2009

Promoting Species Establishment in a Phragmites-dominated Great Lakes Coastal Wetland

Martha L. Carlson
U.S. Geological Survey, macarlson@usgs.gov

Kurt P. Kowalski
U.S. Geological Survey

Douglas A. Wilcox
The College at Brockport, dwilcox@brockport.edu

Promoting Species Establishment in a *Phragmites-* dominated Great Lakes Coastal Wetland

Martha L. Carlson
Kurt P. Kowalski

USGS – Great Lakes Science Center
1451 Green Road
Ann Arbor, MI 48105

Douglas A. Wilcox

Department of Environmental Science
and Biology

SUNY-Brockport

350 New Campus Drive

Brockport, NY 14420

---

[1] Corresponding author: macarlson@usgs.
gov; (734) 994-3331

●

Promoting Species Establishment in a *Phragmites*-dominated Great Lakes Coastal Wetland

Martha L. Carlson
Kurt P. Kowalski

USGS – Great Lakes Science Center
1451 Green Road
Ann Arbor, MI 48105

Douglas A. Wilcox

Department of Environmental Science
and Biology
SUNY-Brockport
350 New Campus Drive
Brockport, NY 14420

●

[1] Corresponding author: macarlson@usgs.
gov; (734) 994-3331

ABSTRACT: This study examined efforts to promote species establishment and maintain diversity in a *Phragmites*-dominated wetland where primary control measures were underway. A treatment experiment was performed at Crane Creek, a drowned-river-mouth wetland in Ottawa National Wildlife Refuge along the shore of western Lake Erie. Following initial aerial spraying of *Phragmites* with glyphosate, this study tested combinations of cutting, raking, and additional hand spraying of *Phragmites* with glyphosate as methods to promote growth of other wetland species and increase plant diversity. Percent-cover vegetation data were collected in permanent plots before and after treatments, and follow-up sampling was performed the following year. Increased species richness, species emergence, and relative dominance of non-*Phragmites* taxa were used as measures of treatment success. We also examined treatment effects on *Phragmites* cover. Dimensionality of seedbank and soil properties was reduced using principal component analysis. With the exception of nitrogen, soil nutrients affected species establishment, non-*Phragmites* taxa dominance, and *Phragmites* cover. A more viable seedbank led to greater species emergence. Treatments had differential effects on diversity depending on elevation and resulting degree of hydrologic inundation. Whereas raking to remove dead *Phragmites* biomass was central to promoting species establishment in dry areas, spraying had a greater impact in continually inundated areas. For treatment success across elevations into the year following treatments, spraying in combination with cutting and raking had the greatest effect. The results of this study suggest that secondary treatments can produce a short-term benefit to the plant community in areas treated for *Phragmites*.

Index terms: control, diversity, invasive plants, *Phragmites australis*, wetlands

INTRODUCTION

Promoting native species establishment and maintaining diversity in wetlands is of great interest to researchers and managers alike. *Phragmites australis* (Cav.) Trin. ex Steud. (common reed) and other invasive species are an ever-increasing challenge to these management goals. *Phragmites australis* (henceforth *Phragmites*), in particular, alters the biotic and abiotic environment of wetlands, thereby excluding native species and reducing plant diversity (Stalter and Baden 1994; Chambers et al. 1999; Keller 2000; Saltonstall 2003; Minchinton et al. 2006). Many researchers have studied the effectiveness of control measures for preventing the spread of *Phragmites* (see review in Marks et al. 1994). However, few studies include efforts that seek to encourage species establishment and maintain diversity in *Phragmites*-dominated areas following initial control.

Although native strains of *Phragmites* are endemic to North America, an introduced, invasive haplotype continues to expand in freshwater wetlands (Saltonstall 2002, 2003) by early emergence (League et al. 2006), aggressive vegetative reproduction (Cross and Fleming 1989; Hara et al. 1993; Marks et al. 1994), and abundant seed dispersal (Ailstock et al. 2001). In fact, recent research in inland freshwater marshes (Campbell 2007; LeBlanc et al. 2007) has supported the early observation by Harris

and Marshall (1960) that *Phragmites* seeds may be more viable in freshwater than in North American saltwater marshes. The invasive haplotype's tolerance of fluctuating water levels makes it particularly suited to wetlands experiencing tidal or seiche fluctuations (Chambers et al. 2003; Pagter et al. 2005; White et al. 2007). Due to perceived threats by *Phragmites* to biological communities and ecosystem function, control measures routinely are taken (Marks et al. 1994; Chambers et al. 1999). However, initial control can be unsuccessful at promoting establishment of native species, and enhancing growth of native flora often requires secondary treatment measures.

Control techniques for invasive species include cutting or mowing, harvesting, burning, flooding, and herbicide application, among others (e.g., Cowie et al. 1992; Hellings and Gallagher 1992; Ailstock et al. 2001; Rickey and Anderson 2004). Although total eradication of *Phragmites* is probably not possible (Warren et al. 2001), herbicide application alone or in combination with other techniques generally is considered most effective for controlling *Phragmites* (Marks et al. 1994). Long-term efficacy (i.e., > 3 years) requires reapplication (Moreira et al. 1999; Ailstock et al. 2001; Warren et al. 2001), especially for maintaining diversity (Turner and Warren 2003). Spot-spraying of glyphosate following aerial spray, along with cutting

(Monteiro et al. 1999; Warren et al. 2001; Findlay et al. 2003), might increase the efficacy of treatments and promote species establishment, but little has been done to examine these secondary treatment effects on species establishment.

