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

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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.

1. Introduction

The plant diversity of urban wetlands can be low because of limited propagule availability, or because site conditions are unfavorable. Propagules could be limited in an isolated site that lacks dispersal corridors, or where only one species is introduced to a constructed wetland (Kadlec and Knight, 1996; Bonilla-Warford and Zedler, 2002; Seabloom and van der Valk, 2003). This suggests that introducing native species through seeding or planting might be sufficient to promote the development of a diverse community of native species. However, limited propagule availability might not be the only reason for low native species richness. The unnatural hydrologic regimes common to urban wetlands might discourage some species and contribute to low diversity (Reinelt et al., 1998; Galatowitsch et al., 2000; Kowalski and Wilcox, 2003). Other stresses, such as sediment and nutrient inputs could also hinder the growth of native plants and stimulate the 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-m^2 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	–

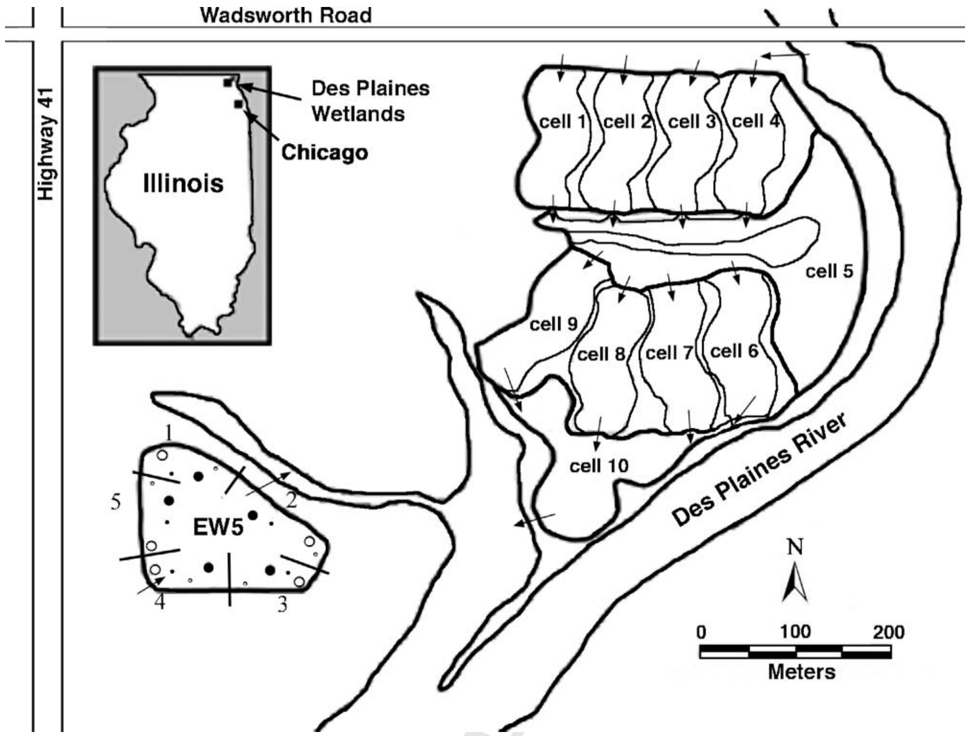

Fig. 1 – Map of DPRWDP. Arrows indicate direction of water flow. In the upper right are the eight cells (cells 1–4 and 6–9) where we sampled vegetation and planted native species. We experimentally seeded in EW5. Small and large circles indicate locations of small and large plots. Black circles indicate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

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

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

Our seeding study was conducted in Experimental Wetland #5 (EW5) of DPRWDP; it is a 1.8-ha wetland created in 1989 (Fig. 1). EW5 is hydrologically separated from the previously described wetland cells. Water is pumped into EW5 from a pipe near the southwestern edge, and a weir on the northeastern edge controls the outflow. The wetland is supplied with both river water (from the Des Plaines River) and ground water. Nearly all of EW5 is a *T.* × *glauca* monotype that is dense and tall (45 ± 2.3 ramets m^{-2} and maximum height >2.5 m). A thick layer of *T.* × *glauca* litter has formed throughout the wetland. 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 October 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 plastic waterproof cases, which were attached to stakes at the water/sediment interface approximately 1 m north of the outlet 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-m^2 plots, for a

