the degree to which plankton communities are molded in composition by small differences in relative availability of N and P, the mechanisms that lead to a high frequency of N limitation in oligotrophic lakes, and the **failure of aquatic N-fixers to compensate significantly for N deficiency** under most conditions. A new N/P paradigm still must acknowledge that suppression of P loading often will be the most effective means of reducing phytoplankton biomass in eutrophic lakes, even if N is initially limiting.

From error to error one discovers the entire truth
SIGMUND FREUD

1. Introduction

Control of phytoplankton in lakes by phosphorus is one of the oldest and most stable paradigms in modern limnology. Phytoplankton biomass and production can be controlled by factors other than nutrients under some circumstances (*e.g.*, strong herbivory, hydraulic displacement, shading, and seasonal deep mixing), but nutrients often are limiting, and phosphorus is cited consistently as the dominant limiting nutrient (Table 1). Persistence of the phosphorus control paradigm in limnology has caused phosphorus dominance to be recognized in related fields, such as environmental engineering.

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Table 1. Textbook generalizations concerning the importance of phosphorus and nitrogen in limiting growth of phytoplankton in lakes.

Source	Phosphorus Limitation	Nitrogen Limitation
Limnology		
HORNE and GOLDMAN, 1994	Lakes in wet climates	Lakes in dry climates
WETZEL, 2001	Foremost limit	About 25%
KALFF, 2002	Oligotrophic temperate lakes	Eutrophic lakes
DODDS, 2002	P key in many systems	Nitrogen can limit
DODSON, 2005	P dominant limitation	N secondary limitation
LAMPERT and SOMMER, 2007	Predominant	Not addressed
Applied Limnology		
WELCH and LINDELL, 1992	P most limiting	Highly enriched lakes
COOKE <i>et al.</i> , 2005	P most often limiting	Highly polluted lakes

Most textbook authors acknowledge the possibility that nitrogen can limit growth of phytoplankton in lakes, but the range of predictions for circumstances under which N limitation will occur is inconsistent or vague (Table 1). In reading multiple texts, one gets the impression that the importance of phosphorus is well established for freshwater lakes, but the role of nitrogen is uncertain or unusual (the prevailing view for hypersaline lakes favors N dominance: JAVOR, 1989). For this reason, transfer of the phosphorus paradigm to applied ecology has occurred primarily through deletion of the confusing possibilities for nitrogen limitation. Thus, when translated outside the discipline, the phosphorus paradigm is even stronger than it is within the discipline.

The accumulation of credible studies of nutrient limitation in numerous lakes, as reviewed below, now suggests that the phosphorus paradigm is not nearly so strong as it appeared to be two decades ago. Evidence that nitrogen limitation in lakes is common rather than exceptional suggests that some of the fundamental arguments supporting the phosphorus paradigm should be reexamined critically, which is the purpose of this paper.

2. History of the Phosphorus Control Paradigm

The phosphorus control paradigm finds its roots in NAUMANN's (1919) classification of lakes according to algal abundance by use of WEBER's (1907) terminology for wetlands. NAUMANN separated oligotrophic from eutrophic lakes on the basis of algal abundance, and attributed the difference between categories to the relative amounts of plant nutrients. Because he could not quantify nutrients, he was unable to move his nutrient-control concept toward identification of one or more specific critical nutrients. Instead, he focused his attention on identifying landscape factors that were consistent with either rich or poor supplies of nutrients known to favor growth of terrestrial plants (N, P, Ca).

JUSTUS LIEBIG (1803–1873) set the stage for identification of specific limiting nutrients in various ecosystem types through his development of the limiting nutrient concept (HUTCHINSON, 1973), which became a general ecological paradigm under which the phosphorus control paradigm for lakes subsequently developed. He postulated that the growth of a plant population at any given place, when constrained by nutrient insufficiency, can be stimulated only by the limiting nutrient, which is the nutrient in shortest supply relative to the needs of the plant. It follows that the limiting nutrient may vary through time and space, and that it must be diagnosed experimentally. While LIEBIG's context was agricultural, the limiting-nutrient concept and its mathematical counterparts (TALLING, 1979) consistently have been of great interest to ecologists for analyzing autotrophy in various kinds of ecosystems.

Given that phosphorus and nitrogen are consistently among the limiting nutrients in agricultural settings, it was natural that limnologists should test the possibility that either or both of these nutrients might be commonly limiting to autotrophs in lakes. JUDAY and colleagues (1931) showed that both N and P are scarce in the water columns of lakes, and PEARSALL (1930, 1932) linked measured N:P ratios to successional stages of phytoplankton development in lakes, thus extending earlier, more hypothetical ideas about control of phytoplankton populations by nutrient ratios (reviewed by HUTCHINSON, 1957). Extensive laboratory investigations were conducted on cultured populations of algae by CHU (1943) and others. Experiments showed limitation of growth for individual algal species at low concentrations of N or P. Subsequent experiments with algae obtained directly from lake water showed lower thresholds of limitation, however, thus undermining confidence in specific thresholds based exclusively on laboratory studies (HUTCHINSON, 1957; VOLLENWEIDER, 1968). Even so, as early as 1930 it was already evident that scarcity of N or P could suppress algal growth. Silica was also recognized at this time as a potentially limiting element for diatom growth (PEARSALL, 1930, 1932). There was also a small but steady interest in limitations caused by micronutrients (VOLLENWEIDER, 1968), but such limitations never have achieved broad credibility.

While stoichiometric analysis of N and P was inherent in PEARSALL's work of the 1930s, HUTCHINSON was first to formulate an explicit phosphorus paradigm based upon stoichiometry: "Of all the elements present in living organisms, phosphorus is likely to be the most important ecologically, because the ratio of phosphorus to other elements in organisms tends to be considerably greater than the ratio in primary sources of the biological elements" (HUTCHINSON, 1957, page 727).

Seeking realism that could not be obtained in a laboratory setting, EINSELE (1941) added phosphorus to a mildly eutrophic German Lake (Schleisee), thereby doubling the amount of organic matter in the water column. This experiment later strengthened HUTCHINSON's conviction, based on stoichiometry, that phosphorus must have the strongest governing influence on autotrophic production in lakes.

After 1940, interest in the relationship between algal biomass or production and limiting nutrients was stimulated especially by recognition of anthropogenic eutrophication as a serious problem. In his thorough review of the subject, VOLLENWEIDER (1968) recorded 13 significant studies of lake eutrophication for 1940–1950, 28 for 1950–1959, and over 50 for 1960–1966. VOLLENWEIDER's coverage of eutrophication included both P and N, but led him to conclude that P provides better prediction of algal biomass. VOLLENWEIDER, following SAWYER (1947), noted that spring concentrations of "assimilable" phosphorus exceeding 10 µg/L or inorganic nitrogen (ammonium plus nitrate) exceeding 200–300 µg/L would suggest eutrophication.

VOLLENWEIDER's main goal in 1968 was to predict phosphorus concentrations from nutrient loading. The result was his now famous double logarithmic graph relating total phosphorus load to mean water depth (VOLLENWEIDER, 1968, Fig. 17). The diagram carries diagonal isolines of uniform concentrations, thus dividing the graphical space into sectors, with eutrophic lakes in the top sector and oligotrophic lakes at the bottom. Linkage of the water column to the watershed, which was inherent in this diagram, satisfied a basic need in the study of lakes, and was widely appreciated outside of limnology because of its usefulness in management. By the late 1960's, limnologists had become broadly committed to studying and controlling eutrophication, but some time elapsed before the key issues came clearly into focus (SCHINDLER, 2006). EDMONDSON (1970) generated great excitement by reducing algal biomass in Lake Washington through sewage diversion, thus validating nutrient-based theories of algal control.

In the late 1960's and early 1970's efforts were made to establish statistical relationships between phosphorus concentration and phytoplankton biomass (chlorophyll). By using a double logarithmic transformation, SAKAMOTO (1966) was able to show a close relationship

between the two variables for 20 Japanese lakes. Subsequently DILLON and RIGLER (1974), seeking predictive capability, measured total P in the spring, *i.e.*, before seasonal development of phytoplankton biomass, and measured chlorophyll *a* as an average over the growing season. They also excluded lakes showing a molar N:P ratio of 12 or less, on grounds that this precaution would allow them to assume a causal relationship between phosphorus and chlorophyll *a*. With double logarithmic transformation, their data for 19 Canadian lakes demonstrated a close statistical relationship between the two variables ($r^2 \approx 0.8$). Adding data from other sources, they found a similarity in relationship with their own study, and proposed a general equation for use when the N:P ratio is $<12:1$, *i.e.*, $\log(\text{chlorophyll } a) = 1.449 \log(P) - 1.136$, where concentrations are given as $\mu\text{g/L}$. The arithmetically expressed confidence limits were disappointingly broad, however. For a total P concentration of $10 \mu\text{g/L}$, the 95% limits were 0.8–5.6; for total P of $21 \mu\text{g/L}$, they were 7.7–58.4. They argued nevertheless that a 50% confidence interval, whose limits differed by approximately by a factor of two, would be useful for managers wishing to know the most likely outcome of an increase or decrease in phosphorus concentrations. They also speculated that future studies would tighten the confidence limits.

A landmark study organized by OECD (1982) encompassing the entire spectrum of relationships between nutrient loading, nutrient concentration, chlorophyll *a*, and other trophic response variables, was in progress as DILLON and RIGLER published their important paper on nutrient–chlorophyll relationships, but was not published in final form until 1982. The OECD study, which was based upon carefully designed protocols for data collection, was international, but dealt only with temperate freshwater lakes and was focused on Europe and North America.

Authors of the OECD study found that concentrations of total nitrogen and total phosphorus in lakes were strongly correlated ($r = 0.75$), but that total phosphorus was better correlated with either chlorophyll or primary production than was total nitrogen. The authors identified a number of lakes that they considered to be nitrogen limited on the basis of N:P ratios. They removed from the data set these and a few lakes that were not strictly under nutrient control, because of suspended inorganic matter or other factors. For the screened data set, correlations between the logarithms of total phosphorus and mean chlorophyll *a* were near 0.9 for all lakes together or for any of the five groups of lakes that were included in the study. They concluded that phosphorus is the primary factor controlling algal biomass in most lakes, and consequently focused the remaining portion of their analysis, which dealt with the relationships between loading and concentration, on phosphorus alone.

Although statistically strong correlations were shown by the OECD study between the logarithms of total phosphorus and mean chlorophyll *a* across lakes, the inclusion of large numbers of lakes and standardized analytical and sampling procedures did not narrow the uncertainty of prediction for chlorophyll *a* from total phosphorus, contrary to the hope expressed by DILLON and RIGLER. The 95% confidence limits of predictions made for individual lakes were approximately one order of magnitude for the OECD study, as they had been for the DILLON and RIGLER study. The OECD results in large part were anticipated by several important studies that were published while the OECD work was in progress (VOLLENWEIDER, 1976; JONES and BACHMAN, 1976; CANFIELD and BACHMAN, 1981).

As the OECD data collection was beginning, Canada established an ambitious program of experiments on eutrophication in its Experimental Lakes Area (ELA), Ontario, under the direction of DAVID SCHINDLER (SCHINDLER, 2006). In 1971, SCHINDLER reviewed the state of knowledge on nutrient limitation of phytoplankton in lakes. He noted the willingness of most authorities to assume that phosphorus is the dominating nutrient limitation on phytoplankton biomass, but also acknowledged a number of observations suggesting limitation by nitrogen or trace elements. He characterized the phosphorus paradigm for nutrient limitation as overly comfortable, in that no study had demonstrated mechanisms of nutrient control experimentally in a realistic way (SCHINDLER, 1971).

Schindler's initial objective was to test the possibility that inorganic carbon might limit the phytoplankton biomass accumulation in a manner comparable to limitations observed through phosphorus or nitrogen (SCHINDLER, 1971; SCHINDLER *et al.*, 1971). His experiments countered earlier work purporting to show limitation of phytoplankton growth by deficiency of inorganic carbon. SCHINDLER's work demonstrated that the combination of an inexhaustible atmospheric source of CO₂, along with efficient transfer of CO₂ across the air-water interface in lakes, restricts carbon deficiency to conditions when both biomass and solar irradiance are very high, *i.e.*, a portion of each day under bloom conditions. Thus, while carbon deficiency can slow the growth of phytoplankton under extreme conditions, it does not establish a cap on total biomass accumulation and has only a weak effect on production (SCHINDLER *et al.*, 1972).

Extending through subsequent publications during the 1970's, SCHINDLER and colleagues presented and interpreted results of experiments with N and P at ELA. SCHINDLER's initial experiments were made with bottles and flasks as well as tubes of 1 m diameter in experimental Lake 227, and subsequent fertilization of Lake 227 with both N and P. The tube experiments showed that addition of phosphorus and nitrogen together could establish dense populations of phytoplankton, even though the CO₂ inventory of the water was the lowest on record for lakes in general (SCHINDLER *et al.*, 1971). Addition of both N and P simultaneously to Lake 227 produced an algal biomass five times background and changed species composition. Overall, SCHINDLER gave an edge to phosphorus in his interpretation of control, but emphasized the strong combined effect of N and P.

SCHINDLER and colleagues conducted enrichment experiments on other lakes as well. The most striking and influential outcome of these experiments occurred through installation of a curtain subdividing Lake 226 into two nearly equal basins (SCHINDLER, 1974). Nitrogen, phosphorus, and carbon were added to one side, where a strong bloom of N-fixing cyanobacteria appeared, whereas the other side was fertilized with nitrogen and carbon but not phosphorus, and did not show the cyanobacterial bloom. Although the experiment continued for 8 years, results after year 4 (1976) were influenced by curtain failure and a forest fire in the watershed (D.W. SCHINDLER pers. comm., 2008). In addition, Lake 304 was fertilized with C, N, and P for two years after having been monitored with no experimental treatment for three previous years (SCHINDLER, 1974). Phosphorus addition was discontinued in 1973, but nitrogen and carbon enrichments were continued as before. Chlorophyll concentration declined in 1973 to concentrations that were typical of background conditions in earlier years. Based on these experiments, SCHINDLER concluded that phosphorus and nitrogen can cause rapid eutrophication, as indicated by drastic increases in phytoplankton biomass. His prescription for abatement of eutrophication was control of phosphorus.

SCHINDLER consolidated his conclusions in 1977. He noted a close relationship between the concentration of total phosphorus and standing crop of phytoplankton in a wide variety of lakes. He described the evidence, largely established by him and his colleagues, showing that carbon is very unlikely to limit phytoplankton biomass in lakes. For nitrogen, SCHINDLER introduced some new conclusions based on experiments with lakes in which amendments of N and P were made at low N:P ratios. Where only P was added to a lake, there was no phytoplankton bloom, but rather a proliferation of attached algae composed of nitrogen fixing taxa. Where nitrogen was added at a low ratio (5:1) with respect to phosphorus, strong blooms of nitrogen fixing cyanobacteria (bluegreen algae) developed. SCHINDLER concluded that the presence of phosphorus at relatively high ratios to nitrogen stimulates growth of N-fixing cyanobacteria, which compensate by fixation for deficiencies in nitrogen. In one of the lakes, compensation by nitrogen fixers for nitrogen deficiency averaged 29% of total N load over two years of fertilization with low N:P ratios.

SCHINDLER's (1977) paper marks the culmination of the formative period for the phosphorus control paradigm. Numerous important developments occurred subsequently, particularly

in the analysis of nutrient supply ratios for natural and anthropogenically perturbed lakes and in analysis of the phosphorus cycle within lakes (SCHINDLER, 2006).

The foregoing overview shows that much of the interest in the nutrient supply of lakes was motivated by a desire to show how cultural eutrophication could be controlled. The scientific question underlying the phosphorus control paradigm in its original form, as stated by HUTCHINSON, was the identity of the nutrient that limits development of algal biomass in lakes. In contrast, the need for a rational approach to the control of eutrophication gave rise to the concept of nutrient restriction, which at first involved simultaneous consideration of nitrogen and phosphorus, but quickly became focused on phosphorus. Initially, priority for phosphorus control was rationalized by the conclusion, based on statistical or experimental information, that phosphorus is the element most likely to limit algal growth in lakes. It became evident very early, however, that the possibility of nitrogen limitation was generally moot from the viewpoint of management, for two reasons (GOLTERMAN, 1975; RYDING and RAST, 1989): (1) control of phosphorus pollution typically is more feasible and cheaper than control of nitrogen pollution, and (2) phosphorus limitation can be induced by aggressive phosphorus control, even if algal populations are initially limited by nitrogen deficiency. Thus, the scientific question (identity of the limiting nutrient) was severed from the management question (most effective control of algal populations). Studies of eutrophication still are motivated by the need to control algal populations, which may be accomplished without any knowledge of the initially limiting nutrient. At the same time, interest in the identity of limiting nutrients in natural or perturbed systems has remained in the literature. Unfortunately, the phosphorus control paradigm for phytoplankton biomass and the eutrophication management principle based on phosphorus control often have been confused.

3. Flaws and Limitations in Evidence Supporting the Phosphorus Control Paradigm

The phosphorus control paradigm is supported by a cluster of mutually consistent types of evidence, including stoichiometric principles, statistical relationships based on sampling of lakes, and experiments. Use of this evidence contains a substantial number of flaws, most of which are related to interpretation or development of the evidence rather than the evidence itself.

3.1. *The Phosphorus – Chlorophyll Relationship*

The double logarithmic empirical relationship between phosphorus and chlorophyll *a* in lakes almost always appears when the subject of nutrient limitation is being presented for lakes. Use of this relationship is so commonplace that unwary readers may see in it substantial evidence for control of chlorophyll by phosphorus.

Phosphorus and chlorophyll both are essential components of phytoplankton biomass. Therefore, measurements of phosphorus and chlorophyll that are taken in a lake over the same span of time (*e.g.*, the growing season) are not independent variables; there must always be a correlation between the two variables, although the strength of the correlation will weaken if concentrations of phosphorus far exceed the need of phytoplankton for phosphorus. The inevitability of the relationship between phosphorus and chlorophyll *a* can be illustrated by use of a simulation, as shown in Figure 1. In this case, phytoplankton (seasonal mean) are assumed to have a cell quota (q_0) for particulate phosphorus equal to the amount of chlorophyll (the ratio varies; for present the ratio is set to $\mu = 1$; $\sigma = 30\%$, normal distribution), and to be capable of luxury consumption producing a cellular phosphorus concentration (q) up to a maximum of $18q_0$ (reviewed by REYNOLDS, 2006). All of the lakes

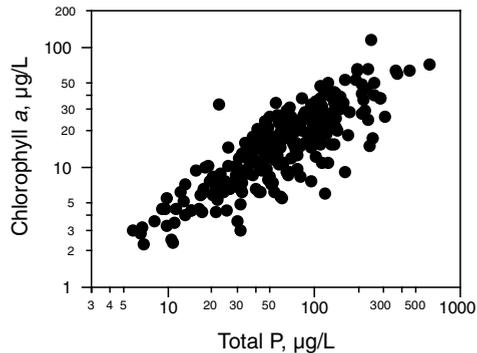


Figure 1. Simulation of the relationship between P and chlorophyll *a* among a hypothetical population of lakes (seasonal averages) when P is not limiting (see text; $r^2 = 0.70$).

in the simulated hypothetical population are phosphorus sufficient, in that all phytoplankton populations have phosphorus concentrations equal to q_0 plus some amount $q - q_0$ that varies between 0 and $17q_0$. Chlorophyll *a* is a random variable with lognormal distribution across lakes (seasonal mean) $\mu = 18.4 \mu\text{g/L}$, $\sigma = 14.8 \mu\text{g/L}$. In this simulation, μ and σ were set at values that represent a full range of trophic categories.

The gap between q_0 and q is treated as a random variable with a lognormal distribution; $\mu = 2.4$, $\sigma = 2.1$ for seasonal averages across lakes. P that is not incorporated into biomass is assumed to equal P in biomass (ratio $\mu = 1$, with $\sigma = 30\%$, normal distribution). As shown by Figure 1, the bivariate distribution of chlorophyll *a* and total P under the conditions of simulation shows a pattern that is characteristic of log-log plots for field data based on total phosphorus and chlorophyll *a* in lakes. Because the two variables are not independent, probability statements regarding their joint distribution are not indicators of cause and effect. The graph only shows that chlorophyll cannot be present in the absence of organically bound phosphorus, *i.e.*, the correlation of chlorophyll *a* with P is a tautology.

DILLON and RIGLER (1974) recognized but did not completely avoid the problem of tautology in comparing phosphorus to chlorophyll *a*. They specified that phosphorus concentration must be measured in the spring, prior to the development of chlorophyll, from which they predicted mean chlorophyll for the growing season. In this case, the two variables are independent, but the outcome (uptake of P simultaneous with increase in biomass) is inevitable and therefore not indicative of nutrient limitation. The purpose of DILLON and RIGLER, however, was to produce a prediction to be used in management rather than to diagnose the cause of growth limitation, and for that purpose the tautological nature of the relationship could be considered admissible. The OECD log-log relationship followed the same pattern, except that the restriction on use of spring concentrations was dropped when it was determined that spring concentrations of total P did not differ much from growing season concentrations of total P in a given lake. The purpose of the OECD analysis, as in the case of the DILLON and RIGLER study, was not to diagnose the mechanism of limitation, but rather to find the most powerful predictor of chlorophyll development. The relationship does not diagnose the nutrient limitation of phytoplankton growth; it only shows what is self evident, *i.e.*, that P has the potential to be limiting, either naturally or by restriction of supply.

A second serious weakness in the quantitative relationship of phosphorus to chlorophyll is its enormous variation, even within a relatively homogeneous set of lakes such as the ones studied by DILLON and RIGLER (Fig. 2). The goodness of fit for the empirical relationship between P and chlorophyll *a* is due entirely to its presentation in double logarithmic form;

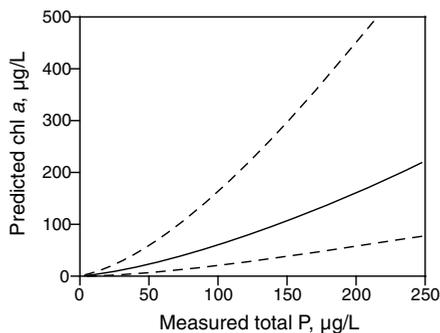


Figure 2. Mean and 95% confidence limits for chlorophyll *a* as predicted from total P for the analysis by DILLON and RIGLER (1974).

in fact, predictions from the relationship are good only within about an order of magnitude for any given lake.

3.2. Uncritical Use of Stoichiometry

HUTCHINSON'S (1957) succinct formulation of the phosphorus control paradigm was firmly grounded in stoichiometry, but the application of stoichiometry to N and P in lakes is very difficult and still mostly unresolved. HUTCHINSON'S stoichiometric argument was extended by the publication of tables showing the relative availability of elements in world rivers as a ratio to the composition of algal biomass (VALLENTYNE, 1974, often reprinted in textbooks). The amount of an element in rivers, however, does not reflect its biotic availability to lacustrine phytoplankton. A relevant parallel example is iron, which shows a tremendously favorable ratio of biomass to source water (18:1 as compared with 2400:1 for P), but is nearly insoluble in water, and consequently is potentially a limiting or colimiting element for phytoplankton in marine waters (GREGG *et al.*, 2003) or lakes (NORTH *et al.*, 2007). Thus, ratios may be an interesting basis for a hypothesis, but are not a secure basis for judging the availability of elements for uptake by autotrophs.