Removing litter promotes species establishment and increases diversity (van der Valk 1986), and lack of litter removal in *Phragmites*-dominated areas adversely affects species establishment (Ailstock et al. 2001; Findlay et al 2003). Therefore, thatch removal following cutting (also known as harvesting) might reduce the frequency of application necessary to maintain species diversity and habitat as well.

Hydrologic inundation also might affect diversity in treated areas. Great Lakes water levels fluctuate over time, and those fluctuations affect wetland plant communities (Spence 1982; Keddy and Reznicek 1986; Wilcox and Meeker 1991; Barry et al. 2004, Wilcox and Nichols 2008). *Phragmites* areal cover decreases when water levels are high and increase following low levels (Hudon et al. 2005). Rolletschek et al. (2000) cited water depth as a factor controlling treatment impacts, specifically mowing *Phragmites*. Therefore, considering inundation when deciding appropriate control measures might optimize benefits to species establishment.

In an effort to obtain a more diverse plant community in an area where managers were controlling for *Phragmites*, we evaluated the efficacy of combinations of cutting, raking, and additional hand spraying of *Phragmites* with glyphosate as secondary treatment options. We chose these treatments over other possibilities due to cited effectiveness (e.g., Cowie et al. 1992; Güsewell et al. 2000) and feasibility. We also tested effects of hydrologic inundation on treatment success. Little attention has been given to secondary efforts to promote species establishment in areas that have undergone control for *Phragmites*. Therefore, our primary objective was to promote species establishment and enhance growth of native flora using secondary control measures.

METHODS

Study Site

Crane Creek, a tributary to Lake Erie along the western shore, supports a drowned-river-mouth wetland complex that lies within the boundaries of the U.S. Fish and Wildlife Service Ottawa National Wildlife Refuge (ONWR) (41° 37' 43" N, 83° 12' 28" W) (Figure 1). The majority of plant assemblages in Crane Creek and surrounding coastal wetlands became depauperate after 30 years of high lake levels coupled with human alterations of coastal waters, such as high nutrient inputs and turbidity (Kowalski and Wilcox 1999; Kowalski et al. 2006). Following lower lake levels that began in 1998, *Phragmites* expanded around the edges of the wetland (Figure 2). In September 2002, the *Phragmites* stands were aerially sprayed with glyphosate. Our study began the following year.

Experimental Design

We designed the study to test for optimal treatment combinations on species establishment, while allowing for effects of time and hydrologic inundation to be ascertained. We arranged treatment plots in a randomized complete block design (Figure 3). Ten 50-m linear stands of aerially sprayed *Phragmites* along the shoreline served as blocks (Figure 1); these stands represented nearly the entire population of aerially sprayed linear *Phragmites* stands in the wetland complex. We divided each block into five permanent plots, 10 m × 13 m (Figure 3). Each plot received one of five treatments at random: (1) cutting (C); (2) cutting and raking (CR); (3) cutting followed by hand spraying (CS); (4) cutting and raking followed by spraying (CRS); and (5) no secondary treatment (NST). Six 1-m^2 quadrats per plot were sampled for vegetation (Figure 3). To ascertain effects of inundation, two of the six quadrats were in a lower, perpetually inundated topographic zone and were mostly devoid of *Phragmites*. Two landward quadrats were in an upper, rarely flooded topographic zone, characterized by dense stands of aerially sprayed *Phragmites* and drier soils. The other two quadrats were equidistant from the lower and upper quadrats. As such, they were in the zone of the expanding *Phragmites* front and experienced frequent inundation and saturated soils (Figure 3).
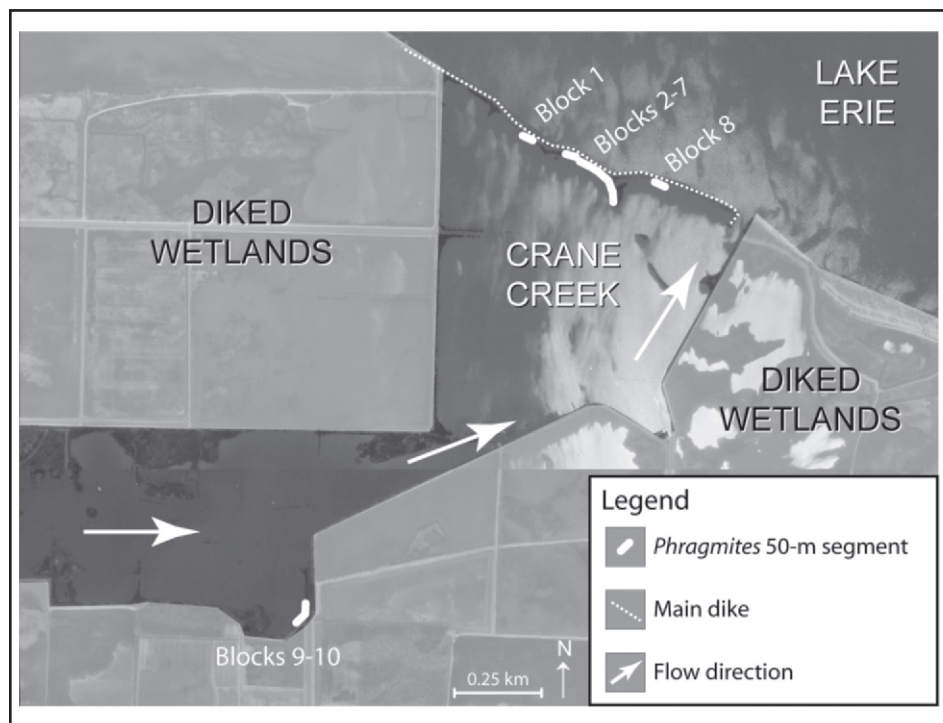