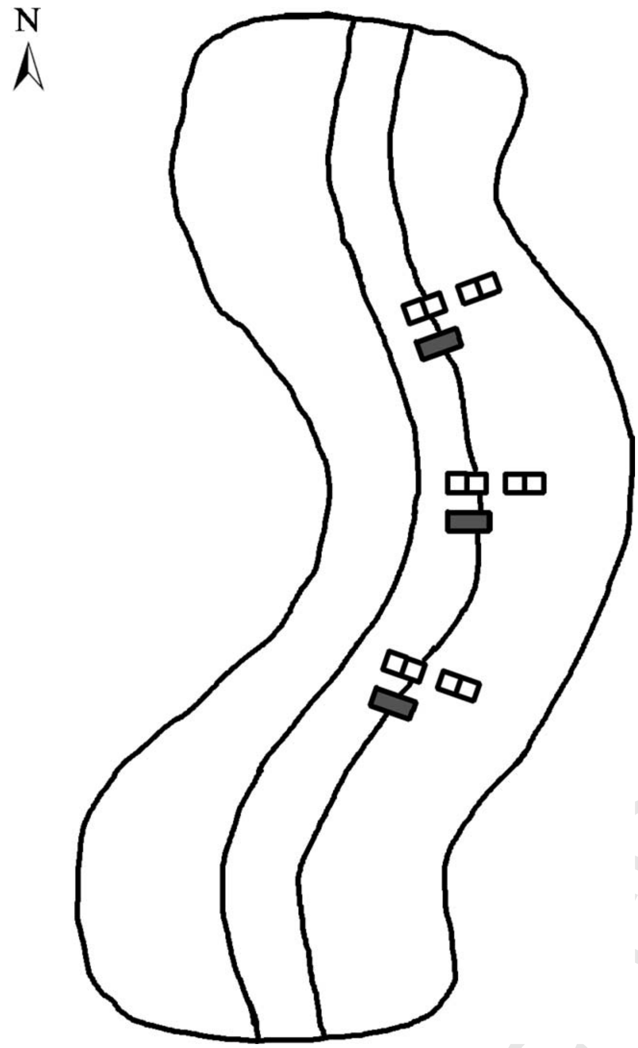

Fig. 2 – Conceptual drawing of a wetland cell (not to scale). A narrow channel runs down the center, with water flowing from north to south. We sampled community composition in the 12 white squares (3 transects, each with 2 pairs of plots). Our planting experiment took place in the three solid rectangles.

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

We determined the elevation of all plots and weirs using a Leica 530 global positioning system, which provides 3-cm vertical precision. To determine the plot elevation, we recorded the elevation at each corner of the plot and used the average of the four measurements. This method was appropriate because there is little vertical relief within each plot. Using plot elevation and wetland water level data, we calculated the average number of days each plot was flooded per growing season from 2001 to 2004 to characterize the hydroperiod of the plots. A plot was considered to be flooded if the water level at the outlet of the wetland cell was higher than the average elevation of the plot.

In 2000 and 2001, we measured standing aboveground biomass and characterized the relationship between *T. × glauca* biomass and biomass of all other species under a range of hydroperiods. We collected biomass from 0.25-m^2 plots adjacent to the permanent plots in each cell. In each 0.25-m^2 harvested plot we cut live plant material at substrate level, separated it into *T. × glauca* and other species, and dried it in a 60 °C oven to constant weight. We did not collect non-rooted species, such as *Lemna minor*, because they flowed in and out of the plots with changing water levels.

In order to characterize the plant species diversity of the 96 1-m^2 permanent plots, we measured stem density of each species in 2000 and 2001, and percent cover of each species from 2001 to 2004. In each permanent plot, we visually estimated percent cover of each species using an 8-point log base 2 scale (i.e. 1, 2, 4, 8, 16, 32, 64, >64). We identified species using Voss (1985) and Chadde (1998); taxonomic nomenclature follows the University of Wisconsin-Madison Herbarium.

