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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 rhizomatously (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-m^2 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-m^2 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

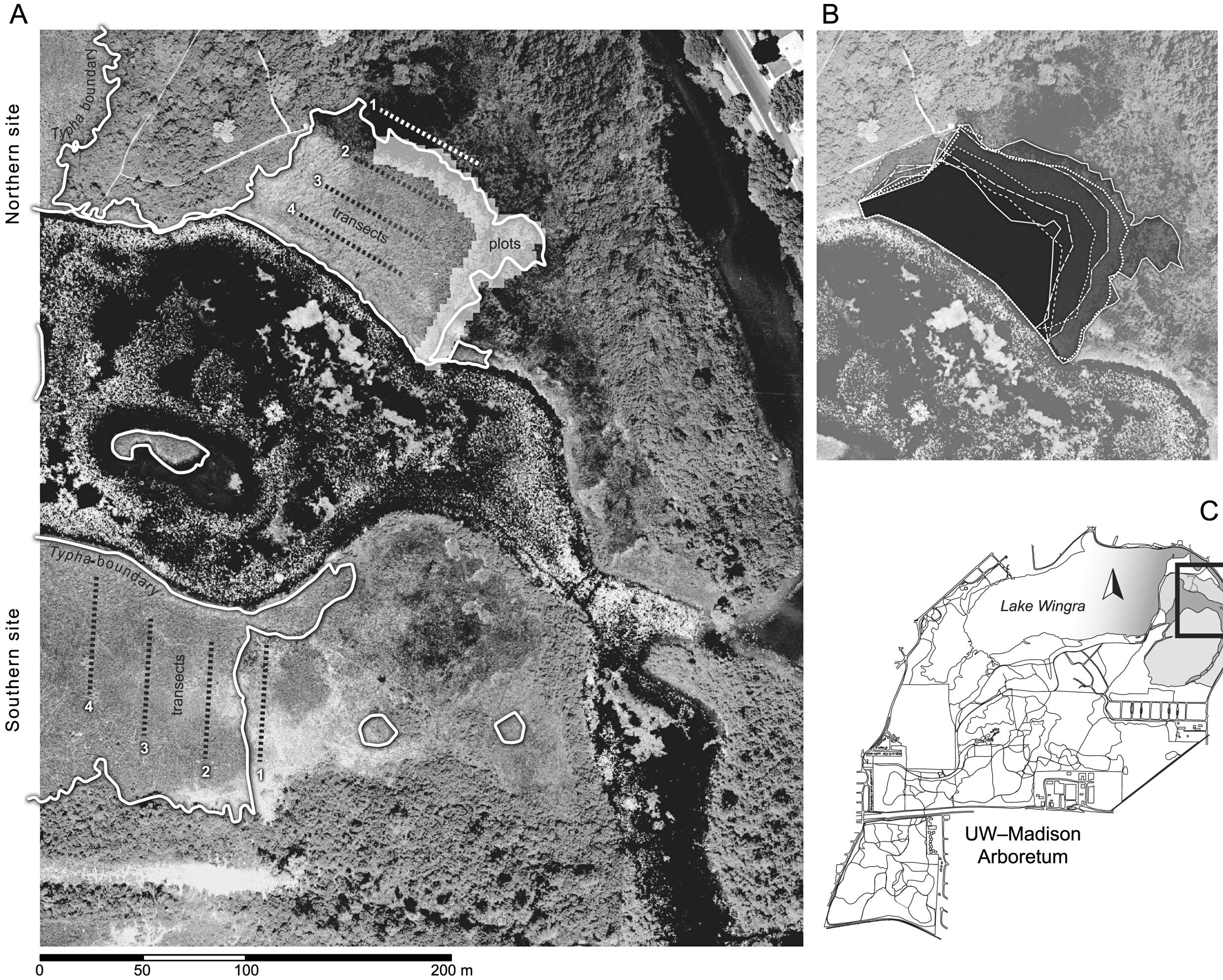

Figure 1. Study site in the University of Wisconsin—Madison Arboretum: (A) Northern Gardner Marsh. Dotted lines represent seed bank sampling transects, whereas the white shaded area in the northern site denotes contiguous 4 × 8–m experimental plots on the *Typha*/sedge meadow ecotone. White lines mark 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 cm^3/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-m^2 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, pretreatment 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 ($\bar{X}$ ± SE) species/m^2. 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-m^2 subplots (Table 1 gives frequency data). Native graminoids had patchy distributions, and two or three species tended to form the canopy in each 1-m^2 subplot, whereas *Eleocharis erythropoda* was nearly ubiquitous in the subcanopy. Forbs were uncommon, except for *Lysimachia thyrsiflora* (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 thyrsiflora*. 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*
Acer rubrum	—	—	—	—	—	1
Andropogon gerardii	—	—	—	x	—	—
Apocynum cannabinum	—	—	x	—	—	—
Asclepias incarnata	—	—	x	—	—	—
Aster sp.	—	—	—	—	—	2
Bidens cernua	1	—	—	—	—	—
Bidens coronata	—	—	—	x	—	—
Calamagrostis canadensis	30	x	x	x	x	42
Campanula aparinoides	1	x	x	x	x	2
Carex aquatilis	34	x	x	—	—	x
Car. flava	—	—	—	x	x	—
Car. lacustris	69	x	x	x	—	x
Car. lasiocarpa	85	x	x	—	—	x
Car. pellita	30	x	—	—	—	—
Carex sp.	—	—	—	—	—	180