The key defect in stoichiometric reasoning involving phosphorus and nitrogen derives from uncertainty about the differential availability of nitrogen and phosphorus fractions in lake water. The early emphasis on N:P ratios involved "assimilable" fractions, but this approach foundered on uncertainties about what is assimilable. In experiments, nutrients can be added in assimilable form, which insures their availability. On the other hand, in the statistical evaluation of N or P among lakes, total N and total P have typically been used in forecasting limitation without any consideration of availability.

Even if phosphorus in a lake is sampled prior to the growing season, at which time algal phosphorus may be only a small proportion of total phosphorus, interpretations of its availability are difficult. Soluble reactive P (SRP), which includes inorganic soluble P plus a fraction of small phosphorus-containing molecules, is most readily available, and shows extremely high rates of turnover (LEAN, 1973). Soluble organic phosphorus is not so readily available as SRP, but can become available through the synthesis of external phosphatases by phytoplankton cells when they experience P deficiency (HEALEY, 1973; RHEE, 1973). Particulate phosphorus that is not part of living biomass spans a tremendous range from potentially available (adsorbed phosphorus on clay or silt) to essentially unavailable (metallic precipitates, hydroxides, and complexes). Furthermore, the fractionation of phosphorus

can be expected to change continuously in the mixed layer of a lake, and can be influenced by phosphorus entering the epilimnion from runoff, release of P from epilimnetic sediments, and exchange between the mixed layer and deeper waters. Thus, quantification of the availability of phosphorus in a lake is infeasible at present. While there has been some use of total soluble phosphorus as a direct indicator of availability (MORRIS and LEWIS, 1988), most statistical work on the importance of phosphorus has been based on total P.

Nitrogen presents problems similar to those of phosphorus. Nitrate and ammonium are highly available, and commonly are scrubbed from the mixed layer by algae and bacteria, as is SRP. Organic nitrogen compounds have a range of availabilities, as in the case of phosphorus. Urea, for example, is highly available (*e.g.*, BERMAN and CHAVA, 1999), as are some DON species previously thought to be unavailable (BRONK *et al.*, 2006), but nitrogen in large molecules may be weakly available or unavailable. Particulate nitrogen is likely to be directly available only to taxa capable of phagotrophy, but could become available by way of microbial degradation.

The tighter log-log relationship between chlorophyll and total P as contrasted with chlorophyll and total N seems to support the idea that phosphorus controls chlorophyll *a*, whereas N typically does not. The weaker correlation for N may be explained, however, by a greater proportion of refractory N than refractory P for inland waters. Lakes commonly show virtual elimination of dissolved inorganic species of N and P from the mixed layer of unpolluted or mildly polluted lakes. Despite the strong demand for inorganic fractions of both N and P, however, particulate N and P tied up in phytoplankton biomass consistently coexists with significant amounts of both N and P in dissolved organic forms (WETZEL, 2001).

The present working hypothesis for P is that the dissolved pool consists of a broad mixture of chemical species having very different turnover rates based on their direct or indirect availability for phytoplankton uptake (LEAN, 1973). Thus, differential phytoplankton uptake of varied species of P maintains a dynamic equilibrium among DOP compounds.

DON also consists of a mixture of readily assimilated chemical species and more refractory chemical species (STEPANAUSKAS *et al.*, 1999; KAUSHAL and LEWIS, 2005). Higher analytical variability for N analyses may contribute to lower correlation between N and chlorophyll as compared with P and chlorophyll (D. W. SCHINDLER, pers. comm., 2008), although the differences between N and P may be expected for other reasons. An important difference between N and P is the ratio of the dissolved organic pool to the particulate pool, most of which is accounted for by phytoplankton. For phosphorus in waters that are unpolluted or mildly polluted, the ratio of dissolved organic P to particulate P is approximately 1:1 (WETZEL, 2001) or even less (VADSTEIN *et al.*, 1993), whereas for nitrogen the ratio can be as high as 10:1 (WETZEL, 2001). Thus, a higher fraction of the DON pool apparently is unavailable or weakly available at any given time.

The effect of a contrast in fractionation for N and P can be illustrated by simulation. The simulation shows the effect of differences in the ratio of unassimilable or weakly assimilable nutrient to the total nutrient pool for the same chemical species. For the simulation, chlorophyll *a* across a group of lakes (growing season mean) is assumed to have a lognormal distribution with $\mu = 18.4 \mu\text{g/L}$ and $\sigma = 14.8 \mu\text{g/L}$ (as in simulation 1, Fig. 3). Particulate phosphorus is set equal to chlorophyll *a* (ratio = 1) but with random variation ($\mu = 1$, $\sigma = 30\%$, normal distribution). Dissolved organic phosphorus is set equal to particulate phosphorus, also with $\sigma = 30\%$ and a normal distribution. Total phosphorus is the sum of dissolved and particulate phosphorus. Particulate nitrogen is set to 16 times (molar) particulate phosphorus (Redfield ratio), implying no overall bias in limitation between phosphorus and nitrogen (and no differential luxury uptake), but with variance ($\sigma = 30\%$, normal distribution). Mean assimilable dissolved nitrogen is set to 2 times particulate nitrogen with $\sigma = 30\%$ and a normal distribution. An additional component of dissolved organic nitrogen is assumed to be refractory, and is set to $\mu = 200 \mu\text{g/L}$, $\sigma = 150 \mu\text{g/L}$, lognormal distribution,

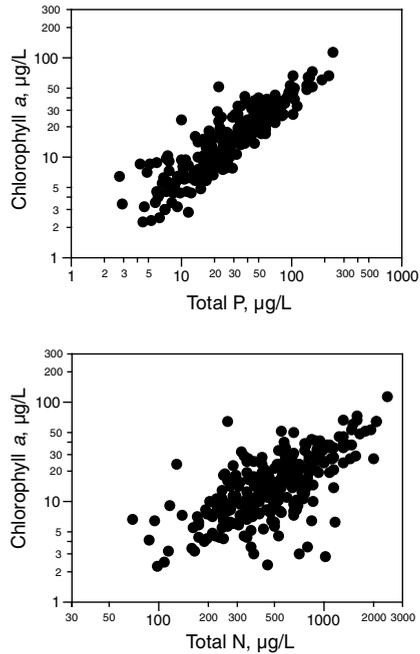


Figure 3. Simulation of chlorophyll *a* in relation to total P ($r^2 = 0.75$) or N ($r^2 = 0.45$) when nitrogen and phosphorus are balanced according to demand (particulate N:P set to the Redfield ratio), and assuming that N has a higher dissolved: particulate ratio than P.

based on characteristic N composition of humic and fulvic acids, from THURMAN (1985), and the assumption that nonhumic refractory N is about as abundant as humic refractory N.

Figure 3 shows the expected effect of a substantial and variable component in the DON pool that is unavailable or weakly available to phytoplankton. Thus, if the assumptions underlying the simulation are reasonable, one would expect a looser correlation between total N and chlorophyll *a* than between total P and chlorophyll *a*, even when both have equal degree of control on biomass (*i.e.*, N:P of biomass set at the Redfield ratio).

3.3. Experiments: Categories of Evidence

Bioassay incubation is the key experiment for diagnosing nutrient limitation at a point in time. For small enclosures, long incubations (> 5 days) produce bottle effects, including changes in community composition of phytoplankton or growth of grazers, and may reveal only potential limitation rather than actual limitation. Very short experiments (<12 hours), which have been conducted with ^{14}C , can produce misleading results because the addition of nutrients may suppress algal growth temporarily (LEAN and PICK, 1981). For enclosures of small to intermediate size, incubation must extend beyond the interval of early response to the addition of nutrients but not last beyond the duration of a few cell divisions, *i.e.*, 2–5 days.

Mesocosms such as those used by SCHINDLER *et al.*, (1971), LEVINE and SCHINDLER (1992), as well as LUND (1975) and many others seem to provide more realism than chambers, but can produce anomalies. For example, the 1 m diameter mesocosms used by SCHINDLER *et al.*

(1971) produced contradictory signals about nutrient limitation, in that P alone showed very little influence on peak biomass, whereas P combined with C produced the highest biomass, even though it is clear from other work by SCHINDLER and colleagues that carbon in the open water of lakes cannot limit biomass accumulation except over very short intervals.

Manipulation of entire lakes is the most realistic measure of ultimate biomass production but experiments of shorter duration most clearly show the time course of differing limitation mechanisms. Also, replication often is weak with whole-lake manipulations.

3.4. *Experimental Evidence: The Canadian Experimental Lakes Area*

The early ELA experiments strongly supported the hypothesis that N and P in combination greatly stimulate algal biomass, and that N limitation can be induced by forcing a low N:P ratio. These points were important for management, but did not make a convincing case for P limitation in the ELA lakes.

HEALEY and HENZEL (1980) evaluated physiological indicators of nutrient limitation for ELA lakes and other Canadian lakes. P was consistently indicated as limiting in the ELA lakes, but most of the lakes that were included in the study had been experimentally manipulated with nutrient additions.

In 1979, FEE published an analysis of relationships between lake morphometry and relative importance of nutrient recycling between epilimnetic sediments and the mixed layer during the growing season. FEE included a table of the results for ELA whole-lake nutrient enrichment studies, as summarized in Figure 4. FEE postulated that both primary production and chlorophyll are affected by the ratio of epilimnetic sediment exposure to epilimnetic volume (A_e/V_e) among unfertilized ELA lakes. If so, A_e/V_e would provide a prediction of expected production and chlorophyll to be used in quantifying degree of departure from expectations in response to experimental enrichment. He demonstrated the relationship of A_e/V_e to production, but found that A_e/V_e and chlorophyll were only weakly related (not significant, but reanalysis with logarithmic transformation shows a significant relationship: W. WURTSBAUGH, unpublished). In his analyses, FEE noted that the ELA experiments support a case for near equality in the importance of N and P among unfertilized ELA lakes, in apparent contradiction to SCHINDLER's evaluation of the same data (SCHINDLER, 1980).

The composite of ELA lake fertilization results indicates that addition of P alone did not markedly increase phytoplankton biomass (Fig. 4), nor did it stimulate the growth of nitrogen-fixing planktonic cyanobacteria, which could have potentially offset a deficiency of N. The results are uniformly consistent with SCHINDLER's observation that enrichment of ELA lakes with significant amounts of phosphorus plus nitrogen increased phytoplankton biomass by a large amount (5–10×). Figure 4 is not consistent, however, with phosphorus limitation of phytoplankton growth in ELA lakes. The results suggest that nitrogen had at least an equal stimulating effect on phytoplankton biomass and therefore may have been a dominant or codominant limiting nutrient in unfertilized ELA lakes.

LEVINE and SCHINDLER (1992) conducted experiments on mesocosms in a lake that had previous large additions of nitrogen in order to determine the degree of compensatory nutrient response in enclosed water columns of ELA lakes with and without contact between water and sediment. They found that compensatory mechanisms for nitrogen were stronger than those for phosphorus in the mesocosms, but the potential influence of the prior N addition was not addressed. Their results were taken as evidence for the dominance of phosphorus control on phytoplankton biomass. These findings were contrary, however, to the results of the whole-lake studies (Fig. 4), which showed that compensation (as indicated by accumulation of biomass above the baseline) for deficient phosphorus is at least as strong as compensation for deficient nitrogen. Of course it is possible that lakes as a whole have compensatory mechanisms that cannot be demonstrated by the use of mesocosms.

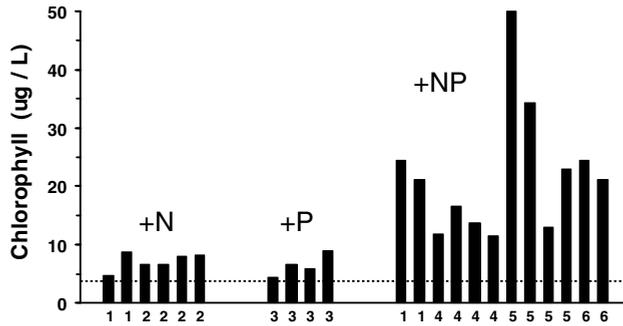


Figure 4. Graphical summary of the results of lake fertilization experiments at ELA from 1973-1976 (mean chlorophyll *a* during ice-free seasons), as reported by FEE (1979, Table 1). The dashed line shows annual mean chlorophyll *a* in unfertilized ELA lakes (from FEE, 1979: 10 lakes, 22 lake years). The numbers below the histograms designate lakes. 1-Lake 304; 2-South basin of divided Lake 226 (data shown here are not affected by a curtain breach that occurred in 1977); 3-Lake 261 (Lake 261 was terminated prematurely and also had an unusual macrophyte flora: D.W. SCHINDLER pers. comm. 2008); 4-North basin of divided Lake 226; 5-Lake 227; 6-Lake 303. All of the lakes were analyzed for 2 or more years. The data from Lake 226N (#4) are frequently cited as evidence for phosphorus limitation in lakes.

3.5. Experiments Beyond the Experimental Lakes Area

Intense interest in N and P limitation, stimulated to a large degree by the ELA studies, led to a geographically broad proliferation of experiments. By short and large, these studies consisted of enrichment of phytoplankton in bottles or small chambers over relatively short durations and involving enrichment with N, P, N + P, and sometimes micronutrients. In addition, whole-lake fertilization studies were done according to the ELA pattern at a number of locations.

ELSER *et al.* (1990) reviewed the accumulated experimental literature on N and P limitation through the 1980's. Based on enclosure experiments for 60 lakes, they showed that a growth response (increase in chlorophyll *a* or increase in carbon fixation) is equally likely for P enrichment or N enrichment, contrary to the prevailing notion that P is much more likely to stimulate growth response than N. They also showed that fertilization with P + N was more likely to produce a response than fertilization with either P or N alone, and that the P + N response was quantitatively stronger (about 2.5 \times). They postulated that the degree of response often is very similar for N and P at a specific time and place.

In surveying 80 lake years of experimentation on whole lakes, ELSER *et al.* (1990) concluded that experiments almost always involved addition of N + P for comparison with a control, rather than experimentation with P and N separately. Only 12 lakes had been fertilized with P and N separately, and only two showed a significant response (both to P). The separate treatment of P and N at ELA, as shown in Figure 4, was not included in the survey by ELSER *et al.* (1990).

ELSER *et al.* (1990) also offered an explanation for the apparent contradiction between bioassays on ambient phytoplankton communities and the U.S. Environmental Protection Agency's test for algal growth potential (MILLER *et al.*, 1978), which involves addition of P, N, and N + P to filtered lake water used for growing cultures of *Selenastrum capricornutum*. Such bioassays show a strong trend toward phosphorus limitation, in contrast to studies of field populations of phytoplankton. The *Selenastrum* bioassay is not a reliable indicator of the status of field populations. As shown much earlier (HUTCHINSON, 1957), laboratory algal

populations differ from field populations in their nutrient requirements. Furthermore, as proposed by ELSER *et al.* (1990), field populations may consist of a balance of species that makes efficient use of both N and P. This concept is supported by experimental evidence that algal taxa differ in optimal TN:TP ratios (SMITH, 1982; SUTTLE and HARRISON, 1988).

DOWNING and MCCAULEY (1992) tabulated information on TN:TP ratios from multiple sources ranging from forests and croplands to sewage. They argued that TN:TP ratios of the predominant sources of N and P in a given watershed will determine the TN:TP ratio in lakes within that watershed, and provided confirmatory statistical evidence from the literature. From a list of nutrient enrichment experiments over a wide range of TN:TP ratios, DOWNING and MCCAULEY also determined that TN:TP molar ratios below 30 are consistently indicative of N limitation according to available experimental data. The presumption of a limiting TN:TP ratio in earlier work had been considerably lower (*e.g.*, 12). Finally, DOWNING and MCCAULEY showed that increasing TP is associated with a declining TN:TP ratio, probably because watershed sources providing the highest TP concentrations tend to have low TN:TP ratios.

Oligotrophic lakes have been of special interest in the diagnosis of nutrient limitation because their TN:TP ratios are higher than ratios for polluted lakes. Experimental evidence has been inconsistent with this general conclusion. For example, MORRIS and LEWIS (1988) conducted repeated bioassays on eight montane lakes in Colorado. The results showed a close balance between N and P limitation in these lakes. Five categories of phytoplankton limitation were identified: no limitation, N limitation, P limitation, concurrent limitation (stimulation only by simultaneous additions of N and P), and reciprocal limitation (stimulation by addition of either N or P). The phytoplankton communities of three lakes were primarily N-limited, one was primarily P-limited, and four showed combined limitation (concurrent or reciprocal). Switching between categories of limitation was also observed within lakes, as it has been in other lakes (*e.g.*, EDMONDSON, 1972; WHITE *et al.*, 1977; 1985, LEWIS *et al.*, 1984; SOMMER, 1987; KÖHLER *et al.*, 2005). Nitrogen, either alone or in combination with P, accounted for 79% of all observed instances of limitation. Nine indices were tested for effectiveness in predicting phytoplankton limitation by N and P. The best chemical indices for discriminating all limitations were ratios of dissolved inorganic N:total P (84% accuracy) and dissolved inorganic N:total dissolved P (80% accuracy). The effectiveness of these indices may be explained by the degree to which they represent N and P fractions that are available to the phytoplankton. The observed parity of N with P limitation is consistent with other studies of oligotrophic lakes (*e.g.*, FEE, 1979; DODDS *et al.*, 1989), while the seasonal alternation of limiting nutrients as well as concurrent and reciprocal limitation are consistent with the concept that limitation by nitrogen and phosphorus often is closely balanced, especially in watersheds that are not strongly influenced by land use or nutrient disposal. High frequency of phytoplankton limitation by nitrogen in montane lakes also has been documented at other locations (DODDS *et al.*, 1989; LAFRANCOIS *et al.*, 2003; MCMASTER and SCHINDLER, 2005; WURTSBAUGH *et al.*, 1997; also see Fig. 5). Thus, while sparsely populated montane environments seemed the most likely prospect for predominance of P limitation, experimental evidence to date suggests that N and P are near parity in these environments. BERGSTRÖM and JANSSON (2006) have argued that significant atmospheric N pollution is reaching a large proportion of oligotrophic lakes (see also STODDARD, 1994). If many of these lakes were at one time N-limited, as seems likely now, some degree of change already may have resulted from modest N enrichment.

The range of algal responses to nutrient additions is shown in a compendium of experiments by WURTSBAUGH (Fig. 5). These experiments, conducted largely in relatively uncontaminated watersheds, demonstrate that nitrogen stimulated accumulation of chlorophyll more frequently than did phosphorus but, as expected, the addition of N and P together almost always provided the strongest stimulation. The frequent but small inhibition of chlorophyll concentrations by phosphorus additions in these experiments could be explained by

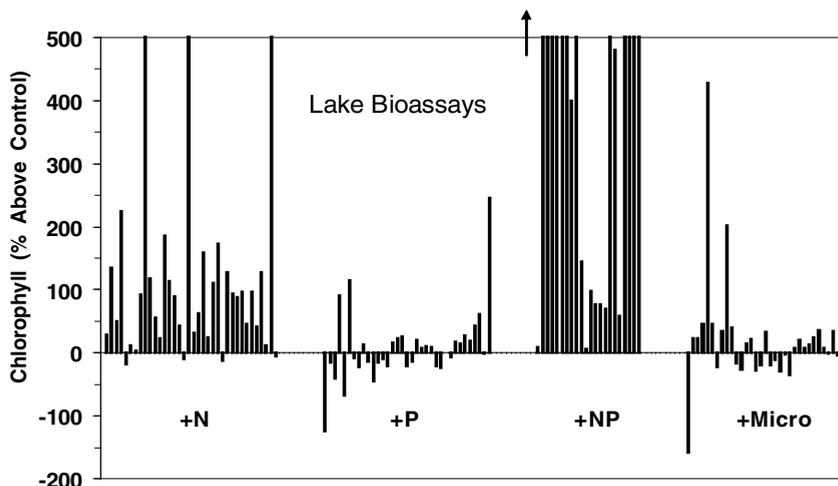


Figure 5. An example of geographically distributed laboratory and field bioassays for phytoplankton responses to nutrients in lake waters from western North America, Peru, and Spain. In these experiments, the laboratory incubations in flasks or field assays in 5–10 L mesocosms typically lasted 5–7 days. The micronutrient (+Micro) additions frequently tested iron limitation but mixed micronutrients were sometimes utilized. (Sources: WURTSBAUGH, 1988; WURTSBAUGH and HORNE, 1983; WURTSBAUGH *et al.*, 1985, 1997; CAMACHO *et al.*, 2003; MARCARELLI *et al.*, 2006 and some unpublished data of W. WURTSBAUGH).

the response of heterotrophic bacteria to phosphorus, and subsequent competition between the bacteria and phytoplankton for nitrogen or increases in phagotrophic predators on phytoplankton and bacteria (THINGSTAD *et al.*, 2005). Micronutrient additions were as likely as P to stimulate chlorophyll accumulation.

3.6. Nitrogen Deficiencies and N Fixation Across Ecosystems

In lakes, the co-limitation of phytoplankton production by N and P may resemble limitations in terrestrial and marine systems, where production is not limited by a single nutrient across broad temporal and geographical ranges (ELSER *et al.*, 2007). HEDIN *et al.* (2003), for example, showed that the nitrogen and phosphorus content of soils, which controls export of N and P to aquatic ecosystems, can show an increasing N:P ratio with age. Disturbances such as fires also can reset the N and P balance in forests by volatilizing accumulations of nitrogen in forest biomass and soils (LEWIS, 1974; MURPHY *et al.*, 2006), so that some ecosystems prone to fires may not export excess nitrate to streams and lakes.

Terrestrial ecosystems typically are unable to ameliorate nitrogen deficiencies fully through nitrogen fixation (VITOUSEK *et al.*, 2002). Similarly, there presently is no evidence for a consistently significant contribution of planktonic nitrogen fixation to oligotrophic and mesotrophic lakes. For eutrophic lakes showing N fixation in the plankton, the median contribution to total load that could be attributed to N fixation is near 22%, and the median fixation as a proportion of the total N necessary to support primary production is less than 5%, according to the data compiled by HOWARTH *et al.* (1988). Therefore, although HOWARTH *et al.* concluded that N-fixation offsets P deficiency, it seems clear that the potential offset is modest, in that N deficiency is likely to persist in most cases that lead to predomi-

nance of N fixers. For example, if a hypothetical lake had an N:P molar ratio of 10:1, implying nitrogen deficiency, a 25% boost in the N component would raise the ratio only to 12.5:1, which is unlikely to bring the lake into phosphorus deficiency. The reasons for the low compensatory potential of phytoplankton nitrogen fixers when phosphorus is abundant are unclear, but micronutrient limitation (WURTSBAUGH and HORNE, 1983), light limitation (LEWIS and LEVINE, 1984; VINER, 1985), and limitation related to the maximum sustainable ratio of heterocysts to vegetative cells (LEWIS and LEVINE, 1984) have been suggested. Nitrogen fixation by lake and stream periphyton appears to be less constrained than is fixation by phytoplankton (BERGMANN and WELCH, 1990; LEVINE and SCHINDLER, 1992; MARCARELLI *et al.*, 2008), but the underlying reasons are not well understood.