We used Swink and Wilhelm's (1994) coefficient of conservatism (CC) for each species to calculate two indicies for each 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.

(Eq. (1)):

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

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

3.3. *Seed introductions*

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

We lowered the water level of wetland EW5 to the soil surface of the lower elevation plots in July of 2002. While the water level was low, we severed all vegetation in all plots at the base using a brush cutter (Fig. 3). We immediately raised the water level by approximately 30 cm to drown the rhizomes of the cut *T.* × *glauca*. Two months of elevated water levels effectively killed *T.* × *glauca* within the plots and had no apparent effect on plants outside plots. In September 2002, we lowered water levels again, at which time the cleared plots were seeded with a mix of 24 native wetland species obtained from Prairie Moon Nursery, Winona, MN (Table 2). We seeded the plots using a split-plot design. Each plot was divided into quarters, two quarters received 8 graminoid and 2 forb seeds per square foot (~0.093 m^2), and the other two quarters received 10 times as many seeds (Fig. 4). We added more graminoid seeds than forbs in an attempt to establish a cover crop of graminoids (Bonilla-Warford and Zedler, 2002). Within the forb and graminoid groups, the number of seeds per species was equal. To allow seeding establishment, we maintained low water levels (no standing water) throughout the winter and early spring. After spring seedling establishment, we increased water levels to create water depth treatments where the shallower plots had water levels that remained saturated throughout the growing season, and the deeper plots had standing water. Staff at the DPRWDP monitored water levels throughout the 2003 and 2004 growing season at the outflow weir.

In order to determine seedling establishment and survival and *T.* × *glauca* re-invasion rates, we measured seedling stem 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				
Bromus ciliatus	0	0	0	0
Calamagrostis canadensis	10	74	14	194
Carex hystricina	0	0	0	0
Carex lacustris	25	154	9	23
Carex stricta	6	70	5	18
Glyceria grandis	0	0	0	0
Leersia oryzoides	12	133	16	110
Schoenoplectus acutus	0	0	0	0
Schoenoplectus tabernaemontani	0	0	0	0
Bolboschoenus fluviatilis	0	0	0	0
Sparganium eurycarpum	3	4	6	27
Spartina pectinata	12	56	7	42
Average	5.7	40.9	4.8	34.5
Forb species				
Alisma subcordatum	6	7	11	17
Angelica atropurpurea	0	0	0	0
Asclepias incarnata	0	0	0	0
Aster novae-angliae	0	0	0	0
Bidens cernuus	24	560	65	342
Eupatorium maculatum	0	0	0	0
Eupatorium perfoliatum	1	1	0	0
Impatiens capensis	1	1	0	0
Lycopus americanus	0	0	0	0
Mentha arvensis	0	0	0	0
Sagittaria latifolia	0	0	2	5
Verbena hastata	1	1	0	0
Average	2.8	47.5	6.5	30.3

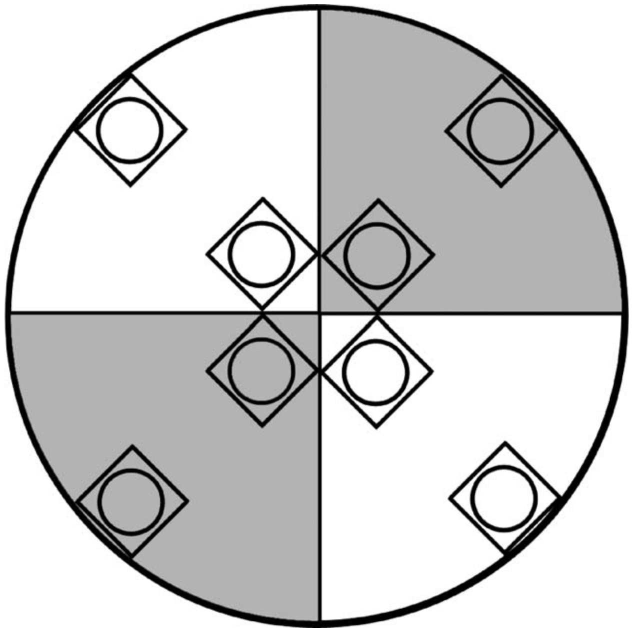

Fig. 4 – A seeded plot in EW5. We used 10× greater seed density in 2 of the 4 quarters of the plot (shaded in gray). In each quarter of the plot we measured *T.* × *glauca* ramet density in two square subplots, and stem density of all other species in two circular subplots.