Figure 1. Map of Crane Creek in Ottawa National Wildlife Refuge showing location of the ten 50-m blocks of *Phragmites***.**

Figure 2. Representative plots in June 2003 prior to secondary treatments illustrating stands of dead *Phragmites* **overstory with new** *Phragmites* **growth underneath. Photo by D. Wilcox.**

We placed quadrats two meters from the plot boundary to avoid edge effects.

FIELD METHODS

We applied the cutting treatment in June 2003 (Figure 4) by mowing the *Phragmites* just above ground level with motorized, steel-blade brush cutters. In the raked plots, we moved *Phragmites* stems outside of the plot boundaries after cutting, using 1.5 m-wide aluminum rakes. In August 2003 following cutting and raking, we hand-sprayed live *Phragmites* plants in designated plots with glyphosate (Figure 4). We applied treatments, singly and in combination, to individual plots. Treatment areas in this study we again sprayed aerially in September 2004 after this study was concluded.
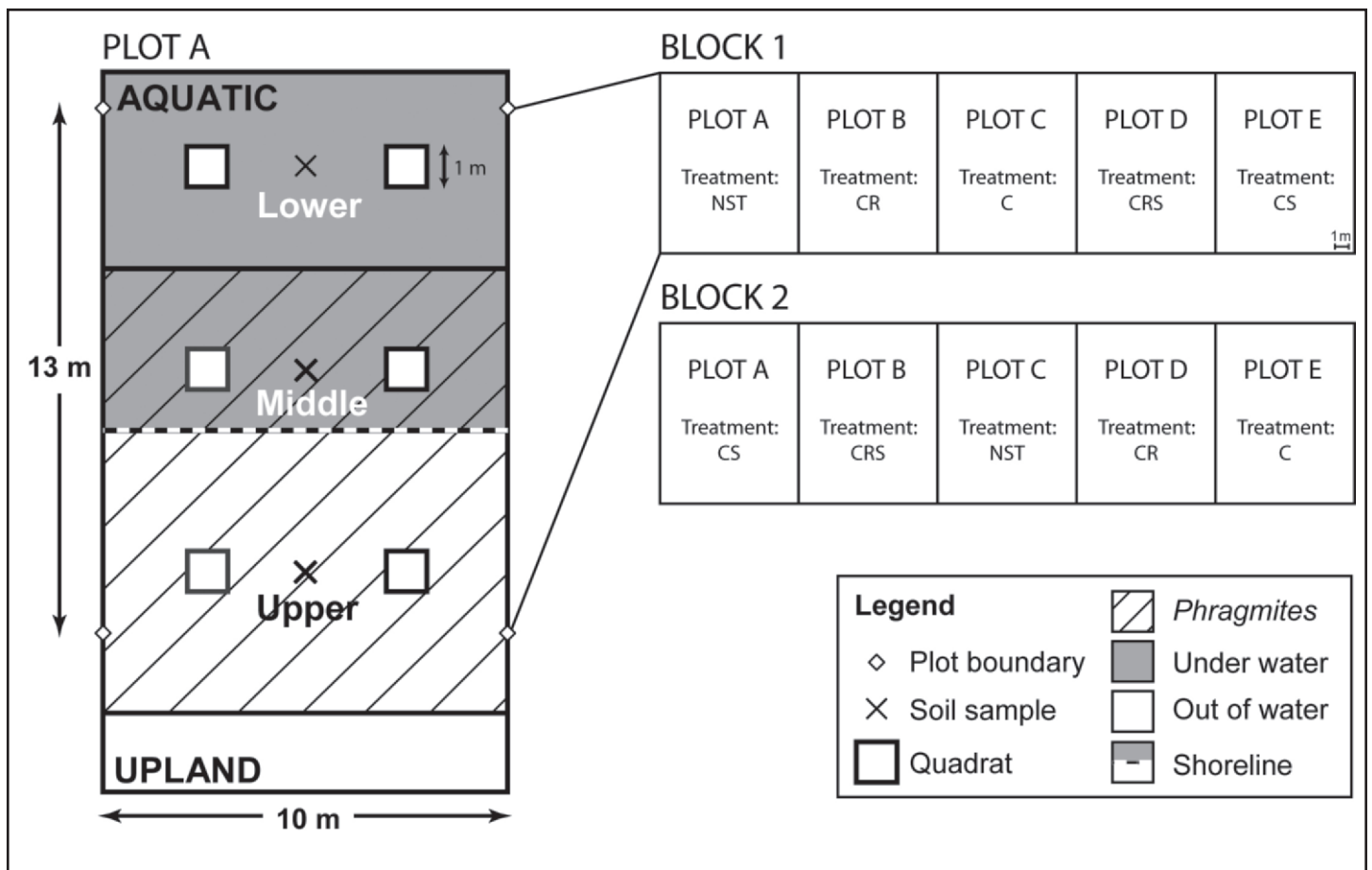
Figure 3. Schematic plot (left) and block (right) diagrams, drawn to scale and illustrating experimental design. Plot contains soil and quadrat sampling locations, determined in relation to the lakeward *Phragmites* **edge. The upper zone refers to the zone of established** *Phragmites*. **The middle zone represents the zone of the expanding** *Phragmites* **front. The lower zone is the area free of** *Phragmites*. **Shoreline in this diagram is arbitrary, as lake levels fluctuated over the study period. Two of the ten blocks are shown with plots within blocks and treatments randomly assigned to each plot (NST = no secondary treatment, CR = cutting and raking, CS = cutting followed by hand-spraying, CRS = cutting and raking followed by hand-spraying).**

Figure 4. Schematic timeline of treatments and sampling.