4. The Emerging Paradigm for N and P Limitation in Lakes

Experimental information on nutrient limitation of phytoplankton now shows that phytoplankton biomass accumulation is as likely to be limited by N as P. Even in unpolluted oligotrophic lakes instances of N and P limitation appear to be equally likely. The hypothesis that N and P enrichment together provide a stronger growth response in phytoplankton than either P or N alone is consistently confirmed, but the hypothesis that phosphorus limitation is consistently offset by N-fixation through cyanobacteria is not valid as a generalization. Although N deficiency in fertile waters often shifts community dominance to N fixers, this shift does not occur in most N-limited lakes of low to moderate fertility. Where it does occur, lakes typically remain N limited despite the presence of fixers.

As recognized early in the study of nutrient limitation, enrichment of lakes with strongly biased N:P ratios can induce either P or N limitation. In particular, N limitation is induced by substantial amounts of treated domestic wastewater or animal waste, which have low N:P ratios and high concentrations of P. Similarly, some lakes in industrialized Europe and North America may have been driven to P limitation by atmospheric deposition of nitrogen and the subsequent N-saturation of watersheds (STODDARD, 1994; BERGSTRÖM and JANSSON, 2006). In addition, some instances are known of high ambient P concentrations that can be traced to geologic sources. In these instances, N limitation is very likely (*e.g.*, WURTSBAUGH, 1988; JAMES *et al.*, 2003; BUNTING *et al.*, 2005; NRC 2004; LEWIS *et al.*, 2008). N limitation of phytoplankton also may be especially important in tropical or subtropical waters (THORNTON, 1987; LEWIS, 1996) and in saline lakes, possibly because evaporation magnifies P concentrations (TALLING, 1992) or because high sulfate concentrations enhance phosphate release from sediments (BLOMQUIST *et al.*, 2004), while denitrification is enhanced by warmth (DOWNING and McCAULEY, 1992; LEWIS, 2002).

Evidence of parity between N and P in the limitation of phytoplankton growth across inland waters as a whole supports a new N + P control paradigm for nutrient limitation that is much more consistent with the accumulated data than the original P control paradigm. Table 2 sets forth the components of the emerging N + P control paradigm for limitation of phytoplankton growth in inland waters.

The new paradigm is essential for an accurate depiction of the manner in which phytoplankton growth is limited in natural lakes and in lakes that are selectively enriched with biased N:P ratios. Even so, the key management principle for control of eutrophication in individual lakes remains the same as it was under the phosphorus paradigm: the most promising management tool for control of phytoplankton growth in most situations is restriction of phosphorus supply. It is also true in some instances, including principally those involving high background P concentrations, that suppression of total phosphorus load by manipulation of anthropogenic sources cannot suppress phytoplankton growth because the background phosphorus load is capable of saturating the P demand of an N-limited phytoplankton community (LEWIS *et al.*, 2008), or because internal loading of P offsets nutrient

Table 2. Components of the emerging N+P control paradigm.

N + P Phytoplankton Control Paradigm for Lakes
1. N and P are equally likely to explain nutrient limitation of phytoplankton in unpolluted lakes.
2. Temporal shifts in N and P limitation often occur, and concurrent or reciprocal limitation by N and P is common, especially among oligotrophic lakes.
3. Near parity between N and P control in many unpolluted or moderately polluted lakes influences development of phytoplankton communities with complementary N and P requirements, which explains concurrent and reciprocal limitation by N and P, as well as seasonal shifts in limitation.
4. Low N:P ratios combined with high P concentration often will shift phytoplankton composition to dominance by cyanobacterial N fixers.
5. Cyanobacterial N fixers do not fully offset N deficiency.
6. Significant anthropogenic bias in watershed sources of N and P can shift a lake toward N or P limitation.
7. Whether N or P limits biomass accumulation, restoration of individual polluted lakes is generally most feasible by restriction of P supply, which either tightens existing P limitation or induces P limitation in an N-limited lake. Interception of anthropogenic P may not be sufficient to induce P control of phytoplankton for lakes with naturally high P supplies or strong internal loading of P. Where atmospheric deposition of nitrogen increases the N:P ratios of large numbers of naturally N-limited lakes, reduction of N loading may be the only possible means of reversing changes in primary production or algal composition.

control (KALFF, 2002). Thus, the feasibility of inducing P deficiency must be evaluated on a case-by-case basis. Also, the occurrence of widespread N enrichment of lakes through atmospheric transport of anthropogenic fixed N cannot be offset by P restriction, as it involves entire landscapes rather than individual lakes. Prevention of broadly distributed changes in lakes by N enrichment can only be achieved by suppression of the atmospheric source of fixed nitrogen.

There remain many issues to be studied as the new paradigm solidifies. Perhaps most interesting is the tendency of oligotrophic lakes in montane environments with low atmospheric nitrogen contamination to show high probability of N limitation for phytoplankton growth. Another is the common failure of heterocystous cyanobacteria to take full advantage of excess phosphorus in many cases, including lakes of high productivity but consistent N limitation and weak or erratic growth of heterocystous cyanobacteria (LEWIS *et al.*, 2008). In addition, the question of micronutrient limitation remains unresolved. The most parsimonious explanation for nutrient limitation at present is achieved without any reference to micronutrient limitation. It is possible, however, that micronutrient limitation comes into play through the unequal requirements of individual species for specific micronutrients, which might explain small or sometimes substantial response of phytoplankton communities to micronutrient enrichment (Fig. 5). Nutrient limitation of periphyton in lakes has not been thoroughly studied; periphyton may influence nutrient availability to phytoplankton in small lakes (LEVINE and SCHINDLER, 1992; AXLER and REUTER, 1996). Finally, there is much yet to be known about the ability of natural phytoplankton communities to conform in species composition to specific N:P ratios, as foreseen by PEARSALL in the 1930s.

Continuing global mobilization of nitrogen and phosphorus by anthropogenic activities (VITOUSEK *et al.*, 1997) and increasing demands on freshwater resources are causing changes in the balance of limiting nutrients in the world's lakes. Knowledge of the effects of N:P ratios on algal growth, species composition, and nitrogen fixation will be required for effective management of inland waters.

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Looking for Surprise in Managing Stressed Ecosystems

Orie L. Loucks

Both natural and anthropogenic sources of stress can produce unanticipated and unprecedented ecosystem responses, such as a new equilibrium with long-term effects. Ecosystem models that simulate the prospective outcomes of management help to analyze responses to stress mitigation but cannot usually anticipate surprises—the emergence of new stable states. In managing stressed systems, we should therefore consider both what we predict and what we cannot predict.

integrated, iterative management approach.

Clearly, the options chosen will be influenced by the scale of the system to be manipulated, on how much is known about it, on the time required to observe a response, and on the potential for natural background variability or stochastic processes to produce significantly altered states while management is underway. This paper explores the third alternative above to illustrate how close (or how far) we are from holistic management of stressors in some systems. Along the way, I will illustrate a few of the pitfalls associated with our still incomplete understanding of ecosystems.

CASE STUDY: A LAKE/LITTORAL ZONE ECOSYSTEM

Shallow-water macrophyte wetlands (Cowardin et al. 1979) include a wide range of plant community types—from the sparse *Isoetes* and *Potamogeton* of oligotrophic lakes to the almost impenetrable beds of submerged macrophytes that can clog eutrophic lakes. The introduced Eurasian milfoil *Myriophyllum spicatum* and several other species often occur as aggressive nuisances and have been particularly competitive with native species as *Vallisneria americana* and *Potamogeton* spp. (Carpenter 1979). Because the fast-growing *Myriophyllum* greatly alters the characteristics of the littoral zone and adjacent shallow lakes, it can be viewed as a stressor of these ecosystems. Physical removal of the macrophyte would reduce the stressor directly, but it is also viewed as a means

A look back over the first decades of research on ecosystems tells us, with all the benefit of hindsight, that few of the systems studied were free of the anomalous inputs or altered conditions that we today identify as incipient stress (Auerbach 1981, Barrett and Rosenberg 1981). Most often, effects from logging, grazing, cultivation, or the introductions of exotic plants, fish, or insects had little consequence for the early questions about ecosystem function. Applying the principles that emerged from the early studies to managing stressed ecosystems, however, requires a reassessment.

Over some 15 years we have come to think of relatively catastrophic events like shoreline destruction by storms (Levin and Paine 1974) and recurring fire (Bormann and Likens 1981, Loucks 1970) as part of the normal renewal process for disturbance-dependent ecosystems. We are now coming to realize that the prevention of such disturbances (thus allowing dominance by climax-adapted species) is itself a stressor that can produce an unprecedented as well as unpredictable ecosystem (West et al.

1981). Various studies are now leading us to consider multiple stable states for ecosystems and to examine the circumstances—sometimes serendipitous and sometimes due to stressors—that produce relatively long-term changes in system equilibrium (Holling 1985). Our incomplete knowledge of the systems involved and the stochastic nature of certain processes imply that surprise will be a continuing part of resource management.

My goal in this article is to examine the efficacy of relatively holistic tools—ecosystem models—for guiding the management of altered ecosystems. The approaches available are few, and none is entirely satisfactory:

- Consider qualitatively the effects of one to several stressors acting on the system and identify management steps likely to bring about a new, target state for the system.
- Proceed iteratively with a series of management steps, observing the response to each one (if time permits), with the goal of establishing a new target state.
- Using a comprehensive computer model, examine the likely response of the stressed ecosystem to each of a series of management manipulations.
- Do all of the above together in an

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of physically removing some of the excess phosphorus from the system. Thus, weed harvesting has frequently been proposed as a lake management strategy for controlling both the plant nuisance and the level of eutrophication in the lake. To address questions about our potential to manage and mitigate the effects of exotic aquatic macrophyte beds, the University of Wisconsin, with support by NSF, sponsored a conference on the effects of macrophyte harvesting (see Breck et al. 1979). This paper draws on information presented at that conference and on new information since then to consider problems in evaluating stressor management strategies for altered lake ecosystems.

Submersed macrophytes are recognized now as playing an important role in lake nutrient cycles, particularly the phosphorus cycle (Breck et al. 1979). A large portion of the phosphorus content of *Myriophyllum* is taken up through shallow roots in the sediment. Measurements from Lake Wingra, Wisconsin, showed that 73% of plant uptake is from sediment (Smith 1978) rather than from the water column. In addition, dissolved P, and possibly N, is released to the surrounding water in relatively large quantities when macrophytes senesce. Excretion of nutrients from healthy macrophyte tissue, however, is negligible.

The relationship between phytoplankton and macrophytes in shallow lake systems is evident in comparing data from Lake Wingra and four other North American lakes (Devol and Wissmar 1978). Apparent phytoplankton use of phosphorus input to the lakes can be estimated as the ratio of phytoplankton production (C_p) to effective phosphorus loading (P/t_w), where P is the allochthonous phosphorus load and t_w is water replacement time. The ratio $C_p t_w : P$ represents the unit production of phytoplankton per unit effective phosphorus load. Under the assumptions of eutrophication models that include total phosphorus loading, this ratio should vary little among lakes. But in fact, the ratios for the five lakes in question differ greatly (Table 1), suggesting that the presence of an aggressive exotic macrophyte might so alter nutrient availability that an entirely new system with a new equilibrium is produced.

Another question, however, concerns the consequences of increasing or decreasing macrophyte cover for fish and invertebrate populations. Normally, a reduction in macrophyte height and density results in reduced cover for small

fish, which are the prey of piscivores and heavy feeders of invertebrates in the water column and on the macrophyte stems. The net effect of macrophyte harvesting for primary and secondary consumers, therefore, depends on the relative effects of such removals on each of the trophic levels involved.

Because changes in macrophyte density also affect cover for the invertebrate prey of fish, invertebrate-feeding fish should be more effective predators after macrophyte density is reduced by harvesting. Crowder and Cooper (1979) provide data from experimental ponds showing that when macrophyte growth is too dense, fish cannot forage effectively for macroinvertebrates. When macrophytes are too sparse, foraging is so effective that fish decimate the preferred, large invertebrates and subsequently grow more slowly on the small prey that remain. An intermediate macrophyte density provides sufficient cover for the preferred invertebrate prey so that the fish do not overexploit them, yet leaves enough open space for the fish to obtain preferred prey.

At another level of analysis, changes in macrophyte density also could have large, indirect effects on zooplankton, thereby reinforcing establishment of an altered stable state in an exotic-dominated ecosystem. Fish that consume invertebrates generally prefer benthos and macroinvertebrates on vegetation over zooplankton, and they prefer large zooplankton over small. As preferred prey become less available, fish will consume more of the less-preferred prey (Werner and Hall 1979). Considering only planktivorous fish, this analysis suggests that lakes with either very dense or very sparse littoral vegetation should have intense predation on the larger zooplank-

ton, and the average size of the zooplankton should be relatively small. If harvesting dense macrophyte beds increases the effectiveness of piscivores and thus reduces the number of planktivores, as suggested by Breck and Kit-chell (1979), the predation pressure on zooplankton would be reduced. This would lead to an increase in the average size of pelagic zooplankton, a result that would be enhanced if weed harvesting made the preferred macroinvertebrates (associated with the vegetation) more available to the forage fish.

A second consumer-related issue concerns the consequences for changes in P remineralization due to changes in the consumer community following macrophyte harvesting. Because planktivorous fish are highly size selective, a decrease in the intensity of predation on zooplankton leads to an increase in the mean size of zooplankton. This shift, in turn, would have important consequences for decreasing the rate of phosphorus remineralization by zooplankton and for altering the grazing pressure on phytoplankton. Peters and Rigler (1973) demonstrated that the P remineralization rate per gram of zooplankton is an allometric function of body size: Small zooplankton excrete P at a much greater rate per gram dry weight than large zooplankton. If a reduction in planktivorous fish, as outlined above, causes an increase in the mean size of zooplankton, then the average gram of zooplankton will remineralize P at a lower rate. In Bartell and Breck's (1979) simulations, reducing fish predation led to an increase in mean zooplankton size, an increase in total zooplankton standing crop biomass, and a decrease in P turnover time.

The size shift in zooplankton and possible changes in total biomass also influ-

Table 1. Total carbon fixed, phosphorus used, and aquatic macrophyte production in five North American lakes. See text for abbreviations. Source, in part: Devol and Wissmar (1978).

	C_p g Cm ⁻² yr ⁻¹	t_w yr ⁻¹	p g Pm ⁻² yr ⁻¹	Macrophyte production g Cm ⁻² yr ⁻¹	$C_p t_w / P$
Macrophyte-poor lakes					
Lake Findley	2.5	7	0.2	0	88
Lake Marion	5	76	12	32	33
Mirror Lake	38	1	0.15	2.8	253
Mean					124
Macrophyte-rich lakes					
Lake Lawrence	43	1.3	0.1	88	599
Lake Wingra	430	2.1	0.96	120	941
Mean					770

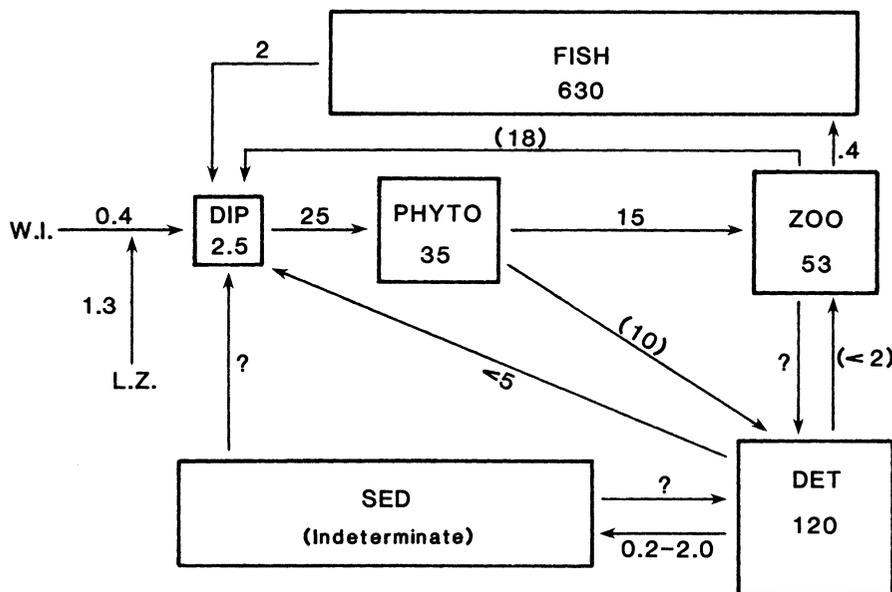


Figure 1. Summary of the pools and fluxes of phosphorus in Lake Wingra during late summer. Pools are $\text{mg} \cdot \text{m}^{-2}$ and fluxes are $\text{mg} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$. Inflows come from the watershed (W.I.) and from the littoral zone (L.Z.). Data were compiled from direct measurements except those in parentheses, which are indirect estimates. Source: Loucks and Weiler (1979).

ence the phytoplankton directly (and therefore the perceived ecosystem water quality) by altering grazing pressure on phytoplankton. Bartell and Breck's (1979) simulations show a shift to smaller phytoplankton when there is little planktivory and when the mean size of zooplankton is relatively large. Over a wide range of fish predation intensities, however, they found little difference in peak algal biomass. Macrophyte harvesting, the proposed stressor management strategy, thus appears likely to increase piscivory, reduce predation on zooplankton, create a size shift to larger zooplankton, reduce P remineralization by zooplankton, shift the size distribution of phytoplankton, and induce decreased total P uptake by phytoplankton.

SIMULATING STRESS MANAGEMENT OPTIONS

My colleagues and I looked at the effects of N and P remineralization following macrophyte removal using a lake ecosystem model to simulate P cycling and the responses of algae and consumers in the presence of whole-lake processes (Loucks and Weiler 1979). The site of an intensive study of lake and watershed relationships for several years, Lake Wingra has an extensive, well-documented data base on the dynamics of the P pools in the ecosystem as well as the inputs and losses (Loucks et al. 1977). Using direct measurements of P concentrations, biomass pools, average content of phosphorus in various

tissue, and other estimates of the rates of feeding and remineralization, one can make a preliminary computation of phosphorus pools and fluxes in Lake Wingra. Such data show that fish comprise the largest active pool of phosphorus in the system, second only to the large but undifferentiated and relatively inactive pool in the sediment. By far the largest daily transfer, however, is from the relatively small dissolved inorganic phosphorus (DIP) pool to the phytoplankton. Remineralization from detritus and from zooplankton are the two largest sources of this daily P uptake. The two smaller contributions to the DIP pool come from external watershed sources and the littoral zone (Prentki 1979).

The potential for changes in nutrient processing to produce a substantially different system equilibrium is evident in Figure 1. Phosphorus pumping and release from the macrophytes, $1.3 \text{ mg} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$, is three times the average daily watershed input of P. A small (10%) change in zooplankton remineralization of P ($18 \text{ mg} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$) would produce an even larger alteration in P availability.

These relationships suggest one might investigate the potential for external intervention to control the magnitude of phosphorus flux from aquatic beds. If the littoral zone is an important day-to-day source of phosphorus that could be altered by a manipulation such as harvesting, and if the remineralization of P by zooplankton also is reduced through the increased pressure of fish on zooplankton (Breck and Kitchell 1979), the amount of DIP available for phytoplankton would be greatly reduced.

The WINGRA III ecosystem simulation model (Weiler et al. 1979) provides a means of making such computations for a series of treatment hypotheses associated with macrophyte harvesting. In this model the dynamics of the pelagic zone are represented through solutions over time of 49 state variables, or pools, in the ecosystem. The behavior and validity of the WINGRA III model have been evaluated against a broad spectrum of in-lake response measurements.

Evaluating the effects from macrophyte harvesting must begin with an examination of the DIP sources within the system. The sources of DIP include the conventional external sources (hydrologic and dryfall inputs, both of which are small) and releases from the littoral zone, zooplankton, suspended detritus, and bottom sediments (all of which are large in comparison, Table 2).

Table 2. Nominal simulation of remineralized P compared to amounts following 50% reduction (harvesting removal of waterborne P inputs) for 28 July 1979, a representative midsummer day. Source: Loucks and Weiler (1979).

DIP source	Estimated daily DIP additions			
	Nominal simulation $\mu\text{g l}^{-1} \text{ day}^{-1}$	%	Reduced loading (A) $\mu\text{g l}^{-1} \text{ day}^{-1}$	%
P release from littoral zone	0.542	17.5	0.542	19.8
Waterborne P inputs	0.035	1.1	0.021	0.8
Dryfall P inputs	0.009	0.3	0.009	0.3
Zooplankton P remineralization	1.230	39.8	1.003	36.7
Benthic insect P remineralization	0.001	0.0	0.001	0.0
P remineralization by fish	0.004	0.1	0.060	2.2
P remineralization by suspended detritus	0.800	25.9	0.698	25.5
P remineralization by bottom detritus	0.472	15.3	0.402	14.7
TOTAL	3.093	100.0	2.736	100.0

We evaluated the consequences of one management approach—simple physical removal of P in an average 50% harvest of the macrophyte biomass—by several additional simulation runs, each incorporating changes in inputs or processing rates to reproduce the whole-system equivalent of the harvesting treatment. The first of these simulations (A, Table 2) presents the hypothesis that the physical removal of P by harvesting could be viewed as the equivalent of a once-only reduction in P loading. Only small differences from the nominal case are evident.

In a second treatment hypothesis (B, Table 3), the daily rate of DIP input from the littoral zone has been cut to 50% of the nominal amounts throughout the simulation period. This decreases the P coming into the pelagic zone by 87 kg during the simulation. Although the effect on total P remineralization is roughly similar in spring and summer, this treatment has greater percentage influence in the spring.

A third treatment hypothesis is shown in C, Table 3. In this run the rate of DIP input from the littoral zone has also been cut in half, but in addition, the zooplankton parameters have been changed to represent the reduced P-cycling rates of larger species anticipated as part of the whole-system response. The total P remineralized ($1.934 \mu\text{g} \cdot \lambda^{-1} \cdot \text{day}^{-1}$) is appreciably below that of treatments A or B—about two-thirds of the nominal case.

Although other treatments were considered (see Loucks and Weiler 1979), an important hypothesis is that the effect of decreasing P releases from the littoral zone and from zooplankton would not preclude an effect through physical phosphorus removal (as expressed through a decrease in external P loading). Thus, a final treatment hypothesis (Table 4) considered together all the parameter changes for the reduced loading treatment, as well as the maximum littoral zone and zooplankton reductions.

Table 5 summarizes the magnitude of the reductions in P remineralization, in $\mu\text{g} \cdot \lambda^{-1} \cdot \text{day}^{-1}$ and as percentages below the nominal model calculations, for five simulation treatments. Given the spectrum of treatment hypotheses and the fundamental importance of changes of 10–40% in daily remineralized P, a substantial potential seems to exist for reducing the eutrophication in Lake Wingra through weed harvesting. A reduction in daily P availability in the range of 30% seems probable, with a maximum of 40–60%.

Table 3. Responses from two additional simulations of harvesting effects on remineralized P for 28 July 1979.