Car. stricta	—	x	x	—	—	—
Car. utriculata	19	x	x	—	—	—
Cirsium arvense	—	—	x	—	—	—
Dichanthelium villosissimum	—	—	—	x	x	—
Eleocharis elliptica	—	—	—	x	—	—
E. erythropoda	135	x	x	—	—	27
Eupatorium perfoliatum	—	—	—	x	x	2
Euthamia graminifolia	—	—	—	x	x	—
Galium boreale	9	x	x	—	x	—
Geum sp.	—	—	—	—	—	1
Glyceria striata	—	—	—	—	x	—
Helianthus grosseserratus	—	—	—	x	—	—
Iris sp.	—	—	x	—	—	—
Juncus arcticus	36	x	x	x	—	—
J. canadensis	—	x	x	—	—	—
J. torreyi	—	—	—	—	x	—
Lycopus americanus	—	—	—	x	x	1
Lysimachia quadrifolia	—	—	—	—	x	—
L. thyrsiflora	27	x	x	x	—	47
Lythrum alatum	—	—	x	x	—	—
Mentha arvensis	—	—	x	x	—	—
Mimulus ringens	1	x	x	—	—	—
Muhlenbergia sp.	—	—	—	x	x	—
Oligoneuron riddellii	—	—	—	x	x	—
Phalaris arundinacea	—	x	—	—	—	—
Phragmites australis	—	x	x	—	x	—
Pilea pumila	—	—	x	—	—	—
Polygonom hydropiper	6	x	x	—	—	—
Rosa blanda	—	—	—	x	—	—
Schoenoplectus acutus	19	x	x	—	—	—
S. fluviatilis	2	x	x	x	—	—
S. tabernaemontani	—	—	—	—	x	—
Solanum dulcamara	—	—	—	x	—	—
Sparganium eurycarpum	—	—	—	x	—	—
Spiraea alba	1	x	—	—	—	—
Symphyotrichum pilosum	—	—	—	x	—	—
Teucrium canadense	1	x	—	—	—	—
Thelypteris palustris	—	—	x	x	x	—
Triadenum virginicum	—	—	—	x	—	—
Typha angustifolia	—	x	—	x	x	—
T. latifolia	—	x	x	x	x	—
Typha × *glauca*	150	x	x	x	x	251
Viola 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.

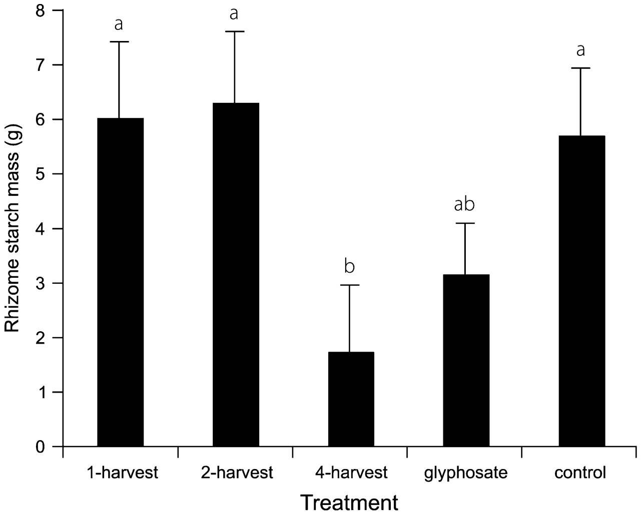

Figure 2. *Typha* rhizome starch mass ± SE by treatment (1-harvest, 2-harvest, 4-harvest, glyphosate, and control) in October 2006; $n = 4$ for each treatment.

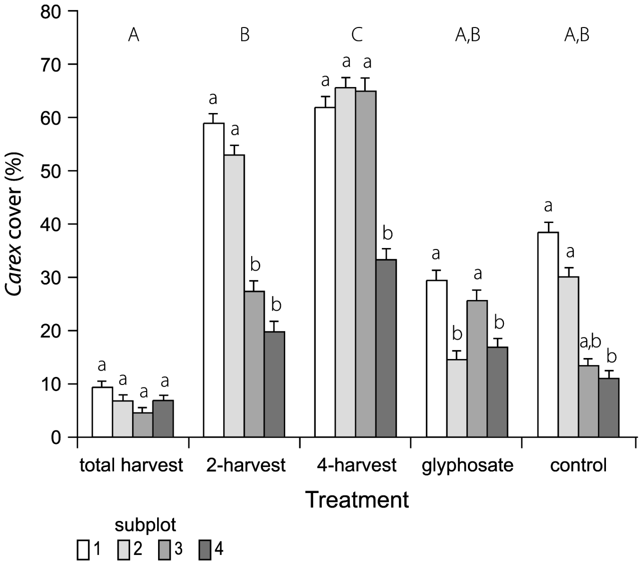

Figure 3. *Carex* cover ± SE by treatment and subplot in October 2007; $n = 8$ for each treatment–subplot combination. Capital letters denote whole-plot treatment contrasts; lowercase letters denote subplot contrasts (within treatments only).