We collected vegetation data in each of the six 1-m² quadrats per plot by ocular estimation of percent cover prior to (YR0), and two months (YR1) and 14 months (YR2) following treatments (Figure 3). One-percent intervals were used up to 10 percent, and five-percent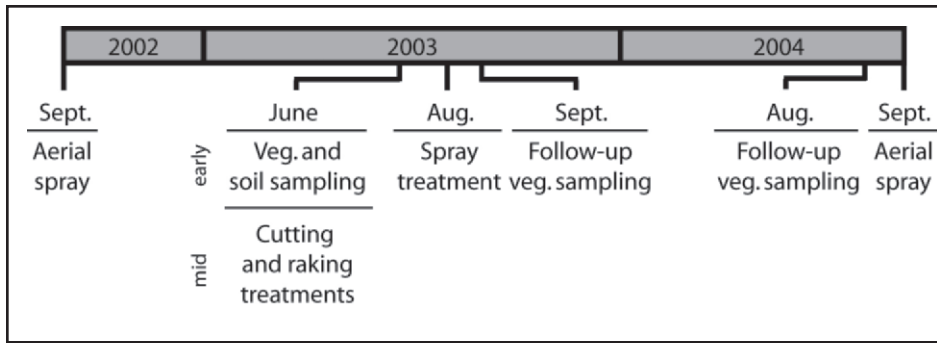 intervals were used for values greater than 10 percent. Plants were identified to species. All taxonomy in this study follows Flora of North American Editorial Committee (1993+).

Soil and Seedbank Methods

To ascertain pre-existing soil and seedbank conditions that might affect treatment results, we collected soil samples prior to treatments between the two quadrats at each topographic zone within plots (Figures 3, 4). We collected the top 7 cm of soil using an aluminum cylinder corer of diameter 7.5 cm. One core was collected for analysis of bulk density and soil organic matter (SOM). A second core was collected for soil chemistry. We collected three additional cores for seedbank analysis. We removed roots and rhizomes manually from samples.

Airtight soil-chemistry samples were refrigerated and sent moist to the Michigan State University Soil and Plant Nutrient Lab (East Lansing, MI), where they were processed for pH, potassium, calcium, magnesium, nitrate-N, ammonium-N, and phosphorus (Olsen P and Bray-P_1). The Olsen method for phosphorus is appropriate when soil pH is greater than 7.4, whereas the Bray method is used for more acidic soils (Bray and Kurtz 1945; Olsen et al. 1954). At the USGS – Great Lakes Science Center, we refrigerated airtight soil

samples (300 cm³ each) prior to gravimetric processing to obtain bulk density and percent SOM. Samples were oven-dried at 105 °C for 24-48 hours and combusted in a muffle furnace at 525 °C for 36-48 hours. To account for variation in bulk density, soil-chemistry data (ppm) were converted to volumetric values ($\mu g\ cm^{-3}$).

For seedbank analysis of emergent species, we spread wetland soil 1-2 cm deep from each plot over potting soil 4-5 cm deep in rectangular containers (25.4 cm × 12.7 cm × 6.4 cm). A flow-through irrigation system was built in a climate-controlled greenhouse (15-30 °C), and water levels simulated water-table drawdown in the natural wetland. We allowed seeds to germinate and grow from August to December 2003. Plants were grown until identifiable, then counted and subsequently removed. We calculated seedbank species richness and stem density per square meter from these greenhouse data.

We calculated importance value (IV) across all plots and treatment types as the sum of the relative frequency and relative density, in the case of the seedbank, or relative frequency and relative dominance for the field vegetation (Curtis and McIntosh 1951). We did not calculate a diversity index because field data were collected as percent cover, and diversity indexes are based on abundance values (Hurlbert 1971).

Statistical Analyses

We performed statistical analyses to make multiple comparisons between treatments and test effects of time and topographic zone. We ran split-plot ANCOVAs on the

data rather than repeated measures, which is limiting in terms of multiple comparisons (Maceina et al. 1994; Littell et al. 1996; Bonate 2000; Aldworth and Hoffman 2002; Federer and Meredith 2005). We determined significance at the $\alpha = 0.05$ level of confidence.

We derived indicators of treatment effectiveness from field vegetation data. These effectiveness indicators consisted of the following dependent variables: field species richness, net species emerged, non-*Phragmites* taxa, and live *Phragmites*. To avoid pseudoreplication (Hurlbert 1984), we combined data by arithmetic average across the two quadrats at each topographic zone or six quadrats per plot, depending on whether effects of time or topographic zone were analyzed, respectively. We calculated relative dominance of non-*Phragmites* taxa and live *Phragmites* as the mean percent cover of an individual taxon. We computed species richness per square meter by arithmetic average. We calculated the net species emerged from in situ wetland soils from field data as the difference between the number of species gained and lost between pre- and post-treatment sampling periods. Treatment success we determined as a significant increase in field species richness, net species emerged, and relative dominance of non-*Phragmites* taxa, and a decrease in live *Phragmites* relative dominance. We used log or arcsine transformation to improve normality and ensure equal variance.