DIP source	Estimated daily DIP additions			
	50% of littoral zone inputs (B)		50% of littoral zone inputs and maximal zooplankton reduction (C)	
	$\mu\text{g} \cdot \lambda^{-1} \cdot \text{day}^{-1}$	%	$\mu\text{g} \cdot \lambda^{-1} \cdot \text{day}^{-1}$	%
P release from littoral zone	0.271	11.5	0.271	13.7
Waterborne P inputs	0.035	1.5	0.035	1.8
Dryfall P inputs	0.009	0.4	0.009	0.5
Zooplankton P remineralization	0.930	39.4	0.469	23.5
Benthic insect P remineralization	0.001	0.0	0.001	0.1
P remineralization by fish	0.116	4.9	0.131	6.6
P remineralization by suspended detritus	0.626	26.5	0.659	33.2
P remineralization by bottom detritus	0.372	15.8	0.409	20.6
TOTAL	2.360	100.0	1.934	100.0

DISCUSSION

Projected responses obtained from simulation models of lake/watershed interactions should not be taken as explicit forecasts of events following management treatments. Rather, simulation results enable us to consider the mechanisms integrating an altered ecosystem systematically and to compare measures of the magnitude of prospective consequences.

Simulation results suggest that several aspects of managing whole ecosystems have been previously overlooked. Linkages in the system are such that the effect from a manipulation is as likely to be magnified as to be damped or to disappear; the problem is in trying to anticipate the direction and magnitude of such responses when no comprehensive

Table 4. Simulated effects of harvesting on daily DIP additions from all sources (28 July).

DIP source	Estimated daily DIP additions	
	$\mu\text{g} \cdot \lambda^{-1} \cdot \text{day}^{-1}$	%
P release from littoral zone	0.271	15.4
Waterborne P inputs	0.021	1.2
Dryfall P inputs	0.009	0.5
Zooplankton P remineralization	0.365	20.6
Benthic insect P remineralization	0.001	0.1
P remineralization by fish	0.186	10.6
P remineralization by suspended detritus	0.567	32.1
P remineralization by bottom detritus	0.343	19.5
TOTAL	0.763	100.0

Table 5. Estimated reduction in daily P remineralization from five simulation treatments.

	Differences from nominal simulation* in total daily DIP additions			
	Spring		Summer	
	$\mu\text{g} \cdot \lambda^{-1} \cdot \text{day}^{-1}$	%	$\mu\text{g} \cdot \lambda^{-1} \cdot \text{day}^{-1}$	%
Reduced loading (removal)	0.63	32	0.35	11
50% reduction in littoral zone inputs	0.68	34	0.73	24
50% reduction in littoral zone inputs and maximal zooplankton reduction	1.34	68	1.09	35
25% reduction in littoral zone inputs and 50% maximal zooplankton reduction	0.81	41	0.56	18
Combined loading, littoral zone, and zooplankton reductions	1.44	73	1.33	43

*See Table 2.

body of knowledge about the system exists.

In the case of Lake Wingra, however, another observation is most significant: Before weed harvesting could be done, the *Myriophyllum* population declined dramatically for unknown reasons, possibly a natural succession to several native aquatic macrophyte species. Processes acting over a longer term than could be represented in the manager's experience, or in an ecosystem model, appear to have become dominant, and the system shifted to a new equilibrium. Some of the higher efficiencies in the cycling of P, as reflected in the analysis of manipulative options, are imbedded in the new system, although not as a consequence of the proposed stress management. Thus, modeling and analyzing the system provided a fuller explanation of what happened as the system itself changed to a new equilibrium.

How should the biologist or resource manager interpret this further illustration of the ecological paradox: beginning at state A, and with a manager targeting state B, the system moves to state C? Presumably these are the surprises of the type Holling (1985) has discussed. Surprise responses are not new in resource management; they may have been less frequent or less dramatic in only mildly stressed ocean, range, or forest systems a century ago, but given the then-meager experience for anticipating responses, the unexpected was also common. Frustration among resource managers may be high now because, despite more quantitative understanding of ecosystem processes, the prevalence of transient states or unstable equilibria (due to mid- and long-term effects of stressors) has made it more difficult than ever to anticipate the secondary consequences of stress management.

One conclusion might be that the management of stressed ecosystems is, at best, guesswork—a fool's paradise. Nature is both diverse and perverse, and we delude ourselves if we seek to manage. However, some stressed systems, such as the Great Lakes, have responded to stressor management. A second conclusion is therefore equally plausible: that quantitative examination of ecosystem responses around a supposed equilibrium state can be insightful and can assist in evaluating stress management strategies. However, management measures should be considered in the larger framework of longer-term successional or bio-

geochemical changes that could interact with the changes needed to achieve a target state. Neither the system-specific nor the larger-framework assessment can be viewed as truly predictive, and neither can stand alone. For well-documented ecosystem types, comparative analysis of possible responses probably provides a stronger basis for proposing management strategies and dealing with subsequent surprise than do conventional prescriptions alone.

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Algal blooms: Noteworthy nitrogen

NUTRIENT OVER-ENRICHMENT in lakes drives water-quality deterioration. The August 2014 water supply shutdown from Lake Erie to over 500,000 residents in Toledo, Ohio (1), highlights this problem, which has been historically addressed by controlling phosphorus (P) inputs. Management and research are based on the premise that P is the limiting factor in freshwater productivity and harmful algal bloom (HAB) formation (2, 3). However, reducing P is no longer adequate for many lakes. Recent studies indicate algal proliferation in response to combined nitrogen (N) and P additions, or in some cases, the addition of only N (4–8). This shift in the freshwater nutrient management paradigm has important implications.

The toxic cyanobacterial genus *Microcystis* often dominates in nutrient-sensitive systems despite P-focused controls. Members of this genus cannot fix atmospheric N_2 (i.e., convert N_2 to ammonia), so they require combined N sources (such as ammonium, organic N, or nitrate) to support growth. Burgeoning usage of N fertilizers, urban and agricultural N wastes, and atmospheric N deposition have increased bioavailable N in receiving waters (9). This global pattern coincides with growing eutrophication issues, especially toxic, non- N_2 -fixing cyanobacterial blooms, as exemplified by China's third-largest lake, Tai; in 2007, massive *Microcystis* blooms cut off drinking-water supplies to approximately 10 million local residents (10).

N occurs in gaseous forms, unlike P, and N is "lost" to the atmosphere through denitrification and other N sinks, whereas P is recycled internally (along with some N), perpetuating N-limitation (8). In-lake N_2 fixation does supply bioavailable N, but this input does not compensate for N loss (8, 11). External N input is thus a key driver of eutrophication. Therefore, the "P-only" management paradigm should be amended to incorporate N-driven eutrophication and HAB abundances.

New nutrient reduction strategies should incorporate point and non-point sources, including N removal in wastewaters, optimization of fertilizer application, and erosion controls. This



Bloom of the toxic, non- N_2 -fixing cyanobacteria *Microcystis* spp. in eutrophic Lake Tai, China.

investment in joint P and N controls will counter the very high costs of HAB events and losses of freshwater resources in Toledo and worldwide.

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Algal blooms: Proactive strategy

CYANOBACTERIAL HARMFUL algal blooms (CHABs) are increasing in severity on a worldwide basis. Combining nutrient-source control with post-bloom control is currently considered the best strategy for dealing with CHABs (1). However, huge investments in this strategy have proven

ineffective in China, as demonstrated by yet another massive bloom last summer in Lake Tai despite over 100 billion RMB (more than US\$16.25 billion) invested since 2007 (2). Further afield, four decades of strict phosphorus loading regulations have not prevented massive CHAB events in Lake Erie of the Laurentian Great Lakes of North America and the adjacent water bodies (3).

The current strategy apparently has limited effectiveness. Furthermore, nutrient-source control may not be feasible for many developing countries because of increasing population pressure and pollution, and elevated CO_2 influx into aquatic systems and climate change will intensify algal blooms (4). Once CHABs have occurred, even the most effective methods to date of removal of cyanobacteria and cyanotoxins cannot eliminate their adverse impacts on ecosystems and human health (5).

We firmly believe that the missing key component in the current strategy is proactive CHAB control. By implementing this approach over the past 15 years, we have achieved effective long-term prevention of CHABs in several severely eutrophic lakes and reservoirs in Eastern China (6), thus showing that this approach is entirely possible and practical. Our strategy also affords valuable time for the implementation of nutrient-source control.

Proactive CHAB control requires appropriate technical expertise aimed at inhibiting algal growth during the spring season, when cyanobacteria is vulnerable to foraging species. This would involve developing new tools to trace pre-bloom algal distribution so that proactive treatments only need to be implemented within algae concentrated areas and in a cost-effective manner. Continuous monitoring and assessment of water bodies would maximize treatment efficacy.

Moreover, supportive laws and government policies are necessary. In particular, governments from different jurisdictions should reallocate resources to where CHABs originate; implement an appropriate merit system for proactive CHAB prevention and other measures related to eco-service enhancement; and curtail counterproductive human practices such as illegal fishing by enhancing law enforcement and providing alternative livelihoods and social learning to affected communities.

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Ocean acidification foils chemical signals

THE CRUCIAL IMPORTANCE of chemical cues to reef resettlement was elegantly demonstrated by D. L. Dixon et al. ("Chemically mediated behavior of recruiting corals and fishes: A tipping point that may limit reef recovery," Research Article, 22 August, p. 892). Similarly, waterborne chemical signals (pheromones) and cues are essential for mediating marine species' behaviors, including those associated with mating, foraging, recruitment, and alarm (1).

Responses to these chemical signals and cues are in danger of global disruption by the effect of rising atmospheric CO₂ levels on aquatic pH. At current rates, ocean pH will drop from the current and historic pH of 8.15 to 8.25 to about 7.8 or below by 2100 (2). Quite apart from effects on calcification, reduced pH has the capability to affect both the signaling (semiochemical) molecules themselves and their interaction

with chemosensory receptor proteins. The interaction of semiochemical ligands with chemosensory receptors changes with pH, through the number, type, and alignment of intermolecular forces (e.g., hydrogen bonding, electrostatic potential, and hydrophilic/hydrophobic regions) on both ligand and chemosensory receptor (3, 4). Examples of the pH-affected semiochemicals are pheromones and cues, including peptides, nucleosides, thiols, and organic acids in nereid polychaete worms, *Aplysia* sea hares, crustaceans, and fish (3).

The current rate of oceanic pH decline is occurring faster than chemosensory systems can evolve; today's systems have evolved over 50 million years under relatively constant pH (2). Every marine species, at every trophic level, is potentially affected by disruption of chemical cues and signals, including responses to predator odors [e.g., (5)], sexual reproduction, sperm attraction, fertilization, social interactions, feeding, and larval settlement (1). Studies into not only the effects of disruption but also the mechanisms of action and resulting predictive ecological models are urgently needed. We risk widespread ecosystem damage by this additional silent danger from rising anthropogenic CO₂ levels.

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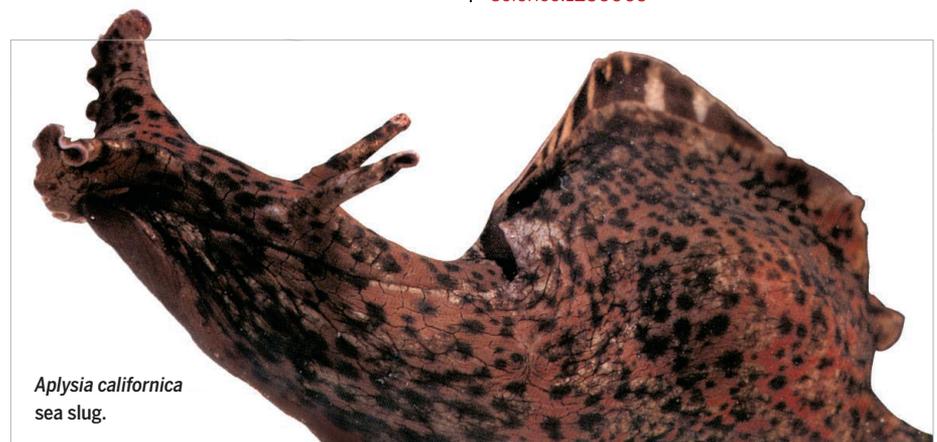
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Aplysia californica
sea slug.

TECHNICAL COMMENT ABSTRACTS

Comment on "Oxytocin-mediated GABA inhibition during delivery attenuates autism pathogenesis in rodent offspring"

Victorio Bambini-Junior, Gustavo Della Flora Nunes, Tomasz Schneider, Carmem Gottfried

■ Tyzio et al. (Reports, 7 February 2014, p. 675) reported that bumetanide restored the impaired oxytocin-mediated γ -aminobutyric acid (GABA) excitatory-inhibitory shift during delivery in animal models of autism, ameliorating some autistic-like characteristics in the offspring. However, standard practices in the study of these models, such as the use of sex-dimorphic or males-only analyses and implementation of tests measuring social behavior, are lacking to definitely associate their findings to autism.

Full text at <http://dx.doi.org/10.1126/science.1255679>

Response to Comment on "Oxytocin-mediated GABA inhibition during delivery attenuates autism pathogenesis in rodent offspring"

Sanaz Eftekhari, Amene Shahrokhi, Vera Tsintsadze, Romain Nardou, Corinne Brouchoud, Magali Conesa, Nail Burnashev, Diana C. Ferrari, Yehezkel Ben-Ari

■ Bambini-Junior et al. questioned whether our treatment in two rodent models of autism has a long-lasting effect into adulthood. In response, we show that bumetanide treatment around delivery attenuates autistic behavioral features in adult offspring. Therefore, the polarity of γ -aminobutyric acid (GABA) actions during delivery exerts long-lasting priming actions after birth.

Full text at <http://dx.doi.org/10.1126/science.1256009>

An invasive exotic grass reduced sedge meadow species richness by half

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Abstract A debate over the impacts of invasive plants is fueled by varied terminology, ecosystem types, response metrics, and conflicting evidence across scales. We quantify the effects of invading *Phalaris arundinacea* (Pa) on species richness and abundance in Wisconsin sedge meadows dominated by *Carex stricta* (Cs). Among species area curves from four nested plots (0.25, 1, 4, and 16 m²) in seven sites, Pa stands averaged 48 % fewer species than the adjacent Cs. Species richness was reduced by about half regardless of plot size. Total richness for Pa stands was 50 species compared to 83 for Cs, and Pa stands had consistently lower additive percent cover of subordinate species at all scales. However, resident species responded differentially to Pa invasion. Only one species, *Calamagrostis canadensis* (a tall clonal grass), had similar importance values (using cover and frequency) in Cs and Pa stands at 0.25 and 16-m² scales. Other species declined with Pa invasion, mostly in frequency. Despite losing half of their resident species, sites did not differ significantly in

their native exotic richness relationship (NERR). NERR confounds the effects of invasiveness with species' origins, and it under-represents impacts of dominant invaders in wetlands. Debates should be fewer if studies specify if the invader is exotic or native, type of invaded ecosystem, the metric used to assess responses, and the spatial scale.

Keywords Native · Exotic · Species richness · Invasive plant · Species-area curve · NERR

Introduction

A debate in invasion biology is based in part on whether or not invasive plants reduce native plant diversity (e.g., Shea and Chesson 2002; Fridley et al. 2007; Davis et al. 2011). Many studies conducted at larger spatial scales have found positive correlations between native and exotic plants (Sax et al. 2002; Hulme 2008), while studies at smaller scales have shown positive, negative, or no such relationships (Rojas et al. 2011; Bennett et al. 2012; Brooks et al. 2013).

The debate over invasive species effects is difficult to resolve because effects of invaders also differ with the terminology (invasive vs. exotic), the type of ecosystem (upland or wetland), and the metric used to assess responses of native vegetation (Richardson et al. 2000; Colautti and MacIsaac 2004). Species that are invasive include, but are not restricted to, exotic plants. For some invasive species, origins are

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uncertain, while ecological aggressiveness is well known. This is notable for *Phragmites australis*, whose multiple origins were only recently clarified (Meyerson and Cronin 2013) and for *Phalaris arundinacea* (hereafter Pa), which has native populations in North America, although most subpopulations are a European strain (Jakubowski et al. 2013, 2014).

Invaders that become dominant can exert strong influence on productivity, canopy strata, nutrient cycling, and soil properties of a community through their abundance, height, shade, belowground biomass, and chemistry (Chapin 2003; Hooper et al. 2005; Simberloff 2011). Such impacts are especially true for wetland ecosystems. Wetlands that occur in the sinks of watersheds are vulnerable to invasions because they accumulate runoff, nutrients and sediments, and propagules of potential invaders. Such conditions facilitate the establishment and expansion of invaders (Galatowitsch et al. 2000; Zedler and Kercher 2004; Kercher et al. 2004, 2007). Invaders can increase biomass production while on-site retention of nutrient and plant richness decrease (Doherty et al. 2014). Despite major effects of dominant invaders in wetland ecosystems, invasions are less studied here than in uplands. Of 1,637 papers reviewed by Lowry et al. (2013), ~1,200 addressed terrestrial ecosystems, while fewer than 100 focused on wetlands.

The most common metric used to test the impact of exotic species has been the “native-exotic richness relationship” (NERR), based on observations (e.g., Stohlgren et al. 2006; Brooks et al. 2013), experiments (e.g., Sandel and Corbin 2010), meta-analysis (e.g., Hulme 2008) and simulations (Fridley et al. 2004). Recent work used the NERR to compare different management options in restored sites (Hill and Fischer 2014). The NERR has also been used to test the scale-dependent effects of invaders. The range of scales used on these studies varies within 0.5 to 7500 m² (e.g., Symonds and Pither 2012; Brooks et al. 2013). Studies are usually scaled up to landscapes by combining areas from multiple sites. The NERR, however, does not consider the effect of a single invasive species as it enters a community and becomes a monotype dominant (displacing other species, sensu Frieswyk et al. 2007). Studies that improve our understanding on how these single invaders that enter in a community can modify its biodiversity are necessary (Simberloff et al. 2013).

Our main goal is to quantify how a dominant wetland invader (Pa) affects resident sedge meadow

species across four plot sizes, among sites and for all-sites in south central Wisconsin. We ask: (1) Does Pa have an effect on plant diversity across plot sizes? (2) Do subordinate species respond differentially to Pa invasion? To answer these questions, we sampled seven sedge meadows being invaded by Pa, while aiming to help resolve the broader invasive species debate by clarifying terms, considering habitat types and comparing metrics for assessing effects.

Methods

Choice of invader and ecosystem

Pa is considered a model invader for the study of invasion (Lavergne and Molofsky 2004); it is also Wisconsin’s “worst wetland weed” (Hatch and Bernthal 2008). This cool season perennial clonal grass reproduces from seed, rhizome tillers and branch fragments; exhibits morphological plasticity; inhabits a wide range of wetland habitats; and occurs across the temperate regions of North America (Maurer and Zedler 2002; Lavergne and Molofsky 2004; Adams and Galatowitsch 2005; Herr-Turoff and Zedler 2007). Introduced European strains and agricultural varieties have hybridized with the native genotype, creating an aggressive plant that leaves little soil space and light for other species (Merigliano and Lesica 1998; Galatowitsch et al. 2000; Perry and Galatowitsch 2003; Lavergne and Molofsky 2007). Rhizomes can subsidize shoots where light is limiting, as under the thick litter, leading to a positive feedback for invader growth (Maurer and Zedler 2002; Eppinga et al. 2011; Kaproth et al. 2013). In mesocosms (1.1-m²), Pa formed monotypes within 2 years when treated with ample water, nutrients or nutrient-rich sediment alone. Pa formed monotypes within 1 yr, when given both ample water and nutrients (either fertilizer or topsoil; Kercher et al. 2004).

Sedge meadows in southern Wisconsin were invaded by Pa following disturbance from agriculture, including planting in pastures, mowing for hay, and conversion of upstream lands to urban uses (Middleton 2002; Zedler and Potter 2008). Upper Midwestern USA sedge meadows are frequently dominated by *Carex stricta* L. (hereafter Cs), a perennial graminoid known as tussock sedge. The ability to produce tussocks allows the species to establish across a broad

hydrological gradient (Lawrence and Zedler 2011). Tussocks also enhance carbon sequestration (Lawrence et al. 2013) and form microhabitats for >30 species that establish on the tussock structures (Peach and Zedler 2006). In recent decades, hydrological changes and human disturbances facilitated invasions, making Pa a wetland dominant in all but three of 323 Wisconsin watersheds (Hatch and Bernthal 2008).

Site selection and sample design

Our first site-selection criterion was that each sedge meadow be dominated by Cs and undergoing invasion by Pa, evidenced by an adjacent stand with ≥ 80 % Pa cover. We confirmed that the invaded portion was previously dominated by Cs using historical vegetation maps (Irwin 1973; Bedford et al. 1974). Sites also had to be large enough to accommodate at least six 16-m² sample plots. Six of our sites had evidence of hydrological disturbance due to urban development (Kercher et al. 2004); one site received agricultural runoff.

Four sites were located within the University of Wisconsin-Madison (UW) Arboretum: Curtis Prairie (CP; 43°2'18"N, 89°25"W, elevation = 266 masl), Southeast Marsh (SEM, 43°2'27"N, 89°24"W, elevation = 261 masl), Wingra Marsh (WM; 43°2'51"N, 89°25"W, elevation = 259 masl), and Lower Greene Prairie (LGP; 43°1'38"N, 89°26"W, elevation = 285 masl). Two sites were located at Cherokee Marsh Madison Park: the East Marsh of the north unit (CH1; 43°9'17"N, 89°21"W, elevation = 260 masl) and the southwestern portion of the south unit (CH2; 43°9'3"N, 89°21"W, elevation = 260 masl). The site receiving agricultural runoff was located on private land in Waubesa Wetland (Z; 42°58'36"N, 89°21"W, elevation = 262 masl).