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-m^2 subplots and stem density of other species (seeded and volunteer species) within a 0.5-m^2 circular frame placed in the center of the subplot; in small plots, we used a square 0.25-m^2 subplot and a 0.125-m^2 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-m^2 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 mgNO_3-N/kg sediment), and extractable ammonium-N (8.3–35.7 mg NH_4-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-m^2 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 × *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.* × *glauca* had greater than 64% cover of the 1-m^2 plots in 37% of the plots throughout the 4-year study. *T.* × *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-m^2 plot over the 4-year study. The maximum richness per 1-m^2 plot (18 species) occurred in cell 6 in 2001 and the minimum (only *T.* × *glauca*) occurred twice in 2002 and 2003, and 17 times in 2004.

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

Average species richness of the 1-m^2 permanent plots over 4 years of sampling was negatively correlated with average *T.* × *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.* × *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.* × *glauca* abundance 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.* × *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.* × *glauca*, with an average of 14%. Plots that averaged greater than 35 days flooded had a broader range of values of *T.* × *glauca* cover, with an average of 49%. The species that occurred in plots with high *T.* × *glauca* density typically had low CC and occurred in plots across a wide range of *T.* × *glauca* densities and plot elevations. For example, *Bolboschoenus fluviatilis* occurred in one plot with 80 *T.* × *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.* × *glauca* densities.

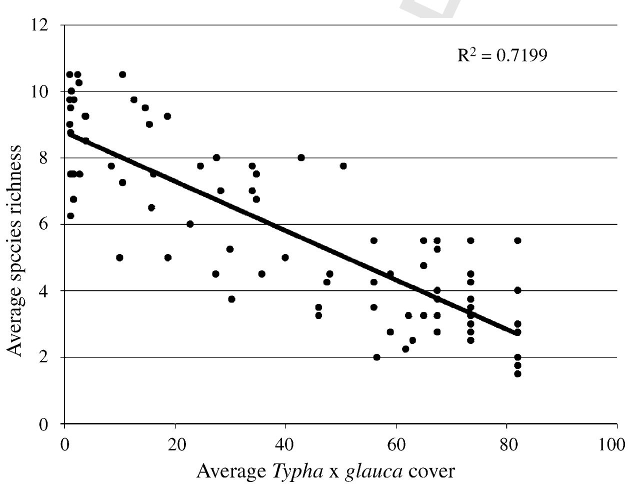

Fig. 5 – Relationship between average species richness of each plot and average *T.* × *glauca* cover. Data points are average values of 4 years of sampling.

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

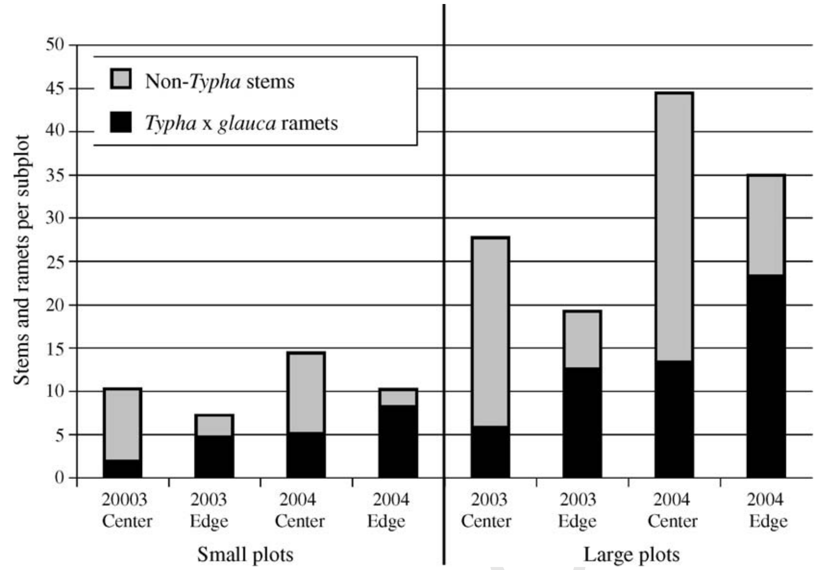

Fig. 6 – Comparison of *T.* × *glauca* ramet and non-*Typha* stem densities in subplots near the center and edges of plots. See Section 3 for subplot sizes.