We determined sources of variation in the split-plot ANCOVAs, in part, by whether the independent variables were fixed or random; the blocks of linear *Phragmites* stands we considered random effects. Although they were not randomly chosen, we sampled sufficient numbers of stands to reflect actual spatial variation (Bennington and Thayne 1994; Newman et al. 1997). The five specific treatments of interest (C, CR, CS, CRS, and NST), topographic zone (upper, middle, lower), and year (1, 2) were specified and, therefore, were fixed effects.

We performed two types of analyses. Analysis Type A tested effects of time, where topographic zones were analyzed

separately, and time and time × treatment were included as sources of variation in the ANCOVA. Analysis Type B tested effects of topographic zone by analyzing Year-1 and Year-2 data separately and included topographic zone and topographic zone × treatment. PROC MIXED in SAS was used with the Satterthwaite method for degrees of freedom for all sources of variation except block and block × treatment, for which PROC GLM was used (Littell et al. 1996). The mixed model (PROC MIXED) allowed for the correct incorporation of fixed and random effects for the split-plot design, and the linear model (PROC GLM) allowed block to be tested against the block × treatment interaction. *Post-hoc* differences between treatments were determined using Fisher's LSD.

We analyzed soils and seedbank data using principal component analysis (PCA) with the correlation matrix to reduce dimensionality. We used the first three principal components as a guide to define four new variables that were used as covariates in the ANCOVAs, along with pre-treatment data. For example, the original variables that loaded highly on PCA factor 1 were standardized to their respective means and then arithmetically averaged to obtain the new covariate.

RESULTS

Seedbank and Soils

The greenhouse seedbank study showed an abundance of mudflat annuals, such as *Ammannia robusta* Heer & Regel, *Eleocharis acicularis* (L.) Roemer & Schultes, *Lindernia dubia* (L.) Pennell, and *Penthorum sedoides* L. (Table 1). *Cyperus* species also were common, and most species were native. Seedbank data also indicated the presence of viable *Phragmites* seeds.

Seedbank and chemical and physical soil properties varied greatly across the study site (Table 2). The first three axes in the PCA accounted for 48.4%, 17.9%, and 13.5% of variance in soils and seedbank data. PCA factor 1 primarily represented the chemical soil properties (pH, Olsen P, K, Mg, Ca). As such, the standardized

Table 1. Importance values (IV) across all plots and elevations for the more common species (i.e., those with an IV > 5.0 in at least one sampling period) observed in the seedbank study (SB), pre-treatment field sampling (YR0), and post-treatment field sampling in Year 1 (YR1) and Year 2 (YR2). IV was calculated as the sum of relative frequency and either relative density (SB) or relative dominance (YR0, YR1, and YR2). Nomenclature follows Flora of North America Editorial Committee (1993+).

	Importance Value			
Taxon	SB	YR0	YR1	YR2
Ammannia robusta	24.84	–	2.17	–
Bidens cernua	0.75	–	7.26	–
Cyperus erythrorhizos	11.42	–	1.26	–
Cyperus odoratus and *Cyperus strigosus*	11.20	–	5.97	–
Eleocharis acicularis	38.97	11.93	14.49	–
Lindernia dubia	11.53	–	3.21	–
Ludwigia alternifolia	7.86	–	0.67	0.23
Ludwigia palustris	5.28	–	5.11	–
Penthorum sedoides	17.06	–	3.04	–
Phalaris arundinacea	–	–	–	9.63
Phragmites australis	5.55	19.93	34.21	47.51
Phragmites australis, dead	–	75.42	14.63	11.46
Polygonum lapathifolium	7.14	5.77	1.44	–
Potamogeton crispus	–	5.86	1.17	3.00
Potamogeton nodosus	–	12.76	8.49	11.89
Ricciocarpos natans	5.96	–	–	–
Sagittaria latifolia	1.97	6.06	11.65	17.60
Spirodela polyrhiza	–	1.64	1.99	6.44
Typha angustifolia	7.65	16.98	20.94	24.42

values were combined into a soil-chemistry covariate. The standardized greenhouse seedbank properties (seedbank species richness and stem density) represented by PCA factor 2 (Table 2) were grouped into a seedbank covariate. Nitrate-N and ammonium-N loaded on factor 3 along with soil organic matter (SOM) and bulk density. The latter two also loaded similarly on factor 1 (Table 2). To separate the influence of nitrogen and physical soil properties on the effectiveness indicators, we generated one covariate for nitrogen and one for SOM and bulk density.

Seedbank properties affected species establishment but not overall species richness. A viable seedbank was positively correlated with species emergence, especially in the upper topographic zone (Tables 3, 4). No

effect of seedbank on non-*Phragmites* taxa or live *Phragmites* was observed within topographic zones (Table 5). Coincidentally, seedbank was significantly related to live *Phragmites* cover across zones in Year 2 (Table 6).

Nitrogen concentration in soils had no observable effect on species emergence, species richness, or plant dominance. However, other soil constituents (pH, Olsen P, K^+, Mg^{2+}, Ca^{2+}) affected species richness in Year 2 (Table 4) and species emergence in both years (Tables 3,4). Availability of these other nutrients also affected relative dominance of non-*Phragmites* taxa but only in the middle zone (Table 5). Effects of soil chemistry on *Phragmites* or non-*Phragmites* taxa were only detected in Year 1 (Table 6).