Sampling

Plot layout We sampled the seven sites in June and July 2012. Because Pa forms an abrupt edge where it invades Cs stands (Werner and Zedler 2002), we laid a 50-m tape along the Cs–Pa boundary at each site. Next, we randomly located sampling points on each side of the boundary so that the largest plots ($4 \times 4 = 16 \text{ m}^2$) would be separated by ≥ 5 m and ≤ 10 m from the boundary (to reduce differences in soil and hydrology). The length of the Cs–Pa

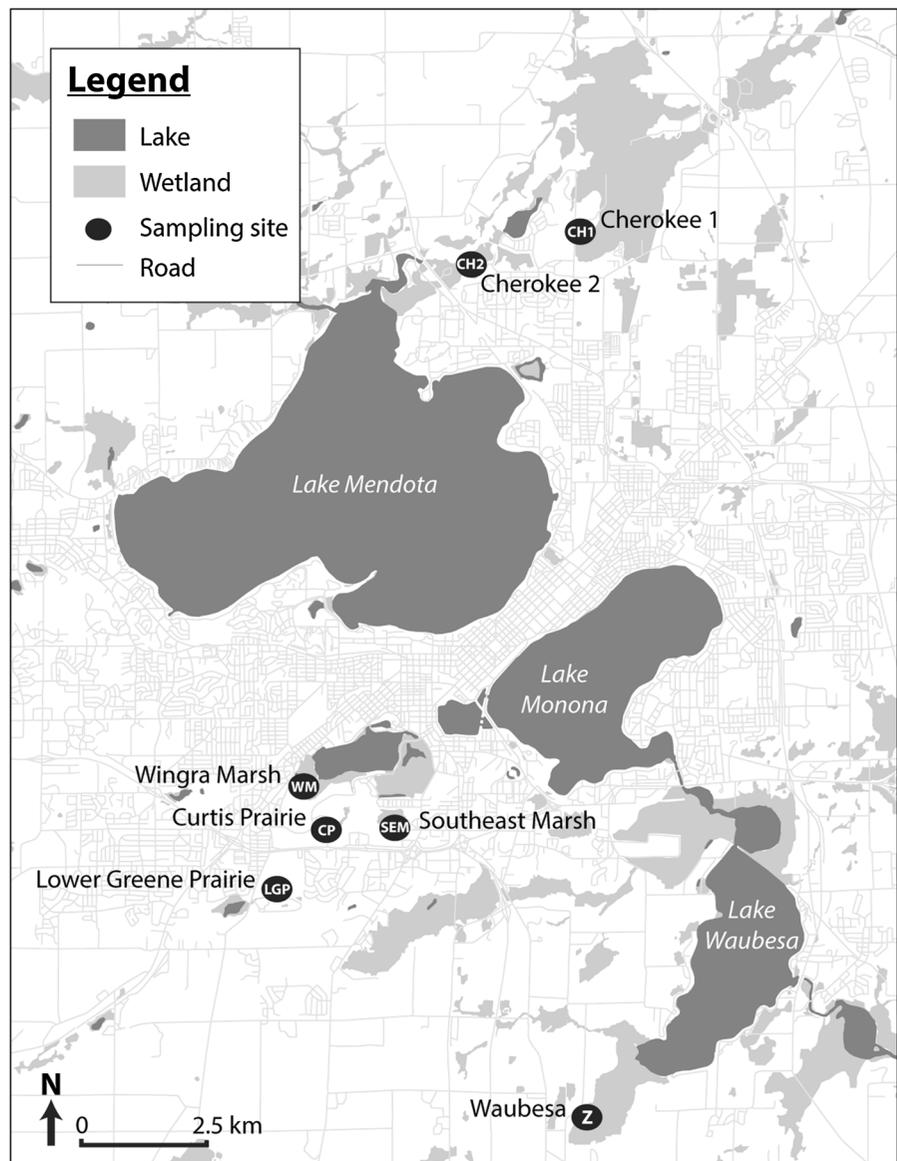
boundary limited the number of 16-m² plots that would fit each site; the range was 6–14 plots. In all, we sampled 70 plots (35 in Cs stands and 35 in Pa; Fig. 1).

Soil description The soil of Cs and Pa stands was sampled to determine texture, organic matter and nutrient availability. We collected the top 15 cm using a 30-cm-long soil corer of 2.5 cm diameter and composited 12 such cores to provide one sample for Cs and one for Pa per site. Cores were placed in plastic bags and refrigerated for up to 7 weeks, then dried, ground and sieved prior to analysis following the procedure of the UW Plant and Soil Laboratory, which analyzed pH, organic matter, plant available P and K, total N, exchangeable cations (Ca^{++} and Mg^{++}), and Cation Exchange Capacity (CEC). Units were mass in ppm. We determined soil texture using the Bouyoucos hydrometer method (Lesikar et al. 2005), treating dried and sieved samples with sodium hexametaphosphate to disperse aggregated particles, then homogenizing for 5 min in a malt mixer. We measured the density of the soil suspension using a hydrometer at 40 s and at 2 h, after sand and silt settled, respectively. Hydrometer readings were corrected for temperature, adding or subtracting 0.36 g/L for every degree above or below 20 °C, respectively. We conducted a Wilcoxon signed rank test to test for differences in soil characteristics between Cs and Pa stands.

Vegetation Within each 16-m² plot, we nested three smaller plots of 4, 1, and 0.25 m², starting at the southeast corner shared by all four plots sizes. In each plot, we recorded the number of plant species and their abundances, progressing from small to large plots and visually assigning each species to a percent cover class: <1, 1–5, 6–25, 26–50, 51–75, and >75 %, then calculating mean cover using cover-class midpoints. We recorded number and cover of species with any aboveground part inside the plot. Nomenclature followed the Wisconsin State Herbarium (WIS 2013).

For each species we recorded its geographical origin and coefficient of conservatism (C). We determined Mean C, the Floristic Quality Index ($\text{FQI} = \text{Mean } C / \sqrt{\text{Total number of native species}}$) (Bernthal 2003), and the number of species with $C > 5$ (excluding 29 unidentified specimens). We used the Shannon–Wiener index to describe diversity for each site ($H' = -\sum p_i \ln p_i$, where p_i = the relative abundance for species i). Similarities among sites were quantified using the Jaccard coefficient, based on number of shared species [$J = c / (a + b - c)$, where

Fig. 1 Location of study areas in and near Madison, Wisconsin



a = total number of species in site a , b = total number of species in site b , and c = the number of species shared by a and b].

Comparing metrics and testing for scale effects

We first calculated NERR at the site level. We were not able to assess correlation at multiple scales because exotic richness data were not continuous at the smaller scales (plots have 0 or 1 exotic species). Therefore, we estimated the relationship at the site

level using Spearman correlation for the total number of native and exotic species for each site.

Second, we used a species area curve to quantify changes in the plant community and test the scale-dependent effect of Pa on native species richness. The log–log transformation of Arrhenius's model ($S = cA^z$) is the most common (S = species number, A = area, c and z are constants). In log–log transformations, c and z become the intercept and slope of a linear model and parameters for comparison between communities. We used the log–log transformations of

the number of species encountered in each plot size (0.25, 1, 4 and 16 m²) separately for invaded (Pa) and uninvaded (Cs) data sets, i.e., we compared the intercept and slope of the species area curve (straight line of log–log transformation) of Cs and Pa plots for each site. Using lme and plot size as a random effect, we accounted for the fact that plots of different sizes were nested.

Third, we pooled all sites to test for scale-dependent effects of the invader among seven urban wetlands. We averaged number of species by sites for each plot size. Again, we used a lme with plot size as random effects, therefore taking into account the fact that plots of different sizes were nested. We compared the intercept and slope for 35 Cs and 35 Pa plots and calculated the species loss in Pa stands by subtracting the number of species in Pa from the number of species in Cs and dividing by the number of species in Cs.

Fourth, to assess the effects of Pa on the cover and frequency of resident species, we calculated an importance value [IV = (mean relative cover + mean relative frequency)/2] for each species. Because Pa, Cs, and *Calamagrostis canadensis* (hereafter Cc) had the highest IVs at all plot sizes, we excluded these three species and calculated the additive mean cover of subordinate species. After transforming the data using log₁₀(X + 1) to improve normality, we compared the additive cover of subordinate species between Cs and Pa stands at all plot sizes (0.25, 1, 4 and 16 m²). We used linear mixed effect regression models (lme) to detect the difference in additive cover of subordinate species between dominant species at each plot size and site as random effect. Finally, for the ten species with highest IVs in Cs stands, we compared their mean cover when present, and their frequency and IV between Cs and Pa stands for 0.25- and 16-m² plots. All statistical analyses used the software R, version 2.15.0 (R Development Core Team 2012) and the base package and nlme version 3.1-103 (Pinheiro et al. 2007).

Results

Site conditions

Maps from the 1970s showed that all seven sites were near historical stands of Pa at that time. Pa was present at site Z and within one kilometer of sites CH1 and

CH2 (Bedford et al. 1974). Pa was first recorded in CP around 1970 (Cottam 1987) but not noted along Curtis Creek until the mid-1980's (Rich Henderson, personal communication to J. Zedler), after Curtis Pond was excavated (1969) and began discharging runoff through a culvert. We do not know when Pa was first observed in LGP, but its distribution increased after 1986 and it now dominates approximately 3.6 ha. Both CP and WM were used as pastures and mowing meadows (Lovely 1984). Friedman (1987) states that Pa was planted near WM, and Pathak (2009) reported Pa expansion after hydrological conditions were altered by urban runoff.

Soil type ranged from silt-loam to sandy-clay-loam. Cs stands were classified as loam (4 stands) or sandy-loam (3 stands), whereas Pa stands included soils classified as loam (1 stand), sandy-loam (3 stands), sandy-clay-loam (1 stand), and silt-loam (1 stand) (Table 1). We found greater total N in plots dominated by Cs than Pa (12,808.8 ± 3,276.2 and 10,280 ± 2,631.8 ppm, mean ± SE, respectively; p value = 0.0469) and lower amount of K in Cs than Pa plots (43.57 ± 4.63 and 52.28 ± 3.19 ppm, mean ± SE, respectively; p = 0.0502). Other soil characteristics were similar in the Cs and Pa stands, but with more variation between sites. Organic matter ranged from ~6 % at CP to 59 % at CH1; P available for plants ranged from ~4 to 33 ppm. Calcium was particularly elevated in WM, where Pathak (2009) found measurable groundwater influence.

Vegetation Species counts, Mean C, FQI, and H' described species richness and conservatism. The seven sites (n = 35 plots for Cs and 35 for Pa stands, but unequal n among sites) supported a total of 96 species, of which 83 occurred in Cs stands and 50 in Pa (Table 2). Combining Cs and Pa plots for each site, we found that: SEM had only nine species (n = 10) while LGP had 47 (n = 10); mean C ranged from 3.20 at SEM to 5.10 at WM (n = 6), and site FQI varied from 8.47 at SEM to 31.45 at LGP. Consistently, LGP and Z (n = 16) had more species, higher floristic quality, and more "conservative" species (with C > 5), while SEM had the fewest species and lowest Mean C, floristic quality, and H'. Four indices were greater for uninvaded stands than in Pa (Cs > Pa), namely, Mean C (4.17 > 3.93), FQI (36.83 > 26.36), H' (1.90 > 1.67) and the number of conservative species (20 > 12) (Table 2). Eleven widely-distributed species (Mean C = 3.3) occurred in Pa stands and not in Cs stands;

Table 1 Soil characteristics in *Carex stricta* (Cs) and *Phalaris arundinacea* (Pa) stands at seven study sites. Each value is from a composite of 12 soil cores. O.M. organic matter; CEC cation exchange capacity

	CP		WM		SEM		Z		LGP		CHI		CH2	
	Cs	Pa	Cs	Pa	Cs	Pa	Cs	Pa	Cs	Pa	Cs	Pa	Cs	Pa
pH	7.0	6.9	7.4	7.5	6.4	6.4	7.1	7.4	6.6	6.3	7.0	7.0	6.5	6.1
O.M. %	5.8	6.2	31.4	32.5	17.0	11.7	14.9	11.0	14.3	13.9	61.7	57.3	61.7	30.0
Total P (ppm)	31	28	4	3	28	38	24	15	19	22	7	9	16	26
Total N (ppm)	2,788	3,160	13,273	12,849	7,878	5,740	8,253	5,679	8,074	8,068	24,671	23,730	24,725	12,738
K (ppm)	53	59	31	34	39	54	46	56	56	53	25	52	55	58
Ca ⁺⁺ (ppm)	1,757	1,573	5,440	5,406	2,846	2,039	3,709	1,855	2,147	1,422	3,651	4,612	3,371	3,165
Mg ⁺⁺ (ppm)	373	401	534	614	380	396	678	512	772	622	981	1,330	816	753
CEC	11	10	16	17	12	10	16	10	14	10	9	14	8	13
Soil texture	Loam	Loam	Loam	Sandy/loam	Loam	Sandy/loam	Sandy/loam	Silt/loam	Sandy/loam	Sandy/clay/loam	Loam	Sandy/loam	Sandy/loam	Sandy/loam
% Clay	4.4	22.7	16.7	9.6	7.4	24.4	18.9	22.5	17.4	22.9	11.9	9.4	7.8	9.4
% Sand	53.8	34.1	51.3	74.8	59.1	55.9	57.5	21.1	52.6	57.0	56.7	68.6	76.9	67.6
% Silt	41.7	43.1	32.0	15.6	33.4	19.6	23.6	56.4	30.0	20.1	31.4	22.1	15.2	23.0

Table 2 Number of plots, total number of species, Mean C mean coefficient of conservatism, FQI floristic quality index, C > 5 number of species with C above 5, and H' = ShannonWiener diversity index by site in *Carex stricta* (Cs) and *Phalaris arundinacea* (Pa) stands

	Number of plots ^a		Total number of species		Mean C		FQI		C > 5		H'	
	Cs	Pa	Cs	Pa	Cs	Pa	Cs	Pa	Cs	Pa	Cs	Pa
	<i>All-sites</i>	35	35	83	50	4.17	3.93	36.83	26.36	20	12	1.90
<i>Sites</i>												
CP	4	4	23	13	3.57	3.36	15.97	10.63	3	2	1.26	1.40
WM	3	3	11	11	4.77	4.00	15.08	12.00	3	2	1.10	0.96
SEM	5	5	8	4	3.14	3.25	7.69	5.63	1	1	0.37	0.22
Z	8	8	32	13	3.89	3.80	20.58	13.16	8	2	1.23	0.64
LGP	5	5	45	16	4.53	4.45	30.05	17.23	11	4	1.29	0.46
CH1	7	7	16	14	4.87	4.54	18.86	16.37	5	5	0.76	1.07
CH2	3	3	19	15	3.83	3.41	15.32	11.31	6	4	0.87	0.71

^a Each plot contains four nested plots of sizes 0.25, 1, 4, and 16 m²

these included two annuals (*Bidens cernuus*, *Cuscuta* sp.) plus *Pastinaca sativa*, *Polygonum amphibium* var. *stipulaceum*, *Polygonum persicaria*, *Salix nigra*, and *Viburnum opulus*. All occur in multiple Wisconsin habitats, including degraded land. In our seven sites, these species had low IVs (0.01–0.06) at all scales sampled; the species were low in both cover (mostly <5 %) and occurrences (range from 1 to 3 plots). The average for all Jaccard coefficients comparing the seven sites (Cs and Pa stands combined) was 0.20, with SEM and LGP being the least similar ($J = 0.12$) and CH1 and CH2 most similar ($J = 0.33$). The Jaccard Index for Cs stands was 0.22 ± 0.02 and for Pa stands was 0.19 ± 0.01 (Mean \pm 1 SE, respectively)

Metrics

NERR. Native species richness of sites ranged from 7 to 46, with 1 to 5 exotic species. We found no significant relationship between native and exotic species ($S = 36.0904$, $p = 0.4338$). The site with the fewest native species (WM) and the site with the most (LGP) each had two exotic species.

Species area curves All seven Pa stands had lower intercepts (indicating lower species richness at the 1-m scale) than Cs stands. The sites with the most species (LGP, 47) and fewest (SEM, 9) both had ~70 % lower intercepts for invaded stands. The smallest difference in intercepts (16 %) was found at CP, with 28 species.

We found little effect of scale using plots ranging from 0.25 to 16 m². There was no difference in the slopes of

log–log transformations of the number of species and plot size for six of the seven sites (Fig. 2, Table 3). Only the WM Pa stand had a significantly greater slope than its Cs stand (0.238 and 0.111, respectively; $p = 0.012$), i.e., the Pa stand had half as many species as the Cs stand at 0.25 m² (2.3 vs. 5.0) but a similar number at the 16 m² plot (7.7 vs. 6.3). Pa decreased species richness by an average of 48 % fewer species than Cs stands at all four plot sizes; 43 % at 0.25 m², 49 % at 1 m², 50 % at 4 m², and 49 % at 16 m². Pooling data for all sites, the intercept of the species-area curve on invaded stands was significantly lower (35 % lower intercept; $p < 0.001$), and the slope was the same as in the uninvaded stand (0.2028 and 0.2047, respectively; $p = 0.9661$) (Fig. 3).

Importance value Cc was the only common species with similar importance values in both Pa and Cs stands at all scales. Cc occurred less frequently in Pa than in Cs stands but had greater mean cover (Table 4). In other areas of the Great Lake region, Cc reached even greater abundance than we observed, completely dominating some wetlands (Frieswyk et al. 2007).

Subordinate species had lower IVs in smaller plots than in larger plots in both Cs and Pa stands. Consistently, the additive percent cover of subordinate species per plot was significantly lower in Pa stands in all plot sizes, i.e., 36, 24, 21 and 51 % less in 0.25, 1, 4 and 16-m² plots, respectively (Fig. 4). Eight subordinate species with relatively high IV in Cs stands had lower IVs in Pa stands at all scales (Table 4). Overall, species had lower frequency and cover at the small

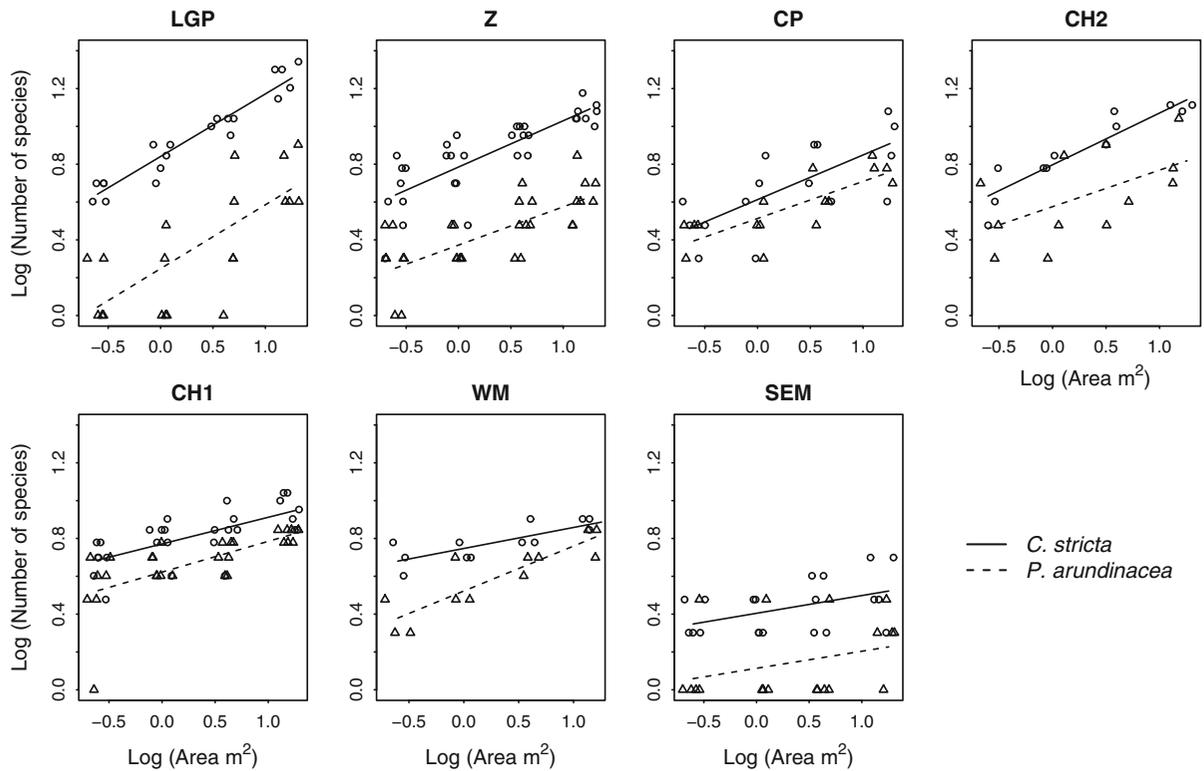


Fig. 2 Log-log transformation of the species-area curves for each site, ordered based on total number of species by site, from the richest to the poorest site. Solid line represents Cs plots and

dashed line Pa plots. Table 4 summarizes the estimated parameters, intercept and slope, and R^2 for each site

Table 3 Estimated parameters for log-log transformed species-area curve

Site	Intercept				Slope				R^2
	Cs	Pa	t	p	Cs	Pa	t	p	
LGP	0.841	0.248	10.367	<0.000	0.331	0.338	6.066	0.933	0.85
Z	0.785	0.372	19.935	<0.000	0.245	0.202	6.379	0.375	0.82
CP	0.613	0.513	14.080	0.077	0.236	0.196	3.966	0.593	0.58
CH2	0.797	0.575	13.110	0.004	0.274	0.193	3.265	0.402	0.67
CH1	0.771	0.622	27.628	<0.000	0.141	0.163	4.761	0.641	0.55
WM	0.747	0.522	24.800	<0.000	0.111	0.238	6.215	0.012	0.84
SEM	0.404	0.113	4.859	<0.000	0.094	0.090	1.642	0.965	0.50

scale, whereas at the larger scale the difference was stronger in frequency but not in cover; in the largest plots, most species had similar cover in Cs and Pa stands (average difference in cover = 1.6 ± 0.21 %) but fewer occurrences in all cases (average difference in occurrence = 10.25 ± 0.5 plots). Most species were at least twice as frequent in Cs plots than Pa plots. For example, at the small scale *Aster novae-*

angliae had higher mean cover and frequency in Cs than Pa stands (mean cover = 9.07 ± 3.0 and 3.00 ± 0.0 %; frequency = 7 and 1 in Cs and Pa, respectively). At the large scale, the species had similar mean cover when present in both stands but lower frequency in Pa stands (mean cover = 4.17 ± 1.5 and 4.25 ± 3.8 %; frequency = 15 and 4 in Cs and Pa, respectively).

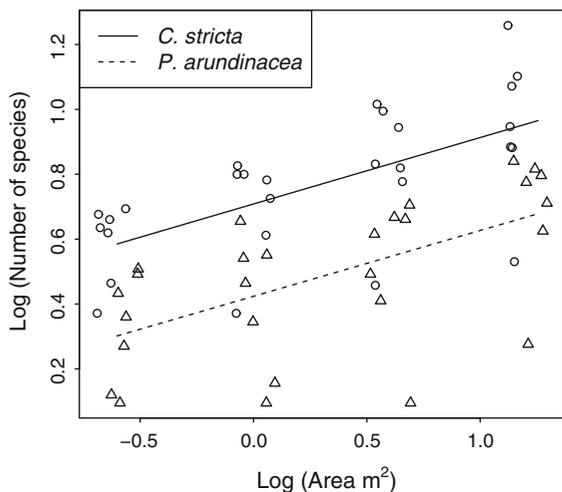


Fig. 3 Log-log transformation of the species-area curve average by site for Cs (solid line) and Pa (dashed line) plots. The equations averaged across site are $\text{Log}(S) = 0.7082 + 0.2047 \times \text{Log}(\text{Scale})$ for Cs stand, and $\text{Log}(S) = 0.4237 + 0.2028 \times \text{Log}(\text{Scale})$ for Pa stands. Pa stands have a significantly lower intercept ($t = 2.475$, $p < 0.001$), and there is no difference in slopes between Pa and Cs stands ($t = 6.614$, $p = 0.9661$). Circles represent averaged number of species by sites in Cs stands and triangles are averaged number of species by sites in Pa stands

Discussion

There should be little debate over the effect of invasive species on native species if authors clarify factors that lead to disagreement, namely, terminology (exotic \neq invasive), type of habitat (upland or wetland), metrics used to assess native vegetation responses (NERR vs. species richness and importance value) and the spatial scales where impacts are detected. Depending on these factors, relationships between an expanding species and residents can be perceived as positive, negative or not significantly different. Here, we specify that an *invasive* grass (most likely exotic) reduced *wetland* species richness across four plot sizes and sites.

Terms

Both native and exotic species can become invasive; the problem is that equating the terms exotic and invasive leads to confusion. Exotic species can be perceived as adding diversity at the regional scale (Davis 2003; Davis et al. 2011), even when they are invasive, form monotypes, and decrease native plant diversity at the plot and site scales. Therefore,

monitoring distributions of exotic species should be a priority, so that managers can implement control regimes early, before exotics invade widely (Schmitz and Simberloff 2001; Simberloff et al. 2012, 2013; Hassan and Ricciardi 2014). Studies that quantify the impacts of invaders are also necessary to alert managers to species needing control regionally.