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% ± 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 ($F_{[3,84]} = 4.3$, $p = 0.007$) 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% ± 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 *Carex* 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 *Carex* 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 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 thyrsiflora* 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).

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.

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

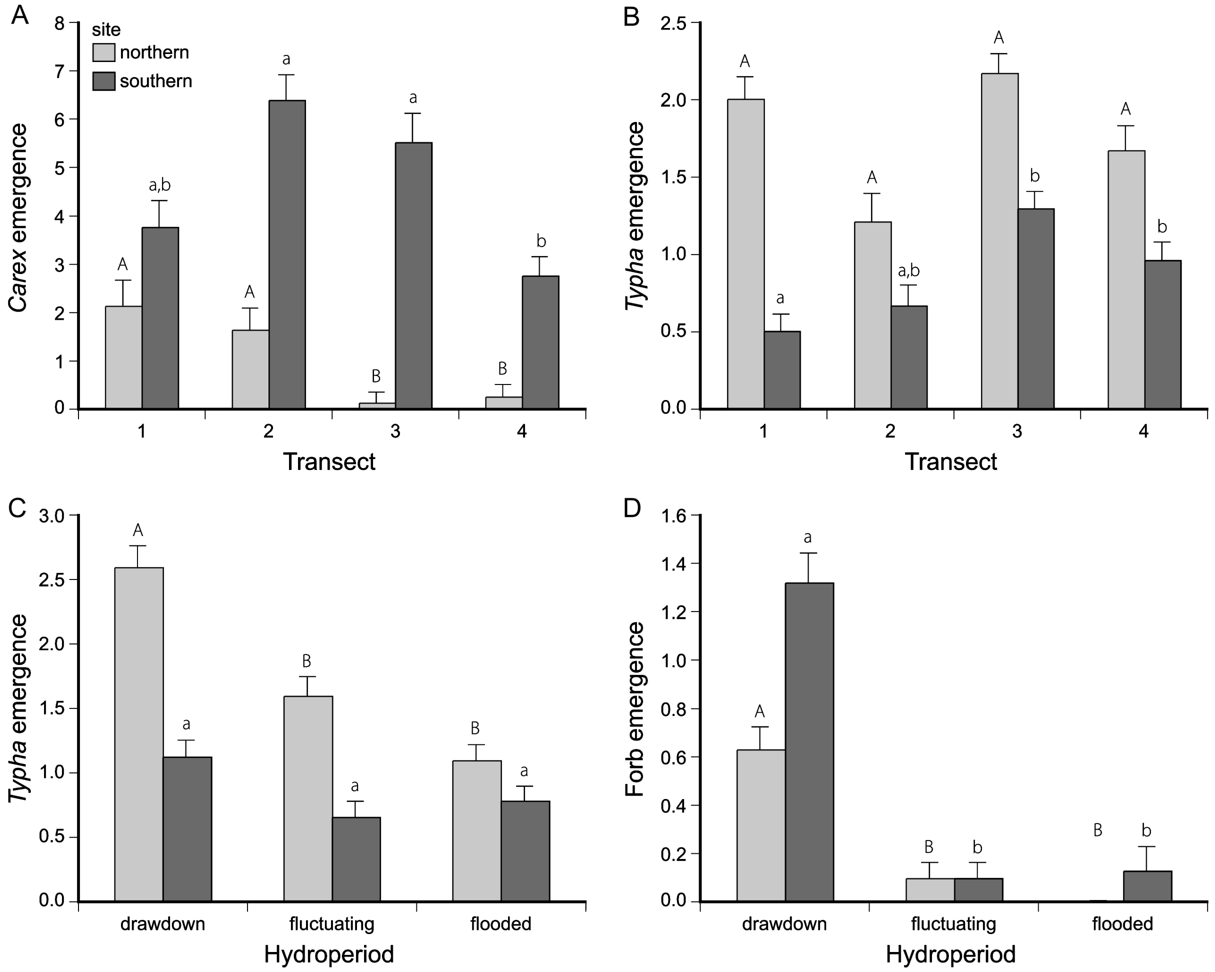

Figure 4. Seed bank emergence ± SE by transect, hydroperiod, and site; $n = 8$ for each transect–site combination; $n = 32$ for each hydroperiod–site combination: (A) *Carex* emergence by transect and site from the low hydroperiod; (B) *Typha* emergence by transect and site averaged over all hydroperiods; (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* × *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 m^2/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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