Table 2. Mean (±SEM), range, and factor loadings for PCA axes 1, 2, and 3 across all plots (n = 150) for chemical and physical soil properties and seed-bank data.

Variable	Mean	Range	Factor 1 Loadings	Factor 2 Loadings	Factor 3 Loadings
Chemical properties					
pH	7.7 (0.02)	6.6 - 8.1	0.32	0.15	-0.19
Olsen P (μg cm^{-3})	15 (0.49)	3 - 30	0.39	0.14	-0.01
K$^+$ (μg cm^{-3})	76 (3.30)	9 - 250	0.39	0.11	-0.13
Mg^{2+} (μg cm^{-3})	278 (7.40)	72 - 597	0.39	-0.02	-0.13
Ca^{2+} (μg cm^{-3})	2501 (54.00)	492 - 4152	0.42	-0.04	0.08
NO$_3$–N (μg cm^{-3})	2.63 (0.18)	0.07 - 14.8	-0.18	-0.07	0.62
NH$_4$–N (μg cm^{-3})	7.99 (0.44)	1.01 - 36.2	0.01	-0.25	0.38
Physical properties					
Bulk density (g cm^{-3})	0.87 (0.02)	0.2 - 1.75	0.33	-0.12	0.43
Organic matter (g g^{-1})	0.91 (0.00)	0.58 - 0.98	0.34	-0.15	0.33
Seedbank					
Species richness (plot^{-1})	7.7 (0.36)	0 - 17	-0.05	0.65	0.22
Stem density (stems m^{-2})	2145 (189)	0 - 10695	-0.01	0.65	0.22

Table 3. F-ratios from ANCOVAs of split-plot on randomized complete block design with time as the split plot (Analysis Type A) for field species richness and net species emerged from *in situ* wetland soils. Data were log-transformed. F-ratios for block and treatment were based on plot-level block × treatment interaction. Significance levels are as follows: *** P < 0.001, ** P < 0.01, * P < 0.05. (NST = no secondary treatment, CR = cutting and raking, CS = cutting followed by hand-spraying, CRS = cutting and raking followed by hand-spraying.)

Sources of Variation		df	UPPER F-ratios Field Species Richness	UPPER F-ratios Net Species Emerged	MIDDLE F-ratios Field Species Richness	MIDDLE F-ratios Net Species Emerged	LOWER F-ratios Field Species Richness	LOWER F-ratios Net Species Emerged
Covariates								
Pre-treatment		1	34.62 ***	-	1.20	-	23.52 ***	-
Soil Chemistry		1	0.29	4.43 *	4.44	6.00 *	3.56	16.32 **
Seedbank		1	0.12	5.20 *	0.90	1.51	0.45	0.42
SOM and bulk density		1	0.64	5.66 *	2.90	5.25	2.79	7.75 **
Block		9	3.39 **	3.55 **	3.19 **	4.28 ***	3.13 **	3.13 **
Treatment		4	6.58 ***	3.08*	3.44 *	2.43	0.55	1.13
Block × treatment		36	1.10	1.00	1.03	2.22 **	0.75	2.57 **
Time		1	0.07	5.26 *	0.56	44.17 ***	0.07	47.45 ***
Time × treatment		4	3.32 *	2.33	1.08	1.36	0.86	0.57
Residual MS			0.03	0.02	0.02	0.01	0.04	0.01
Significantly	Overall		CR**, CRS**	CR**, CRS**	CS*	CS*	-	-
different	*Year 1*		CR***, CRS*	CR**	CS*	CR*, CS**	-	-
from NST	*Year 2*		-	CRS*	-	-	-	-

Table 4. F-ratios from ANCOVAs of split-plot on randomized complete block design with topographic zone as the split plot (Analysis Type B) for field species richness and net species emerged from *in situ* wetland soils. Data were log-transformed. F-ratios for block and treatment were based on plot-level block × treatment interaction. Significance levels are as follows: *** P < 0.001, ** P < 0.01, * P < 0.05. (NST = no secondary treatment, CR = cutting and raking, CS = cutting followed by hand-spraying, CRS = cutting and raking followed by hand-spraying.)

| | | YEAR 1 F-ratios | | YEAR 2 F-ratios | |
| | | Field Species Richness | Net Species Emerged | Field Species Richness | Net Species Emerged |
Sources of Variation	df				
Covariates					
Pre-treatment	1	44.98***	-	17.77***	-
Soil Chemistry	1	0.26	14.24***	8.64**	8.52**
Seedbank	1	0.38	3.45	1.08	12.61***
SOM and bulk density	1	0.01	15.19***	13.01***	15.53***
Block	9	2.38*	3.83**	6.18***	2.50*
Treatment	4	3.50*	3.18*	3.55*	1.12
Block × treatment	36	0.99	1.11	0.52	0.98
Topographic zone	2	0.12	5.44**	1.89	6.67**
Topographic zone × treatment	8	2.28*	2.74**	0.88	1.01
Residual MS	89	0.04	0.02	0.03	0.02
Significantly different from NST	Overall	CR**, CRS*	CR*	-	-
	Upper	*CR**, CRS**	*CR***	-	*CRS**
	Middle	-	*CR*,CS***	-	-
	Lower	-	-	-	-