When species' geographical origins are not known, researchers will know less about what limits a species in its native land. For Pa, both native and European genotypes are present in North America (Lavergne and Molofsky 2007; Jakubowski et al. 2013), but there is strong evidence that the native genotype is scarce in our region and that an exotic population has invaded our wetlands (Jakubowski et al. 2014). Pa's dominance in Wisconsin wetlands is due in part to widespread planting for pastures and streambank erosion control, long before its impacts to natural wetlands were anticipated (Moore 1934).

Ecosystem type

Wetlands tend to develop monotypes of Pa and other clonal graminoids (e.g., *Typha* spp. and *Phragmites australis*), which in turn displace native species and reduce plant diversity. The main reason that wetlands facilitate expansion of aggressive clonal species is their watershed position; downstream from disturbed lands that discharge excess water, nutrients and sediments (Zedler and Kercher 2004). For example, Pa planted in 1.1-m² mesocosms containing 14 wet-prairie plants displaced most natives within 1 year where water and nutrients or nutrient-rich sediments were added (Kercher et al. 2007). In addition, using satellite imagery and ground truthing, Bernthal and Willis (2004) found that Pa was strongly dominant wherever it was present, with no cases of co-dominance with other plant species.

Wetlands need to be included in reviews of invasive species' effects on native plant diversity because the invaders that form monotypes and decrease native species (Vilà et al. 2011) can change ecosystem structure and function (Simberloff 2011) and sometimes cause local extinctions (Hooper et al. 2005). Once an invader forms a monotype, it becomes too late to achieve eradication (Hooper et al. 2005; Healy and Zedler 2010). The *Spartina alterniflora* invasion of San Francisco Bay is a convincing example; years of effort have reduced this tall, clonal, exotic grass, but

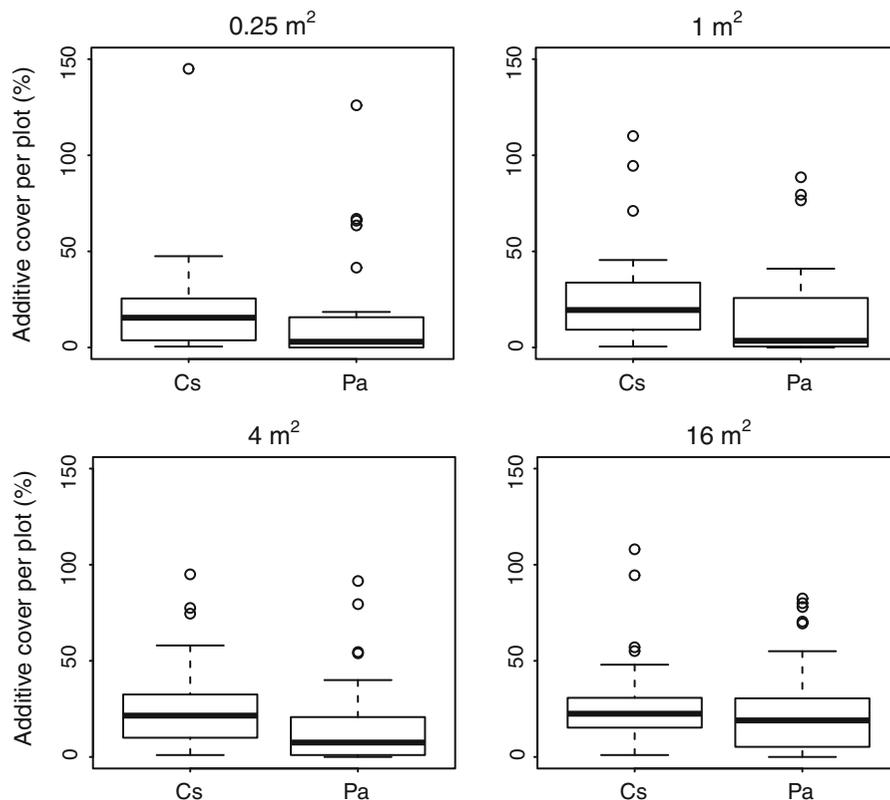


Fig. 4 Additive cover of subordinate species per plot in Cs and Pa stands at four spatial scales: 0.25, 1, 4 and 16 m². Cs stands had higher additive cover than Pa at all plots sizes ($t = -3.169$, $p < 0.002$ at 0.25 m²; $t = -4.993$, $p = 0$ at 1 m²; $t = -5.717$,

$p = 0$ at 4 m²; $t = -3.301$, $p < 0.001$ at 16 m²). We used original data in the figure and transformed data ($\text{Log}(X + 1)$) in the statistical analysis

its genes persist in hybrids that are indistinguishable in the field. The native *S. foliosa* population was depleted first by the invader and then by herbicides used to control the exotic. Thus, the population of endangered clapper rails (*Rallus longirostris obsoletus*) declined, when it was supposed to benefit (San Francisco Estuary Invasive Spartina Project 2015, spartina.org). If wetlands are not included, analyses of upland invaders will lead to incomplete generalizations about invader effects.

Metrics and the spatial scale

Responses to invasion can differ with the metric and the scale used to assess effects of exotic invaders. Several authors indicate that scale-dependent effects of invaders can occur (a) where larger-scale patterns are driven by regional variations in the environment (e.g., climate) and where conditions favorable to

native species richness also favor exotic richness and, at the same time, (b) small-scale processes are influenced by species interactions that positively affect (facilitate) some species' abundances and/or negatively affect others (e.g., via competition; Shea and Chesson 2002; Fridley et al. 2004; Bartomeus et al. 2012). The NERR has been useful in describing this biogeographic pattern, but it does not account for the effects of single plants that invade aggressively and become dominant. Stohlgren et al. (2006) suggest that the NERR is negative, neutral or positive at the small scale and progressively more positive with increasing spatial scale in most forests, grasslands, and wet meadows. However, in our study of sedge meadows, the NERR was neither positive nor negative at the site level, even though Pa consistently reduced species richness by about one-half, regardless of plot size. Relying on NERR would indicate no effect of the invader on diversity, whereas our assessment of

Table 4 Abundance [mean cover, frequency, and Importance Value (IV)] for the ten most abundant species; IV > 0.1 in the large plots in *Carex stricta* (Cs) and *Phalaris arundinacea* (Pa) stands. Abundances are summarized for small (0.25 m²) and large (16 m²) plot-sizes. Values include all seven sites, total of 70 plots, 35 in Cs stands and 35 in Pa; mean cover is average of cover class midpoint in plot where species was present; frequency is the number of plot present; and IV is based on relative frequency and mean relative cover

Species	Mean cover ± 1 SE		Frequency		IV	
	Cs	Pa	Cs	Pa	Cs	Pa
Small plot-size (0.25 m ²)						
<i>Carex stricta</i>	73.43 ± 4.0	21.18 ± 7.0	35	11	–	0.37
<i>Phalaris arundinacea</i>	6.85 ± 1.9	70.29 ± 4.4	24	35	0.46	–
<i>Calamagrostis canadensis</i>	7.47 ± 2.8	15.50 ± 7.2	19	12	0.38	0.34
<i>Lycopus americanus</i>	3.00 ± 2.5	–	6	0	0.10	–
<i>Eupatorium maculatum</i>	1.75 ± 1.3	–	2	0	0.03	–
<i>Aster novae-angliae</i>	9.07 ± 3.0	3.00 ± 0.0	7	1	0.15	0.02
<i>Campanula aparinoides</i>	1.21 ± 0.5	0.50 ± 0.0	7	1	0.11	0.02
<i>Galium obtusum</i>	4.00 ± 2.9	0.50 ± 0.0	5	1	0.09	0.02
<i>Impatiens capensis</i>	5.00 ± 2.7	0.50 ± 0.0	5	1	0.09	0.02
<i>Scutellaria galericulata</i>	8.00 ± 7.5	–	2	0	0.04	–
<i>Solidago gigantea</i>	9.25 ± 6.3	–	2	0	0.04	–
Large plot-size (16 m ²)						
<i>Carex stricta</i>	85.21 ± 2.2	14.07 ± 8.2	35	21	–	0.47
<i>Phalaris arundinacea</i>	4.09 ± 0.3	82.29 ± 2.5	32	35	0.53	–
<i>Calamagrostis canadensis</i>	4.61 ± 1.1	11.16 ± 4.0	28	19	0.47	0.39
<i>Lycopus americanus</i>	2.02 ± 0.9	0.50 ± 0.0	23	5	0.35	0.07
<i>Eupatorium maculatum</i>	4.03 ± 2.3	6.33 ± 4.6	17	3	0.28	0.05
<i>Aster novae-angliae</i>	4.17 ± 1.5	4.25 ± 3.8	15	4	0.25	0.07
<i>Campanula aparinoides</i>	1.65 ± 0.4	0.50 ± 0.0	13	5	0.20	0.07
<i>Galium obtusum</i>	0.71 ± 0.2	0.50 ± 0.0	12	4	0.18	0.06
<i>Impatiens capensis</i>	2.77 ± 1.3	8.00 ± 3.1	11	5	0.17	0.09
<i>Scutellaria galericulata</i>	0.73 ± 0.2	0.50 ± 0.0	11	1	0.16	0.02
<i>Solidago gigantea</i>	4.11 ± 2.2	1.75 ± 1.3	9	2	0.15	0.03

species richness and IV showed substantial impacts of a single invader. NERR is insensitive to species' behaviors and is not useful for testing the effect of a single invader on plant community diversity.

As an alternative to the NERR, we used species area curves to analyze our four plot sizes (0.25–16 m²). We saw that Pa reduced species richness similarly across those scales. In six of our seven sites, Pa and Cs stands did not differ in the slope of the log–log species-area curve for plots of 0.25–16 m². Similar slopes suggest that the Pa invasion does not change the aggregation and evenness of the sedge community, i.e., both stands are dominated by one species and other species occur in low abundance and frequency. Most sites had similar degrees of reduction in species richness. WM was the exception; its significantly higher slope in Pa than Cs stands was due to fewer species in smaller plots (while larger plots had similar richness). The Pa stand at WM had the coarsest soil (75 % sand); we

suggest that it retained less water and nutrients, made Pa less competitive and allowed more species to co-exist.

Although we did not find scale-dependence at plot sizes ≤16 m², outcomes for other species across a larger range of plot scales have shown spatial variance. Two previous tests using species area curves found scale-dependent effects of invasive plants. Jackson (2005) reported that perennial buffel grass (*Cenchrus ciliaris*) reduced species richness to 53 % in seven invaded areas compared to nine uninvaded Australian grasslands sampled in 1–64-m² plots, with greater reduction in smaller plots. In USA, Powell et al. (2013) compared nested plots from 1 to 500 m² and found a lower intercept and steeper slope in the invaded conditions of 3 forest biomes: hardwood hammock forests in central Florida invaded by a perennial herb (*Dianella ensifolia*, umbrella dracaena); oak-hickory forests in eastern Missouri being

invaded by a shrub (*Lonicera maackii*, honey-suckle), and tropical mesic forests on the Big Island of Hawai'i being invaded by a nitrogen-fixing tree (*Morella faya*, firetree). In each case, the effect of the invader on species richness was scale-dependent within sites. The invaded stand had fewer species at the smallest scale and similar numbers than the un-invaded stands at the larger scale. In addition, both studies reported decreased species abundance in the invaded stand at all scales sampled. Both studies were from uplands. Because more species can occur in larger areas, effects of invaders at larger scales are confounded by microhabitat diversity created by topographic, soil and hydrological variability. In our study of sedge meadows, we focused on the invasion border where differences in species richness are more attributable to the invader.

At the site and all-sites levels, we also saw reduced total richness in Pa versus Cs stands. A statewide study of Wisconsin wetlands used remote sensing data and found that Pa dominates (>50 % cover) approximately 26 % (124,261 hectares) of the surface area of Wisconsin wetlands and 35–52 % of the area of Dane County open wetlands (Hatch and Bernthal 2008). Our results suggest that areas that were dominated by Cs and now invaded by Pa have lost resident species.

Finally, Importance value (IV, the mean of relative cover and relative frequency) was also helpful in distinguishing responses of resident species to invasion. In our sites, Cc, a perennial annual grass, had similar IVs along the Pa and Cs stands; it had the highest frequency and abundance when present. In contrast, subordinate native wetland species responded differentially to Pa invasion. Some had reduced frequency and cover in Pa vs. Cs stands. For example, *Lycopus americanus* is a widespread perennial herbaceous plant that can inhabit in various types of wetlands and resist human perturbation ($C = 4$). Other species decreased mainly in frequency, e.g., two tall perennial forbs (*Aster novae-angliae*, *Eupatorium maculatum*) that tend to exceed the height of the Cs canopy in summer (Peach and Zedler 2006) and three short perennials (*Campanula aparinoides*, *Impatiens capensis*, and *Scutellaria galericulata*) that are preferential associates of Cs (Johnston and Zedler 2012). Lower IVs can identify subordinate species that are the most affected by an invader; also, the component of IV, cover or frequency, that is most reduced can indicate the nature of the impact.

The consistent reduction in species richness occurred despite differences in soil characteristics, species composition and species abundances across sites. Sites varied in their soil characteristics but we found higher amount of total N and lower amount of K in stands dominated by Cs across sites. Similarly, in a mesocosms experiment, species rich meadows have shown higher amount of total N in soil compared to meadows invaded by Pa (Herr-Turoff and Zedler 2005). Here, Herr-Turoff and Zedler (2005) found that Pa did not increase N soil concentration while higher amount of N increased Pa invasion. However, studies on soil conditions usually have detail soil data across time to quantify nutrients dynamics, especially for N concentration that have fast turnover in wetlands. Therefore, our one time soil sampling does not allow us to explain our richness pattern but it highlights that Pa reduced plant richness in a wide range of soil conditions. Moreover, species that occur in sedge meadows usually have low fidelity to this type of wetlands (Galatowitsch et al. 2000; Johnston and Zedler 2012); only a few species are considered preferential associates (Johnston and Zedler 2012). In our study, Jaccard's similarity index averaged only 0.20 among the seven sites (Cs and Pa plots together) and 0.22 among the seven Cs stands. Most species had low abundance, and many species that were absent in one Pa stand were present in another. Few of the species that remained were considered conservative (Mean C = 3.93 in Pa stands). Pa is consistently associated with lower species richness, as well as fewer conservative species, lower Mean C, lower floristic quality (FQI), and lower diversity (H'). Despite considerable variation in soils and vegetation across site, the responses to Pa were consistent and clear—native vegetation was degraded in richness and quality.

Implications for management

Debating the merits of benign exotic “colonists” does not help managers deal with the most aggressive invasive plants. Claims that exotic invaders increase diversity at the regional scale (Sax et al. 2002; Davis et al. 2011) should not interfere with plans to control tall clonal invaders (such as *Typha x glauca* and *Phragmites australis*) that become dominants at the site scale. Nutrient-rich sites will lose native species in just a few years after colonization by such invaders

(Dickson et al. 2014). In our study area (Fig. 1), only small areas of wetland remain, and management at the site level is imperative to maintain native sedge meadow diversity.

Because Pa has become dominant locally and regionally, it is now extremely difficult to eradicate (e.g., Lavergne and Molofsky 2006; Healy and Zedler 2010). New invasions need to be controlled early in order to retain native species richness in wetlands. Local stakeholders can use our findings to advise against planting Pa near uninvaded wetlands. Simultaneously, we recommend that managers work with upstream landowners to reduce off-site factors that facilitate Pa invasion (nutrients, sedimentation, flooding and other hydrological changes; Kercher et al. 2007). Neighbors who live upstream from urban wetlands can improve yard care to reduce nutrients in runoff (Zedler et al. 2014). In urban and agricultural areas, watershed approaches, monitoring, and adaptive restoration will be needed to minimize reinvasion where control measures are underway (Jakubowski et al. 2010, Zedler et al. 2012).

We urge continued testing of grass-selective herbicides, especially swabbing on leaves following mowing and/or burning to remove dry biomass. Annual reconnaissance and treatment will likely be needed for years to come.

Conclusions

Impacts of invaders at the community level are best assessed using species area curves and IV. Species area curves showed reduced species richness at four plot scales, at individual sites, and all-sites combined. Sedge meadows that were historically dominated by Cs lost about half of their plant species where invaded by Pa. IV helped identify changes for individual species. Resident native species that persist where Pa invades can show reduced cover, frequency or both. In contrast, the NERR is not adequate to quantify the impact of single invaders at the community level. This metric confounds the behavior of invaders and exotic species.

Reduced richness and abundance of native species at the site level should not be ignored in broad generalizations about invader effects. The discussion of invader effects should include wetlands, because Pa and other clonal graminoids can aggressively invade and form monotypes at the site scale, regardless of

effects on diversity at the regional scale. Monitoring and management at the site level is imperative to maintain native sedge meadow diversity.

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CAN NUTRIENTS ALONE SHIFT A SEDGE MEADOW TOWARDS DOMINANCE BY THE INVASIVE *TYPHA* × *GLAUCA*?

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Abstract: Where wetlands receive urban runoff, *Typha* spp. and other invasive plants often displace the native vegetation. We tested the ability of nutrients (N and P) to increase vegetative growth of *T. × glauca* (a hybrid of *T. latifolia* and *T. angustifolia*). In the greenhouse, 17 treatments revealed that *T. × glauca* required both N and P for growth, and total leaf length was most stimulated where a higher proportion of P was added (7N:1P vs. 14N:1P, with N constant and P changed), regardless of concentration (the High treatment was 4× the Low treatment). In Gardner Marsh (Madison, Wisconsin, USA), we set up 28 plots (1 × 6 m) that bisected the boundary between sedge meadow (graminoids) and *T. × glauca*, and we added a common lawn fertilizer (9N:1P:4K) at high (62.5 g/m²), medium (31.3 g/m²), low (15.6 g/m²), and control (0 g/m²) rates on five dates, with n=7 plots/treatment. After one growing season, fertilizer addition increased *T. × glauca* ramet density, height, and biomass, especially where the sedge meadow graminoids were initially dominant. Aboveground biomass of *T. × glauca* in the high nutrient addition treatment (1029 ± 256.1 g/m²) was more than double that for control plots (431 ± 80.52 g/m²) overall, with the greatest percent increase in sedge meadow subplots. In contrast, native graminoids (mostly *Carex* spp.) did not respond to treatment, either in biomass or percent cover. *Typha × glauca* allocated nutrients to both growth and storage, as indicated by higher N and P concentrations in leaves, shoot bases, and rhizomes in plots with high nutrient addition. Because fertilizing the marsh enhanced the shoot growth of *T. × glauca* but not native graminoids, and because the 7N:1P treatment stimulated growth in the greenhouse, we suggest that wetland managers focus on reducing P inflows to urban wetlands. Fertilizer additions below those recommended by the manufacturer for new lawns (5× that of our highest treatment) should be more economical and have fewer impacts on receiving wetlands.

Key Words: fertilizer, *Typha × glauca*, *Carex* spp., invasive plant, hybrid, clone, urban runoff, nitrogen, nutrient allocation, phosphorus

INTRODUCTION

The invasiveness of plant species is a function of both plant traits and habitat modifications (Mooney et al. 1986, Galatowitsch et al. 1999, Mack et al. 2000). Changes to hydrologic and fire regimes, disruptions to soil or canopies, and pollution by nutrients and other contaminants often act in concert to enhance the susceptibility of habitats to invasion (Burke and Grime 1996, Mack et al. 2000). In urban areas, hydrologic regimes have become more pulsed due to surface-water runoff from impervious surfaces, and the increased runoff carries nutrients, salts, and heavy metals to downstream wetlands. Collectively, these alterations could trigger expansions of invasive species (Galatowitsch et al. 1999); however, nutrient addition is

known to increase invasibility on its own (Aerts and Berendse 1988, Huenneke et al. 1990).

The shift from a diverse wetland plant community to a stand of cattail, *Typha* spp., has often been associated with changes in hydrology and nutrients (Runhaar et al. 1996, Newman et al. 1998, Galatowitsch et al. 1999). While changes in the water table can influence plant communities (Wilcox et al. 1985, Runhaar et al. 1996, Newman et al. 1998), the literature suggests that water levels alone are not sufficient to facilitate invasions of *Typha* spp. (Neill 1990, Newman et al. 1998). In several cases, the expansion of *Typha* sp. has been associated with elevated nutrients (Bastian 1993, Miao and Sklar 1998, Newman et al. 1998). Our observations of the expansion of *Typha* hybrids in urban wetlands led us to ask if nutrients alone could

cause a multi-species sedge meadow to shift to a monotype of the hybrid, *Typha* × *glauca* Godr.

We performed experiments in the greenhouse and at Gardner Marsh (adjacent to Lake Wingra in Madison, Wisconsin, USA), where both hydrology and water quality have been altered (stabilized water levels, nutrient-rich runoff; Lee 1971, Irwin 1973) and where much of the historical sedge meadow is now dominated by *Typha* × *glauca*, a sterile hybrid of *T. latifolia* and *T. angustifolia*. Because *T. × glauca* spreads vegetatively (Smith 1967) and tolerates a wide range of water levels (Waters and Shay 1992), we focused on nutrient-facilitated expansion. Our greenhouse experiment tested nitrogen (N) versus phosphorus (P) limitation, as well as the effect of two N:P ratios applied at two levels. In Gardner Marsh, we tested the effect of a lawn fertilizer (N, P, and potassium [K]) at low, medium, and high application rates (the high rate was 1/5 that recommended for new lawns). We assessed both the effect on *T. × glauca* biomass and expansion into a sedge meadow by adding fertilizer to rectangular plots that crossed the sedge meadow-*Typha* border. Finally, we tested the hypothesis of Gerloff and Krumholz (1966) and Miao and Sklar (1998) that *Typha*'s rapid growth was associated with an abundance of nutrients in leaves (for light capture) compared to shoot bases and rhizomes (for storage) or roots (for nutrient acquisition). We analyzed nutrient concentrations in *Typha* leaves, shoot bases, rhizomes, and roots. High concentrations in leaves indicate high photosynthesis rates (Chapin et al. 1990) and rapid growth in productive environments (Grime 1979).

METHODS

Greenhouse Test of N, P, and N+P Addition

Before selecting a fertilizer for use in the field experiment, we asked if both N and P were needed to stimulate growth. A greenhouse experiment was conducted at the University of Wisconsin from July 19 to September 4, 1999. *Typha* × *glauca* rhizome fragments with pre-existing shoot buds were dug from Gardner Marsh and grown hydroponically in deionized water. Starting wet weights ranged from 5 to 20 g, with an average of 11.8 ± 0.5 g. Rhizome fragments were grown individually in 1-L pots (18-cm diameter, 22-cm height) that were lined with plastic bags that were easy to replace when algal growth became noticeable. Water levels were maintained at 15-cm depth by adding deionized water. After a 12-week conditioning period (April 14 to July 8) with trace amounts of nitrogen, phosphorus, and micronutrient solution, shoots were pruned so that each pot contained one shoot bud (~2cm).

Table 1. Treatment levels in the greenhouse experiment, with *Typha* rhizomes grown in hydroponic solution. Ramets were given six levels of N and no P, or six levels of P and no N, or 2 ratios of N:P at 2 concentrations. Note that N:P ratios were varied by changing P concentrations. N and P additions had 5 replicates; N+P had 6 replicates, as did the control.