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

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

4.3.2. *T.* × *glauca* reinvasion

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

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

Fig. 7 – Large plots with *T.* × *glauca* removed and seeds added (photo by Boers). (a) One year after seeding showing low density of *T.* × *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.* × *glauca* and fewer seeded species.

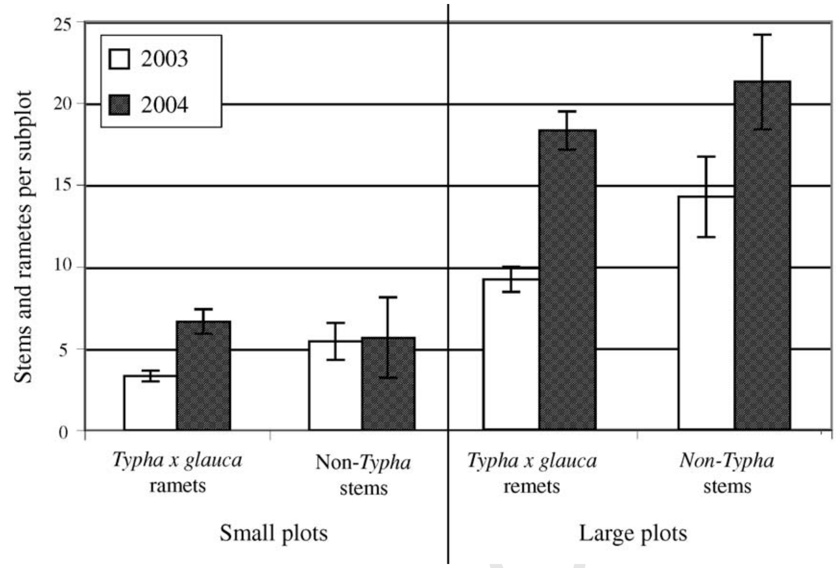

Fig. 8 – Changes in T. × *glauca* ramet and non-*Typha* stem density in large and small plots from 2003 to 2004. See Section 3 for subplots sizes.

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.* × *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.* × *glauca* stand other species became established and may be competing with the re-invading *T.* × *glauca*. There were negative correlations between *T.* × *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.* × *glauca* ramets doubled from 2003 to 2004, but stem density of other species did not change (Fig. 8). In contrast, in large plots *T.* × *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.* × *glauca*, have more time to develop a native plant community before *T.* × *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.* × *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.* × *glauca* was found in 20 of the 24 plots; more than any of the species