Treatments in Upper Topographic Zone

Prior to secondary treatments, the upper topographic zone was characterized mainly by standing dead *Phragmites* (Table 1). Live *Phragmites* was common, along with *Polygonum lapathifolium* L., *Salix exigua* Nutt., *Lythrum salicaria* L., *Eleocharis erythropoda* Steudel, and *E. acicularis*. *Sagittaria latifolia* Willd. and *Schoenoplectus tabernaemontani* (C. C. Gmelin) Palla were found primarily in depressions. Two months after treatments were applied, *Phragmites* still was dominant, but emergent plants (i.e., *S. latifolia*, *S. tabernaemontani*, *Typha angustifolia* L.) and mudflat annuals (i.e., *Polygonum punctatum* Buch. – Ham. ex D. Don, *Bidens cernua* L., *Ludwigia palustris* (L.) Elliott, *Cyperus odoratus* L. and *Cyperus strigosus* L.) represented a greater proportion of vegetated cover. Fourteen months following treatments, *Phragmites* dominated, and *T. angustifolia* and *S. latifolia* were common.

P. punctatum was also noteworthy, but presence of the invasive *Phalaris arundinacea* L. was considerable.

In Year 1, cutting and raking (CR) and cutting, raking, and spraying (CRS) were the most effective treatments in the upper zone. Dominance of non-*Phragmites* taxa was greatest for CRS, followed closely by CR (Figure 5A). CRS also showed the least live *Phragmites*, followed by CR (Figure 5B). Field species richness and emergence were greatest in the CR plots, followed by the CRS plots (Figures 5C, 5D). CR and CRS also showed significant differences from no-secondary treatment (NST) in *post-hoc* tests for all indicators except *Phragmites*.

Although treatment success into Year 2 was limited, CRS was most effective. CRS plots had greater species richness, species emergence, and non-*Phragmites* taxa dominance, and lower live *Phragmites* cover (Figure 5). CRS was significantly

different from NST for net species emerged (Tables 3, 4). Treatments had a significant effect on field species richness (Table 4), non-*Phragmites* taxa, and live *Phragmites* (Table 6).

Differential effects of treatments on topographic zone were observed for field species richness and net species emerged. The significant topographic zone × treatment interactions in Year 1 for these two indicators showed that effects of treatments varied with topographic zone, with CR and CRS most effective in the upper zone (Table 4).

Treatments in Middle Topographic Zone

Prior to treatments, the non-*Phragmites* taxa included emergent plants such as *S. latifolia* and *T. angustifolia* (Table 1). Also, floating plants (i.e., *Potamogeton nodosus* Poiret, *Lemna minor* L., *Nelumbo lutea*

Table 5. F-ratios from ANCOVAs of split-plot on randomized complete block design with time as the split plot (Analysis Type A) for relative dominance of non-*Phragmites* taxa and live *Phragmites* derived from field vegetation data. Non-*Phragmites* taxa data were arcsine-transformed; live *Phragmites* data were log-transformed. F-ratios for block and treatment were based on plot-level block × treatment interaction. Significance levels are as follows: *** P < 0.001, ** P < 0.01, * P < 0.05. (NST = no secondary treatment, CR = cutting and raking, CS = cutting followed by hand-spraying, CRS = cutting and raking followed by hand-spraying.)

Sources of Variation	df	UPPER F-ratios Relative Dominance Non-*Phragmites* Taxa	UPPER F-ratios Relative Dominance Live *Phragmites*	MIDDLE F-ratios Relative Dominance Non-*Phragmites* Taxa	MIDDLE F-ratios Relative Dominance Live *Phragmites*
Covariates					
Pre-treatment	1	7.12*	0.27	1.31	21.15***
Soil Chemistry	1	3.38	5.75*	6.18*	12.11**
Seedbank	1	0.01	0.01	0.04	0.08
SOM and bulk density	1	3.89	8.35**	2.94	7.92*
Block	9	3.06**	4.39***	3.97**	2.76*
Treatment	4	3.43*	0.75	3.65*	2.51
Block × treatment	36	1.64	0.77	0.79	0.54
Time	1	17.58***	47.24***	3.9	12.47***
Time × treatment	4	1.69	0.53	1.42	0.49
Residual MS		0.10	0.24	0.15	0.31
Significantly different from NST	Overall	CR*, CRS**	-	CRS*	CRS*
	Year 1	*CR**, CRS**	-	-	-
	Year 2	-	-	-	-

Willd.) were prevalent. Two months after treatments, *S. latifolia* and *T. angustifolia* were co-dominant with *Phragmites*. As water levels receded in summer and soils were exposed, mudflat plants such as *E. acicularis*, *B. cernua*, *P. punctatum*, *L. dubia*, and *N. palustris* were common. Also, submersed (e.g., *Ceratophyllum demersum* L.) and floating (e.g., *P. nodosus)* plants were present. Fourteen months after treatments, *S. latifolia* and *T. angustifolia* still were co-dominant with *Phragmites*, but *P. arundinacea* was expanding, and fewer mudflat species were observed.

In Year 1, CR and CRS plots had the greatest relative dominance of non-*Phragmites* taxa (Figure 6A); however, none was significantly different from NST in Year 1 (Tables 5, 6). The greatest decrease in live *Phragmites* cover was observed in the CRS plots (Figure 6B). A significant difference between CRS and NST was not detected in Year 1 alone but was detected across both years (Table 5). CS was most

effective at increasing species richness and species emergence, followed by CR (Figures 6C, 6D). Significant differences were observed: (1) between NST and CS for species richness and (2) between NST and both CR and CS for net species emerged (Table 3).