N level	N (g/L)	P level	P (g/L)	N and P	N:P (g/L)
1N	0.07	1P	0.02	7:1H	2.24 : 0.32
2N	0.14	2P	0.04	14:1H	2.24 : 0.16
3N	0.28	3P	0.08	7:1L	0.56 : 0.08
4N	0.56	4P	0.16	14:1L	0.56 : 0.04
5N	1.12	5P	0.32	Control	0 : 0
6N	2.24	6P	0.64		

Rhizomes were subjected to 17 nutrient addition treatments (Table 1): nitrogen alone as NH_4NO_3 (6 levels), phosphorus alone as KH_2PO_4 (6 levels), a ratio of 7N:1P (high and low levels), a ratio of 14N:1P (high and low levels), and a control (Table 1). All rhizomes received a modified 50% Hoagland's micronutrient solution that contained no nitrogen or phosphorus. The control pots (n=6) received only this solution. The N and P treatments had 5 replicates; we increased replication for the N+P treatments to 6, as we tested fewer concentrations. In all, there were 90 pots located on two greenhouse benches, with locations randomized biweekly.

Every two weeks, we measured total leaf length and completely replenished nutrients and micronutrient solutions. At the end of the experiment, plants were separated into above- and belowground parts, dried to a constant weight at 60°C, and weighed. Total leaf length was used as a nondestructive measure of growth. Data were log-transformed to provide homogeneous variances and analyzed using Analysis of Variance (ANOVA). Least Significant Difference (LSD) was used to group plots by treatment and to rank the treatments by the mean.

Field Test of Fertilizer Effects on Invasion

Experimental Site and Design. Within the University of Wisconsin-Madison Arboretum and adjacent to Lake Wingra, Gardner Marsh (89° 42' W, 43° 6' N) is a shallow lacustrine marsh that was once dominated by *Carex stricta* Lam., *C. lasiocarpa* Ehrh., *C. aquatilis* Wahlenb., *C. lacustris* Willd., and *Calamagrostis canadensis* (Michaux) Beauv. (Irwin 1973). In the early 1970s, Lake Wingra received 80% of its total P and roughly 90% of its soluble inorganic P from urban runoff (Lee 1971). During this time, Irwin (1973) documented a small and stable distribution of *Typha* spp.

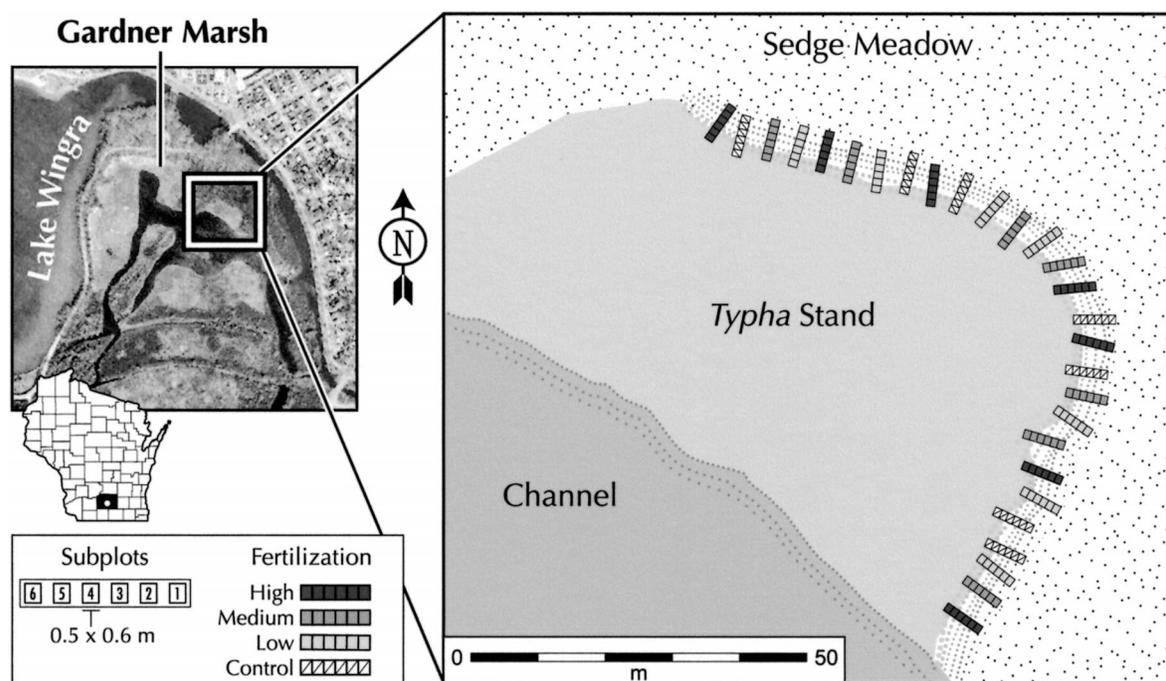


Figure 1. Experimental field setup within Gardner Marsh, Madison, Wisconsin. Each rectangular plot had 6 subplots. Fertilization treatments were H = High, M = Medium, L = Low, and C = Control. The boundary of the *Typha* × *glauca* stand and elevation were measured at the end of the growing season using a Leica 530 GPS unit. The range of elevations among all subplots was 24 cm.

in Gardner Marsh. Since then, a monotype of *Typha* × *glauca* has displaced most of the sedge meadow.

We selected a sharp boundary between the cattails and the native sedge meadow to test the effects of nutrient loading on the *Typha* × *glauca* invasion front. We fertilized 21 rectangular plots (1 × 6-m) across this boundary, with sedge meadow dominant at one end and cattail at the other (Figure 1). Seven additional plots served as controls. The 28 plots were placed 5 meters apart. To reduce edge effects, we sampled six subplots (0.5 × 0.6 m or 0.3 m²) within the 1 × 6-m plot, for a total of 168 subplots (Figure 1). We chose a split-plot-with-block design because cattail density increased from the sedge meadow into the clone center. To test the fertilizer effect on *T. × glauca* growth, we used data from the whole plot. To test the effect of nutrient addition on the expansion of *T. × glauca*, we compared data among subplots of the 6-m plot. Although we did not collect data on conditions prior to fertilization, we set up control plots and designed the experiment to test for block effects, where seven blocks were located from southeast to northwest along the boundary (Figure 1).

Fertilization Experiment in Gardner Marsh. Treatments were assigned to plots in a completely randomized block design with 7 replicates (Figure 1). Fertilizer (Ideal Lawn Food®) provided N [as urea], P [as P₂O₅], and

K as [K₂O]. The fertilizer had a ratio of 9N:1P, similar to that of the 7N:1P treatment that most stimulated *T. × glauca* growth in the greenhouse. The granular fertilizer was sprinkled by hand and readily sank into the shallow water (generally < 25 cm). The fertilizer was uniformly spread in five equal applications over the 1999 growing season (May–August).

The low nutrient addition level was 15.6 g fertilizer/m² applied 5 times for a total of 78 g fertilizer/m². This low level provided 15.6 g N/m², 1.7 g P/m², and 6.5 g K/m² after 5 applications. The medium level was twice the low level, and the high level was four times the low level.

Aboveground biomass (sorted as *Typha* × *glauca* and graminoid biomass) was harvested in each subplot in the fall (August 27 to September 5, 1999) and dried in forced-air drying ovens at 60° C for >48 hours until a constant weight was reached. To test for a treatment effect for each subplot, we used the SLICE option in the LSMEANS procedure in SAS (ANOVA, SAS Institute 1996). The SLICE option specified effects by which to partition LSMEANS.

Percent Cover and Soil Sampling. The density of *Typha* × *glauca* ramets was recorded in each subplot in the middle (July 23) and end (August 24) of the 1999 growing season. On the same dates, the percent cover of *Carex* spp. was estimated at each subplot using six

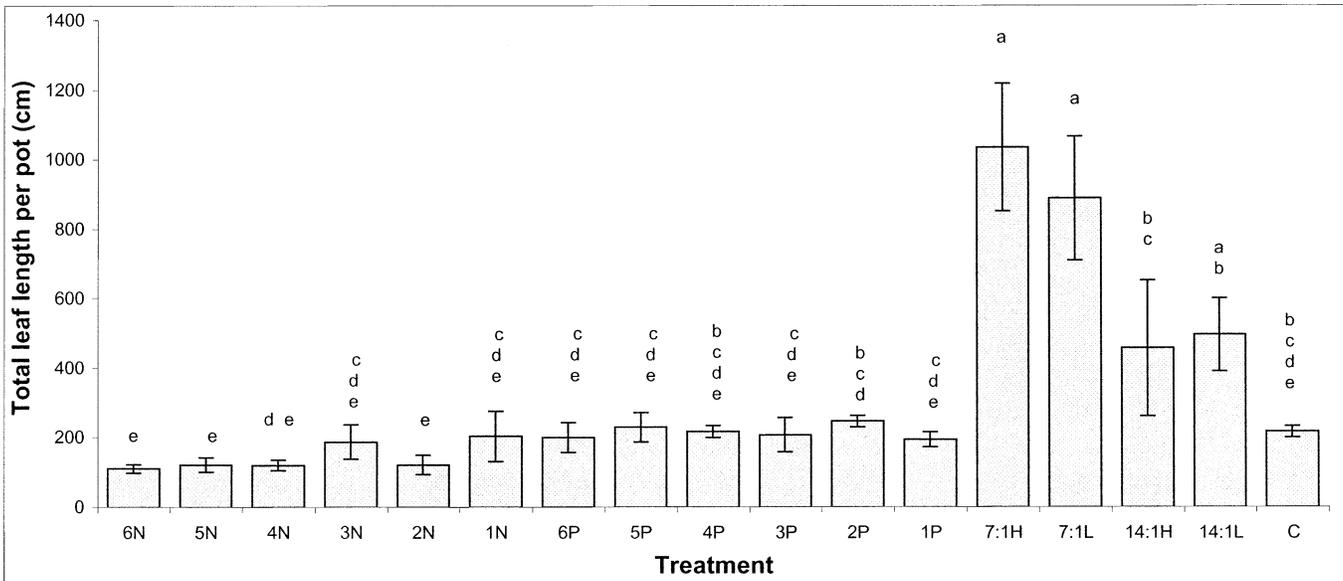


Figure 2. Average total leaf length of *Typha* × *glauca* per pot in the greenhouse for treatments with N addition (6 levels), P addition (6 levels), and N and P additions (4 treatments, varying N:P ratio and concentration). N:P ratios were 7:1 and 14:1. H = High concentration L = Low concentration, C = Control. Means with the same letter are not significantly different. Error bars represent 1 S.E.

classes (<1%, 1–5%, 6–25%, 26–50%, 51–75%, and 75–100%). Data were analyzed with ANOVA. Individual treatment effects of graminoid cover/*Typha* × *glauca* density were analyzed by using a t-test to detect differences in least squares means (LSMEANS procedure with the DIFF option, SAS Institute 1996).

In mid-October 1999, we took soil samples (10 cm in diameter, 20 cm deep) with a razor-edged corer, with one core from the center of each of 111 subplots, sampling all subplots in plots 20–28 and subplots 1, 4, and 6 in plots 1–19 (to reduce the cost of nutrient analyses). Belowground samples were separated into cattail rhizomes and roots (pooled for cattails + graminoids). These samples were washed over a 3-mm screen, dried in forced-air drying ovens at 60° C for >48 hours until a constant weight was reached, then weighed. We analyzed for treatment, position, and interaction effects using ANOVA.

Tissue Nutrient Concentrations. Nutrient (N and P) allocation in *T. × glauca* tissues (leaf, shoot base, roots, and rhizomes) was measured following Miao and Sklar (1998). After oven drying, the largest cattail from subplot 6 of each high fertilizer and control plot was chosen for tissue N and P analysis; we chose this innermost subplot of the cattail clone to minimize chances of interspecific effects on tissue nutrient concentrations. Tissue samples of leaves (top 10 cm of longest leaf), shoot bases (bottom 3 cm of ramet), roots (directly attached to a cattail rhizome), and rhizomes (entire rhizome sampled in soil core) were ground in

a Wiley Mill (#20 mesh, openings ~1 mm). Samples were then analyzed for total nitrogen (TN) and total phosphorus (TP) by the University of Wisconsin Soil and Plant Analysis Lab.

We used PROC MIXED with repeated measures ANOVA because leaf tips and ramet bases were taken from the same plant (the largest cattail from subplot 6); therefore, these samples were not independent. This procedure takes into account any correlation that samples from the same plant might have (SAS Institute 1996). PROC MIXED was a better SAS syntax than PROC GLM because we had unequal sizes of samples (one had insufficient mass). Data for TN and TP were log-transformed to meet the assumptions of equal variance.

RESULTS

Greenhouse Test of N, P, and N+P Addition

We tested the initial starting weight of the rhizome as a possible covariate to total leaf length (TLL = sum of all leaf heights in a pot) using regression analyses for each treatment and found no significant effect (all p values >0.05). TLL was consistently low for plants in control pots (mean ± S.E. = 216.2 ± 16.6 cm/pot) and treatments receiving only nitrogen (N) or only phosphorus (P) (180.3 ± 10.5 cm/pot). Regardless of concentration, adding N or P alone did not increase TLL over that of control plants (Figure 2, ANOVA; $F_{12} = 1.64$, $p = 0.1115$). In contrast, the addition of

N+P increased TLL 4-fold (761.6 ± 89.2 cm/pot; Figure 2). Comparing treatments with both N and P added, the two factor ANOVA for concentration (high or low) and N:P ratio (7:1 or 14:1) showed a significant effect of ratio on TLL ($F_2 = 24.76$, $p < 0.0001$) but no effect of concentration ($F_1 = 0.38$, $p = 0.5450$) or interaction ($F_2 = 0.68$, $p = 0.5146$). The 7N:1P ratio doubled the average TLL over that with the 14:1 ratio (Figure 2).

Field Test of Fertilizer Effects on Invasion

We found no block effects during the study and hence focus on treatment effects, i.e., responses of native graminoids (cover and aboveground biomass), *Typha* (aboveground biomass, density and height), and combined belowground biomass. Tissue nutrient data are presented last, as these were obtained only for *Typha* and from a subset of subplots.

Percent Cover of Native Graminoids. Because the cover of individual species was highly variable, we pooled the cover of native graminoids within subplots for each sampling time (June 23 and August 25, 1999). August graminoid percent cover averaged 19.2 ± 1.5 % cover in control plots and 13.6 ± 1.7 % cover in high fertilizer plots, but there was no significant treatment effect (ANOVA; $F_{3,144} = 2.21$, $p = 0.0901$). There was a subplot position effect ($F_{5,144} = 5.62$, $p < 0.0001$), with greater graminoid cover within the sedge meadow than within the *T. × glauca* stand (subplot 6) but no interaction between treatment and position ($F_{15,144} = 0.69$, $p = 0.7872$).

Changes in percent cover were calculated as differences between sampling times. Although treatments did not affect the seasonal decrease of native graminoid cover ($21.1 \pm 1.3\%$ in June to $16.9 \pm 0.88\%$ in August 1999; ANOVA; $F_{3,144} = 1.08$, $p = 0.3617$) (Table 2), there was a position effect ($F_{5,144} = 3.22$, $p = 0.0087$), with the rate of decrease 10 times greater in subplot 1 (*Carex* spp. dominant) than subplot 6 (*T. × glauca* dominant). There was no interaction between treatment and position ($F_{15,144} = 0.71$, $p = 0.7716$).

The average cover of native graminoids was negatively correlated with *T. × glauca* biomass ($R = -0.47$, $p < 0.01$), and there was evidence that higher densities of *T. × glauca* ramets reduced native graminoid cover. We found a position effect for the ratio of native graminoid cover: *T. × glauca* density in June (ANOVA; $F_{3,131} = 9.00$, $p < 0.0001$) but no treatment effect ($F_{3,131} = 1.08$, $p = 0.3607$) or interaction ($F_{15,131} = 0.89$, $p = 0.5742$). Both treatment ($F_{3,142} = 4.63$, $p = 0.0041$) and position effects ($F_{5,142} = 6.43$, $p < 0.0001$) were found in August (but no interaction, $F_{15,142} = 1.16$, $p = 0.3079$). T-tests of this ratio in August in control plots vs. each treatment showed that

controls had a significantly higher ratio than the medium ($T_{142} = 2.36$, $p = 0.0194$) and high ($T_{142} = 3.47$, $p = 0.0007$) nutrient addition rates (but not the low rate, $T_{142} = 0.88$, $p = 0.3811$).

Aboveground Biomass of Native Graminoids. Native graminoid biomass did not respond to fertilizer addition. The average aboveground biomass ranged from 390 ± 47.3 g/m² in the control treatment to 475 ± 44.1 g/m² in the low treatment (split-plot ANOVA; $F_{3,127} = 0.82$, $p = 0.4847$; Figure 3, Table 2). Although we did not directly test the effects of competition between native graminoids and *T. × glauca*, the lower graminoid biomass within the *Typha* stand ($F_{5,127} = 0.82$, $p < 0.0001$) did not result in a differential response to treatment by position (SLICE option on subplots, $F_{3,127} = 1.63$, $p = 0.1846$). This lack of response and lack of an interaction between treatment and position ($F_{5,127} = 0.73$, $p = 0.7531$) indicate little capacity of native graminoids to increase aboveground biomass in response to fertilizer over one growing season, in contrast with the strong responses of *T. × glauca*.

Aboveground Biomass of *T. × glauca*. Overall, there was a strong fertilizer effect on *T. × glauca* biomass (split-plot ANOVA; $F_{3,130} = 18.73$, $p < 0.0001$; Table 2). The total standing crop (all species) increased with low, medium, and high fertilizer treatments (Figure 3), largely due to the increase of *T. × glauca* biomass. Plots receiving the most fertilizer had 85% more total biomass (1434 ± 70 g/m²) than controls (777 ± 38 g/m²). *Typha × glauca* biomass in the high treatment (1029 ± 256.1 g/m²) was more than double that of the control (431 ± 80.52 g/m²). Pairwise comparisons of the difference of least-squares means across treatments revealed significantly greater biomass under high fertilization than medium ($T_{124} = 2.91$, $p < 0.0043$), low ($T_{124} = 4.64$, $p < 0.0001$) and control ($T_{124} = 6.78$, $p < 0.0001$) treatments. Low and medium treatments also exceeded the control ($T_{124} = 2.37$, $p = 0.0193$ and $T_{124} = 4.00$, $p < 0.0001$, respectively).

As expected, *T. × glauca* biomass was significantly greater within the *Typha* stand ($F_{5,130} = 6.81$, $p < 0.0001$; Figure 4) than where *Carex* dominated, with no interaction between treatment and position ($F_{5,130} = 1.26$, $p = 0.2352$). It was the response of biomass to treatment by subplot position that was of interest. In the *Carex*-dominated position (subplot 1), we observed increased *T. × glauca* biomass with high fertilization (962.9 ± 135.0 g/m²), compared to medium (324.0 ± 88.8 g/m²), low (197.1 ± 50.1 g/m²), and control (321.8 ± 82.9 g/m²) plots. We then tested for a fertilizer effect for each position along the 1×6 -m plot using the SLICE option. The treatment effect was strongly significant for subplots 1, 3, and 4 ($F_{3,124} = 5.90$, $p = 0.0009$; $F_{3,124} = 7.44$, $p < 0.0001$; $F_{3,124} =$

Table 2. Responses of Gardner Marsh to fertilizer addition. Data are treatment means and ANOVA p-values.

Response variable	Fertilization treatments												ANOVA p-values		
	Control			Low			Medium			High			Treatment effect	Position effect	Inter-action
	mean	S.E.		mean	S.E.		mean	S.E.		mean	S.E.				
Graminoid % cover (June)	21.5 a	2.1	16.9 a	1.8	22.3 a	2.3	18.3 a	2.1	18.3 a	2.1	—	—	<0.0001	—	
Graminoid % cover (August)	18.7 a	1.8	22.9 a,b	3.5	18.1 a,b	1.7	13.6 b	1.7	13.6 b	1.7	—	—	<0.0001	—	
Change in graminoid cover (August–June)	-1.9 a	2.5	-6.0 a	3.2	-4.3 a	2.1	-4.6 a	2.1	-4.6 a	2.1	—	—	<0.01	—	
<i>Typha</i> density as ramets/m ² (June)	11.4 a	1.3	12.8 a	1.7	13.4 a	1.6	15.4 a	1.6	15.4 a	1.6	—	—	<0.0001	—	
<i>Typha</i> density as ramets/m ² (August)	15.5 a	1.3	19.4 a,b	1.8	22.7 b	1.9	29.2 c	2.1	29.2 c	2.1	<0.0001	<0.0001	<0.0001	—	
Graminoid cover/ <i>Typha</i> density (June)	2.8 a	0.5	3.4 a	0.9	3.1 a	0.5	2.3 a	0.4	2.3 a	0.4	—	—	<0.01	—	
Graminoid cover/ <i>Typha</i> density (August)	6.4 a	0.8	5.3 a,b	0.9	3.6 b,c	0.9	2.3 c	0.9	2.3 c	0.9	<0.01	<0.0001	<0.0001	—	
<i>Typha</i> height as cm (August)	196.4 a	8.2	213.8 a	7.9	215.4 a	7.7	238.1 b	8.0	238.1 b	8.0	<0.01	<0.0001	<0.0001	—	
<i>Typha</i> aboveground biomass as g/m ² (August)	431.0 a	45.4	645.6 b	57.9	721.5 c	75.4	1028.9 d	74.5	1028.9 d	74.5	<0.0001	<0.0001	<0.0001	—	
Graminoid aboveground biomass g/m ² (August)	389.6 a	30.7	474.5 a	44.1	474.4 a	46.7	415.8 a	47.3	415.8 a	47.3	—	—	<0.0001	—	
<i>Typha</i> total belowground biomass as g/m ³ (October)	2174.9 a	170.9	2356.9 a	220.6	2251.3 a	178.0	2529 a	166.6	2529 a	166.6	—	—	<0.01	—	
<i>Typha</i> rhizome biomass as g/m ³ (October)	431.4 a	127.5	752.5 b	166.6	626.1 b	116.8	617.8 b	139.1	617.8 b	139.1	—	—	<0.0001	—	
Root biomass pooled as g/m ³ (October)	1743.5 a	89.3	1604.5 a	118.8	1625.2 a	136.3	1911.2 a	119.4	1911.2 a	119.4	—	—	—	—	

Means with the same letters per response variable are not statistically different from each other; p > 0.05. —, not significant. p > 0.05.

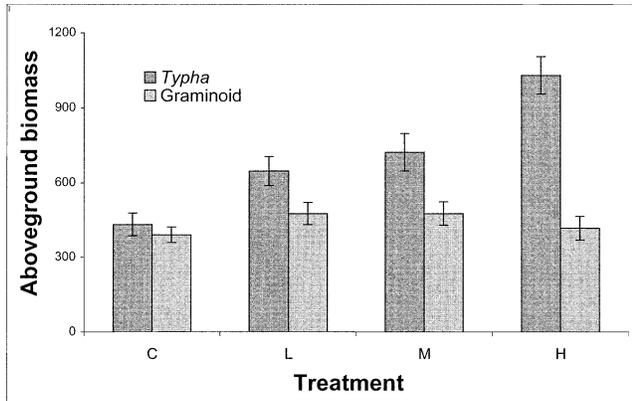


Figure 3. *Typha* × *glauca* and graminoid aboveground biomass (g/m²) by treatment on August 1999. C, L, M, and H as in Figure 3. Error bars represent 1 S.E.