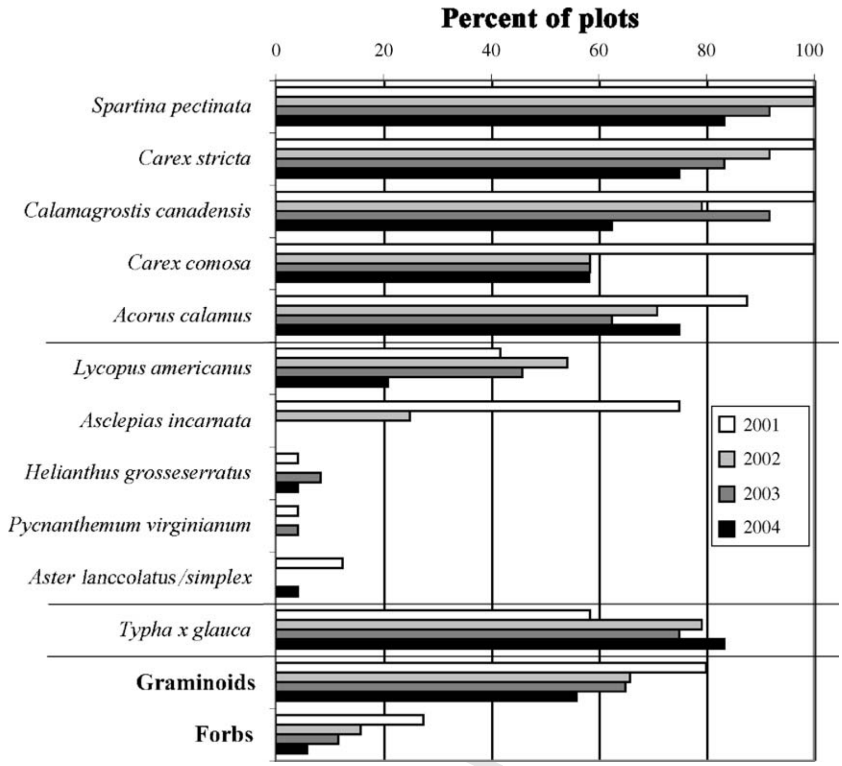

Fig. 9 – Percent of plots containing planted species and *T.* × *glauca* from 2001 to 2004. Species are arranged by life form: graminoids (*Spartina* to *Acorus*), forbs (*Lycopus* to *Aster*), then *T.* × *glauca*. The species list is followed by the average frequency of the planted graminoids and forbs.

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

5. Discussion

5.1. *T.* × *glauca* suppressed species richness

T. × *glauca* was able to suppress other species and dominate wetland EW5 and the eight-wetland cells, despite low nutrient concentration of inflowing water relative to many urban wetlands (Mitsch and Gosselink, 2000). Total species richness of the eight-wetland cells was high, but species richness and floristic quality were low where *T.* × *glauca* abundance was high. Most of the diversity of the wetlands was found in plots away from the channel where they were less flooded and had low cover of *T.* × *glauca*. The negative correlation between *T.* × *glauca* cover and species richness can be explained by *T.* × *glauca*'s rapid growth and its ability to tie up resources (light, nutrients, root space) (Galatowitsch et al., 1999). The *T.* × *glauca* was able to produce a canopy over 3 m tall at a density of 80 ramets m^{-2}. Dry *T.* × *glauca* litter shaded the ground with up to 100% cover by accumulating horizontally and diagonally up to 1.5 m above the ground. Thus, *T.* × *glauca* continued to intercept nearly all of the light long after its leaves died. These characteristics prevented most other species from coexisting with *T.* × *glauca*.

In the permanent plots of the eight-wetland cells, *T.* × *glauca* density was positively correlated with the number of days a plot was flooded. Plots that were flooded for only a short time during the growing season (less than 35 days) each had low cover of *T.* × *glauca*, and plots flooded longer than 35 days frequently had higher *T.* × *glauca* cover values and had a much higher average cover, suggesting a threshold. Plots that were flooded beyond the threshold were likely to be dominated by *T.* × *glauca*, and those flooded less were not. Plots that had high cover of *T.* × *glauca* were strongly correlated with low species richness. On average, plots with 80% *T.* × *glauca* cover had one third as many species as plots with 10% *T.* × *glauca* cover. Eutrophication is associated with frequent flooding, and it favors *Typha* over native plants (Newman et al., 1996; Woo and Zedler, 2002). Not only do floodwaters bring in nutrients, but they also cause wetland soils to release P, via a process called internal eutrophication (Koerselman et al., 1993; Venterink et al., 2002; Aldous et al., 2005). Only a few species were present where *T.* × *glauca* had dense cover, and all were generalist perennials. They were *P. arundinacea*, an aggressive invasive species, and four species that tolerate deep water: *Schoenoplectus tabernaemontani*, *Leersia oryzoides*, *Polygonum punctatum*, and *Bolboschoenus fluviatilis* (Chadde, 1998).

5.2. *Seedling establishment*

T. × *glauca* can be effectively removed by cutting plants at the soil surface and flooding the site to smother roots and rhizomes. This technique is likely to be most effective in midsummer when plants are transporting resources above ground to support flowering and seed production (Beule, 1979; Sale 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-m^2 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-m^2

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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