1.76, $p < 0.0001$, respectively). Most of this effect was due to increased *T. × glauca* biomass in the high fertilizer treatments and was not a response of native graminoids. The effect was marginal for subplot 6 ($F_{3, 124} = 1.74$, $p = 0.0596$) and lacking in subplots 5 and 2 ($F_{3, 124} = 1.71$, $p = 0.1626$ and $F_{3, 124} = 1.23$, $p = 0.3016$, respectively). Responses of *T. × glauca* to fertilizer were spatially variable, with a tendency for greater treatment effect where the *Typha* stand overlaps the sedge meadow.

Typha × glauca Density and Height. To determine whether the increase in *T. × glauca* biomass was due to an increased density of ramets or increased *T. × glauca* height, we analyzed density and height separately in ANOVA (Table 2). The number of *T. × glauca*

ramets increased from June 23 to August 25, 1999 (Table 2), with nearly twice the increase in high fertilizer plots ($29.2 \pm 2.1/m^2$) as in control plots (16.4 ± 1.5 ramets/m²). The experimental plots were laid out across a gradient of *Typha* density, which persisted through August 1999 ($F_{3, 138} = 9.79$, $p < 0.0001$, with *T. × glauca* density in subplot 6, 30.3 ± 2.2 ramets/m² greater than in subplot 1, 13.9 ± 1.7 ramets/m², and no interaction between treatment and position, $F_{3, 138} = 0.59$, $p = 0.8795$). The shift to *Typha* was thus accelerated by fertilizer but not complete within one growing season.

Typha × glauca height also increased significantly with treatment ($F_{3, 115} = 5.15$, $p = 0.0022$). Maximum heights in the high fertilizer treatment exceeded 3 meters and were 20% taller than plants in control plots. There was also a position effect ($F_{5, 115} = 4.87$, $p = 0.0004$), in which plants within the *Typha* stand (subplot 6) were nearly 20% taller than those in the sedge meadow. No interaction was found between treatment and position ($F_{15, 115} = 0.43$, $p = 0.9674$). *Typha × glauca* height and density were positively correlated ($R = 0.5762$, $p < 0.01$).

Belowground Biomass. Rhizome alone did not respond to fertilizer treatment (Table 2). There was an effect of subplot position ($F_{5, 63} = 4.73$, $p = 0.0010$) but no treatment effect ($F_{3, 63} = 2.00$, $p = 0.1229$) or interaction ($F_{15, 63} = 1.23$, $p = 0.2806$). For roots alone, there was no treatment, position or interaction effect ($F_{3, 87} = 0.58$, $p = 0.6322$; $F_{5, 87} = 0.89$, $p = 0.4883$; $F_{15, 87} = 0.40$, $p = 0.9756$, respectively). Root and rhizome biomass (pooled because cattails and other gra-

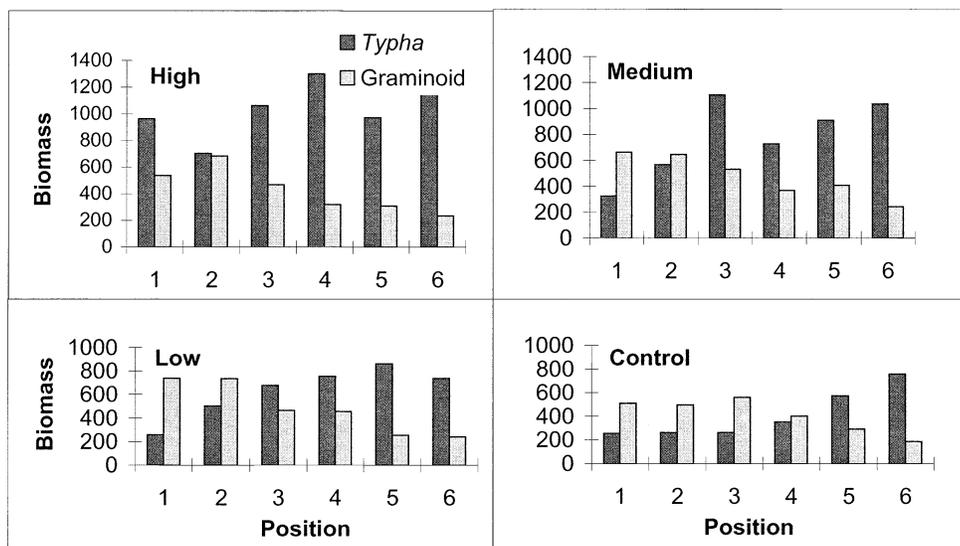


Figure 4. Aboveground *Typha × glauca* and graminoid biomass (g/m²) by nutrient-addition treatment for each subplot position. Subplots numbered 1 were toward the sedge meadow and those numbered 6 were toward the interior of the cattail stand (Figure 1). Error bars represent 1 S.E.

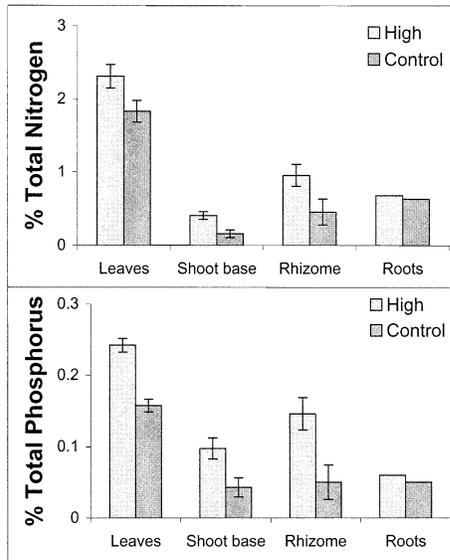


Figure 5. Concentrations of nitrogen (top graph) and phosphorus (bottom graph) in *Typha × glauca* leaves, leaf bases, rhizomes and roots (data are percent of dry weight). Note: roots directly attached to *Typha × glauca* were pooled and do not have error bars. Error bars represent 1 S.E.

minoids could not be distinguished) was highly variable among subplots, ranging nearly 12-fold, from 395 g/m² in one medium fertilizer subplot to 4710 g/m² in a low fertilizer subplot, but the variation was not a treatment effect ($F_{3, 87} = 0.80$, $p = 0.4947$) or interaction ($F_{15, 87} = 0.62$, $p = 0.8548$). The only pattern for the pooled belowground biomass was a subplot position effect ($F_{5, 87} = 3.67$, $p = 0.0046$).

Comparing control and high-fertilizer plots, the mean belowground biomass was similar (2175 ± 171 g/m² and 2529 ± 167 g/m², respectively), while the ratio of below- to *Typha* aboveground biomass was substantially higher for controls (2.6 vs. 1.8), largely due to differences aboveground. This ratio was log-transformed to equalize variances, and the ANOVA showed a treatment effect ($F_{3, 79} = 2.88$, $p = 0.0411$) and a subplot position effect ($F_{5, 79} = 5.62$, $p = 0.0002$) but no interaction ($F_{15, 79} = 0.98$, $p = 0.4883$), as for aboveground biomass.

Tissue Nutrient Concentrations. Total nitrogen (TN) concentrations of *T. × glauca* tissues increased with fertilizer addition ($F_{1, 6} = 35.06$, $p = 0.0010$). Leaves had significantly higher TN concentration than shoot bases ($T_{19} = 21.27$, $p < 0.0001$) and rhizomes ($T_{19} = 7.55$, $p < 0.0001$). Leaves had 2.0 and 5.6 times the nitrogen concentration of shoot bases and rhizomes, respectively, and shoot bases had significantly higher TN than rhizomes ($T_{19} = 5.84$, $p < 0.0001$) (Figure 5). We found an interaction between treatment and plant part ($F_{2, 19} = 5.20$, $p = 0.0158$) mainly due to

increased TN in rhizomes of fertilized vs. control plots.

Fertilization increased the concentration of total phosphorus (TP) in plant tissues (Figure 5; ANOVA, $F_{1, 6} = 22.19$, $p = 0.0033$), with differences in TP among plant parts ($F_{2, 21} = 56.54$, $p < 0.0001$). Leaves contained the most TP, rhizomes were intermediate, and shoot bases lowest. Leaves had about 2.5 times the TP as shoot bases ($T_{21} = 10.30$, $p < 0.0001$), and rhizomes had about 1.6 times that of shoot bases ($T_{21} = 4.94$, $p < 0.0001$) in the high fertilizer treatment. Shoot bases and rhizomes did not differ in TP ($T_{21} = 1.04$, $p = 0.2884$), and there was no interaction between treatment and plant part ($F_{2, 21} = 1.52$, $p = 0.2421$).

Tissue N:P ratios (square root transformed to equalize variances for ANOVA) showed no treatment effect ($F_{1, 6} = 0.60$, $p = 0.4686$) or interaction but strong differences among plant parts ($F_{2, 19} = 90.74$, $p < 0.0001$). Leaves had more than twice the N:P ratio of shoot bases (9.7 ± 0.5 vs. 4.4 ± 0.7 ; $T_{19} = 13.27$, $p < 0.0001$) and a significantly higher N:P ratio than rhizomes (8.2 ± 1.4 ; $T_{19} = 2.78$, $p = 0.0119$), and rhizomes had a significantly higher N:P ratio than shoot bases ($T_{19} = 4.10$, $p = 0.0006$). Although TP was most concentrated in leaves (Figure 5), the low N:P ratio of shoot bases suggests rapid allocation of N to leaves or preferential retention of P by shoot bases. N:P ratios showed a tendency to decrease with fertilization in the leaves (11.5 ± 0.5 mean \pm s.e for control; 9.6 ± 0.5 for high treatment) and rhizomes (8.4 ± 0.3 ; 5.7 ± 0.5), but not in the shoot bases (4.4 ± 0.8 ; 4.3 ± 0.3).

DISCUSSION

Did Nutrient Addition Accelerate the Expansion of *Typha × glauca* into the Sedge Meadow?

In Gardner Marsh, *T. × glauca* responded to nutrient addition with increases in aboveground biomass, ramet density, and height, with the high fertilizer plots producing more than twice the biomass in control plots. Ramet density was increased by ~25%, 47%, and 90% for low, medium, and high nutrient addition, respectively. Plants were 20% taller in plots with high fertilizer than controls, the tallest exceeding 3 meters.

Rapid responses to nutrient addition typify opportunistic invaders (Grime 1979, Montague and Givnish 1996, Mack et al. 2000). In the Everglades, *Typha domingensis* Pers. expands into the native *Cladium jamaicense* Crantz community when phosphorus levels are elevated (Davis 1991, Urban et al. 1993). *Typha domingensis* can take advantage of short-term nutrient supplies, while sawgrass responds much more slowly

Table 3. Comparison of *Typha* spp. biomass (*Typha* × *glauca* was dominant in all cases). Locations are Wisconsin (this study) and Delta Marsh, Manitoba, Canada (Neill 1990).

Reference	Habitat	Application Rate	Total Nutrient addition/m ² /yr	Biomass (g/m ²)	
				Above-ground	Below-ground
This study	Sedge meadow	0	Control	431 ± 45	na
		5 equal applications from May to August	(15.6 g N + 1.7 g P + 6.3 g K)	646 ± 58	na
			(31.3 g N + 3.4 g P + 12.6 g K)	722 ± 75	na
			(62.5 g N + 6.9 g P + 25.2 g K)	1029 ± 75	na
This study	Position 6 in the <i>T.</i> × <i>glauca</i> stand	0	Control	756 ± 126	2286 ± 295
		5 equal applications from May to August	(15.6 g N + 1.7 g P + 6.3 g K)	736 ± 124	2502 ± 497
			(31.3 g N + 3.4 g P + 12.6 g K)	1035 ± 194	2528 ± 273
			(62.5 g N + 6.9 g P + 25.2 g K)	1161 ± 197	2759 ± 269
Neill 1990	Deep marsh	0	Control	1387 ¹	4990
		Equal application May and June. Biomass taken after 2 years of nutrient addition	25 g N	1740 ¹	4725
			100 g N	1925 ¹	4796
			20 g P	1043 ¹	3582
			60 g P	1062 ¹	3601
			(100 g N + 60 g P)	2294 ¹	4033

¹ Biomass estimated from published graphs.

(Davis 1991). The situation in Gardner Marsh appears to be similar. In nutrient-rich environments, species that preferentially allocate nutrients to storage risk being outcompeted by opportunistic species that put resources into vegetative growth.

Overall, nutrient addition stimulated cattail above-ground biomass. Although there was no statistical interaction between nutrient addition and all subplot positions, when we isolated the fertilization effect according to each position, we were able to show an increase in aboveground cattail biomass at subplot 1, at the sedge meadow end of the fertilized plot (SLICE option in SAS). Under high fertilization, subplot 1 had three times the cattail aboveground biomass found in the control, while graminoid biomass was relatively unchanged (Figure 4). At low to medium fertilization levels, cattail aboveground biomass remained low, suggesting that large amounts of fertilization stimulated the expansion of *T.* × *glauca*. Our inability to detect belowground responses to fertilization could be influenced by the small size of the soil core compared to the scale of spatial variability in belowground biomass, the subsampling of subplots, or the single growing season evaluated (i.e., belowground responses could lag behind those of shoots).

Did Nutrient Addition Benefit Native Graminoids?

Although some studies of sedge meadow species have shown increased biomass with fertilization (Tables 3 and 4), our native graminoids had the most aboveground biomass (475 ± 44 g/m²) under our lowest fertilizer rate (using 9N:1P:4K). In Michigan, Richardson and Marshall (1986) showed a response of *Carex* spp. to fertilization in a single growing season. Their high treatment had a 3N:1P ratio and yielded an aboveground biomass of 506 ± 49 g/m² (Richardson and Marshall 1986). In The Netherlands, Aerts et al. (1992) fertilized fens with 20 g N/m² and found that highly productive species of *Carex* (*C. lasiocarpa* and *C. acutiformis* Ehrh.) allocated biomass and nitrogen to leaves, while less productive species (*C. diandra* Schrank and *C. rostrata* Stokes) allocated N to belowground tissues. In the Florida Everglades, *Cladium jamaicense* did not respond until year two of fertilization (4.8 g P/m², comparable to our medium to high treatments), at which time, the aboveground biomass was two to three times that of controls (Craft et al. 1995). In our one-year study, native graminoids did not respond in cover or aboveground biomass, and there was no detectable response of roots (pooled for all species). The maximum height reached by native graminoids

Table 4. Biomass of sedge meadow species and cattails in this and other studies.

Reference	Site	Habitat	Dominant Species	Application Rate	Total Nutrient addition g/m ²	Biomass (g/m ²)	
						Aboveground	Belowground
This study	Wisconsin, U.S.A.	Sedge meadow	<i>Carex stricta</i> , <i>C. lasiocustris</i> , <i>C. lasiocarpa</i>	na	Pooled ¹	622.6–45	2176–135 ²
Aerts et al. 1992	The Netherlands	Experimental ponds (1 × 50 m)	<i>Carex lasiocarpa</i>	Every 3 weeks	20 g N	940	910
Richardson and Marshall 1986	Michigan, U.S.A.	Fen	<i>C. aquatilis</i> , <i>C. lasiocarpa</i> , <i>C. oligosperma</i>	0 Every 2 weeks from May to September	0 (17 g N + 5.5 g P)	385–28 506–49	2500 4300
Bernard and Solsky 1977	New York, U.S.A.	Sedge meadow	<i>C. lacustris</i>	na	none	965	208
Jervis 1969	New Jersey, U.S.A.	Sedge swale	<i>Carex</i> spp (<i>C. stricta</i>)	na	none	1492	na
Gorham and Somers 1972	Alberta, Canada	Fen	<i>C. aquatilis</i>	na	none	380	na
Auclair et al. 1976	Quebec, Canada	Sedge meadow	<i>Carex lacustris</i> , <i>C. aquatilis</i> , <i>Catalpa grostis canadensis</i> , <i>Typha angustifolia</i>	na	none	807	na
Craft et al. 1995	The Florida Everglades, U.S.A.	Subtropical freshwater wetland	<i>Cladium jamaicense</i>	Control Every 2 months after 2 years	0 4.8 g P	1158 3284	1556–162 1974 ³
Garver et al. 1988	Minnesota U.S.A.	Minerotrophic fen. <i>Typha</i> rhizomes planted in paddies	<i>Typha</i> × <i>glauca</i> <i>Typha latifolia</i> <i>Typha angustifolia</i>	Before planting Before planting Before planting	15 g P 15 g P 15 g P	781 727 265	401 307 166
Bernard and Bernard 1973	Minnesota, U.S.A.	Cattail marsh in October	<i>Typha</i> × <i>glauca</i>	na	noen	946–98	954–70
Bernard and Fitz 1979	Central NY, U.S.A.	Cattail marsh	<i>Typha</i> × <i>glauca</i>	na	none	1360	na
Boyd and Hess 1970	Southeastern U.S.A.	30 wetlands	<i>Typha latifolia</i>	na	none	946–2252	na
Weisner 1993	Sweden	Cattail marsh next to a hypertrophic lake	<i>Typha latifolia</i> <i>Typha angustifolia</i>	na na	none none	236–38 386–31	na na
Miao and Sklar 1998	The Florida Everglades, U.S.A.	Subtropical freshwater wetland	<i>Typha domingensis</i>	na	none	1240–126	na
Jervis 1969	New Jersey, U.S.A.	Cattail marsh	<i>Typha</i> spp.	na	none	1905	na

¹ Treatments were not significantly different, and aboveground biomass from all fertilization treatments were pooled.² Belowground biomass was calculated for position 1 only.³ Estimated values from published graphs.

was roughly 1 meter, while *T. × glauca* leaves exceeded 3 meters. We surmise that *Carex* species were much less capable of acquiring nutrients and light than the invasive *Typha*.

Was N or P Limiting?

While nitrogen limits plant growth in salt marshes (Valiela and Teal 1979, Boyer and Zedler 1998) and some freshwater wetlands (Bowden 1987), phosphorus limitation is indicated in fens (Boyer and Wheeler 1989), and co-limitation of N and P has been shown for freshwater wetlands (Hayati and Proctor 1991, Bedford et al. 1999). In our greenhouse experiment, *T. × glauca* did not respond when we added N or P alone, but it did respond to N+P; i.e., 7N:1P increased total leaf length of *T. × glauca* four-fold over that of controls, while growth in the 14N:1P treatment was indistinguishable from controls, although variable. Co-limitation is more difficult to demonstrate in field settings, where ambient conditions and nitrogen fixers complicate supply rates. The watershed of Gardner Marsh is known to receive pulses of both N and P in early spring (Prentki et al. 1977), so our fertilizer (9N:1P) additions were in addition to inflows via surface water. We analyzed four tissues from *T. × glauca* plants and found most N:P ratios to be <14. Leaf tips and rhizomes from the high-fertilizer treatments generally had lower N:P ratios than controls (N:P = 9.6 ± 0.5 vs. 11.5 ± 0.4 for leaf tips and 5.7 ± 0.5 vs. 8.4 ± 0.3 for rhizomes), although shoot bases were similar. While Koerselman and Meuleman's (1996) index would suggest N limitation, we think that light and/or space were more limiting than nutrients at the high fertilizer rate and that low N:P ratios could reflect luxury uptake of P. Furthermore, a single ratio might not accurately represent a species' N or P limitation status. For example, one plant had a leaf N:P ratio of 13.7 while its shoot base ratio was 8.5. A shift in N:P ratios, in response to fertilization, especially in growth tissues, could reflect fundamental differences between aggressive invasives and conservative plant growth, a topic that merits further attention.

What Makes *T. × glauca* so Invasive?

Typha × glauca readily allocated nutrients to growing tissues, its clonal growth likely enhanced its ability to invade and displace native graminoids, and its hybrid status might confer vigorous growth. Nutrient allocation was investigated by Miao and Sklar (1998) in the Florida Everglades, where the invasive *Typha domingensis* had more P in leaves than the native *Cladium jamaicense*. Likewise, we found elevated levels of TN and TP in *T. × glauca*, comparing our high fertiliza-

tion rate to controls. The higher concentration of TN and TP in leaves than storage tissues is consistent with opportunistic growth, while increased N and P concentrations in belowground tissues indicate an ability to conserve nutrients for future growth (Chapin et al. 1990). In our greenhouse experiment, rhizomes that received no nutrient treatment persisted for 12 weeks, while those fed 7N:1P exhibited robust growth. Such plasticity in growth also contributes to invasiveness (Hutchings and Wijesinghe 1997).

Other factors also enhance invasion ability. Ellstrand and Schierenbeck (2000) reviewed 28 invasive hybrids, of which more than 50% involved at least one non-native parent, and 25% were clonal species. *Typha latifolia* and *T. angustifolia* readily hybridize and form *T. × glauca* where the parents are sympatric (Smith 1967). Hotchkiss and Dozier (1949) consider *T. angustifolia* to have arrived on the US eastern seaboard in the early 1900s, after which it spread north to Manitoba and west to South Dakota (Galatowitsch et al. 1999). Its ability to invade roadside ditches likely relates to its tolerance of salt (Wilcox 1986) and a wide range of water depths (Waters and Shay 1992).

Like its parents, *T. × glauca* forms clones, but it surpasses both parents in the densities of its roots and ramets (Marsh 1951). In this study, nutrient addition increased *T. × glauca* biomass, height, and ramet density. The ability to take up and store nutrients helps clonal species grow rapidly and preempt space (de Kroon and van Groenendael 1997); hence, it is no surprise that clonal species comprise ~70% of invasive species in the global temperate zone (Klimes et al. 1997). Vegetative expansion of *T. × glauca* clones was documented as 5m/yr for the shores of Lake Erie (McDonald 1955) and from 8 to 70 ha in two years in a Michigan site (Smith 1967). Large rhizomes not only store nutrients but also allow resource sharing among ramets (de Kroon and van Groenendael 1997, Hutchings and Wijesinghe 1997, Amsberry et al. 2000).

The rapid uptake of nutrients, hybrid vigor, and clonal habit not only confer invasion potential to *T. × glauca*, but also are likely to facilitate its formation of monotypes (single-species stands). Even in restored marshes and wastewater treatment wetlands that have been planted with multiple species, *Typha* clones eventually form monotypes when nutrients are plentiful (Bastian 1993, Brown and Bedford 1997).

Conclusions

Native graminoids did not increase in cover or aboveground biomass when nutrients were added to Gardner Marsh, not even in subplots with the fewest *T. × glauca* ramets. In contrast, *T. × glauca* took up more nutrients when fertilized and readily allocated

them to growth, as well as storage. Such differential responses to nutrient addition can shift native wetland vegetation to monotypes of invasive species (Tilman and Wedin 1991, Miao and Sklar 1998).

In this study, the addition of a general lawn fertilizer (9N:1P:4K) at 1/5 the rate recommended for new lawns was more than enough to stimulate the expansion of *Typha* × *glauca* into a remnant sedge meadow. To reduce the spread of *T. × glauca* and other invasive species, nutrient inflows (especially via urban runoff) must be managed across entire watersheds. A vigorous and far-reaching program of public education will be needed to reduce nutrients in runoff.

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