In Year 2, the CRS plots had greater mean field species richness, net species emerged, and relative dominance of non-*Phragmites* taxa, and lower relative dominance of live *Phragmites* (Figure 6). Year-2 significant differences were detected between CRS and NST for relative dominance of non-*Phragmites* taxa and live *Phragmites* (Tables 5, 6).

Treatments in Lower Topographic Zone

P. nodosus and *T. angustifolia* continually were dominant in the lower zone (Table 1). Additionally, *Potamogeton crispus* L.

and *N. lutea* were common prior to treatments, and *S. latifolia* and *C. demersum* were common after treatments.

Little *Phragmites* was observed in the lower zone, generating relative non-*Phragmites* cover values at or near 100%. Furthermore, the substrate in the lower zone was submersed for much of the growing season. The effectiveness indicators that passed tests for normality and homoscedasticity were field species richness and net species emerged (Table 3). However, no significant treatment effects were detected.

DISCUSSION

Effects of Inundation

Site hydrology is an important consideration when designing secondary treatment strategies to promote species establishment in *Phragmites*-dominated areas where control efforts are underway.

Table 6. F-ratios from ANCOVAs of split-plot on randomized complete block design with topographic zone as the split plot (Analysis Type B) for relative dominance of non-*Phragmites* taxa and live *Phragmites* derived from field vegetation data. Non-*Phragmites* taxa data were arcsine-transformed; live *Phragmites* data were log-transformed. F-ratios for block and treatment were based on plot-level block × treatment interaction. Significance levels are as follows: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$. (NST = no secondary treatment, CR = cutting and raking, CS = cutting followed by hand-spraying, CRS = cutting and raking followed by hand-spraying.)

Sources of Variation	df	YEAR 1 F-ratios Relative Dominance Non-*Phragmites* Taxa	Live *Phragmites*	YEAR 2 F-ratios Relative Dominance Non-*Phragmites* Taxa	Live *Phragmites*
Covariates					
Pre-treatment	1	41.54***	7.48**	5.65*	14.97***
Soil Chemistry	1	31.63***	21.52***	0.30	1.70
Seedbank	1	0.01	0.71	4.29*	6.95*
SOM and bulk density	1	15.29***	19.45***	8.37**	0.26
Block	9	1.02	3.77**	0.74	0.83
Treatment	4	2.14	0.37	5.19**	3.87*
Block × treatment	36	0.81	0.66	0.88	1.20
Topographic zone	2	0.16	17.26***	23.98***	100.25***
Topographic zone × treatment	8	1.55	0.96	0.89	0.63
Residual MS	88	0.18	0.32	0.10	0.10
Significantly	Overall	CR*, CRS*	-	CRS**	CRS**
different	*Upper*	*CR*, CRS**	-	-	-
from NST	*Middle*	-	-	*CRS**	*CRS***
	Lower	-	-	-	-

Wetland topography and its relationship to water-level fluctuations affect *Phragmites* density and ability of species to establish. Therefore, degree of inundation partially determines effectiveness of secondary control measures, as evidenced by differences in treatment effectiveness at the various topographic zones (Figures 5, 6). Attention to site hydrology when designing secondary control treatments can help maintain a more diverse plant community. At the same time, inundation can be an invitation for other flood-tolerant invasive plants, such as *Typha* (Kercher and Zedler 2004), to establish, as seen in this study (Table 1). Although *Typha* is preferred by managers at ONWR for waterfowl habitat, in other areas, they can be nuisance plants that spread readily, given appropriate water levels and elevated nutrients (Miao and Sklar 1998; Newman et al. 1998; Woo and Zedler 2002; Wilcox et al. 2008).

In higher, drier areas where *Phragmites* stands were well established prior to aerial spray (upper zone), standing dead biomass was thicker and more ubiquitous, and biomass removal was important. Litter has been shown to have deleterious effects on seedling recruitment (van der Valk 1986), primarily due to light limitation (Haslam 1972; Güsewell and Edwards 1999; Windham and Lathrop 1999). *Phragmites* may limit growth of other species through litter production and retention even where new shoots are not present (Minchinton et al. 2006). Therefore, biomass removal by cutting and raking was critical at this elevation for providing species other than *Phragmites* with sufficient light availability for growth (Tables 3, 5).

Where soils were saturated (middle zone), herbicide application following cutting was more critical than litter removal (Figure 6). Here, the *Phragmites* front was expanding, likely by clonal integration, where parts of a clone in a favorable area support parts in less favorable environments (Amsberry et al. 2000). Initial dead *Phragmites* biomass levels were lower, and cut debris was carried away from the area by water-assisted transport (pers. observation). However, more importantly, flooding following cutting also probably led to die-back (Husak 1978; Hellings and Gallagher 1992; Vestergaard 1994; Smith 2005) by reducing the ability of *Phragmites* to tolerate anoxic conditions (Rolletschek et al. 2000). Since this frequently inundated zone was below mean water level, cutting of *Phragmites* stems in these areas likely produced harmful effects on the live plants. Herbicide application in the upper and middle zones further stunted the ability of *Phragmites* to expand by clonal integration, thereby allowing for establishment of other species.

In areas that were submersed regularly (lower zone), treatments had little observable effect (Table 3). The deeper zones had
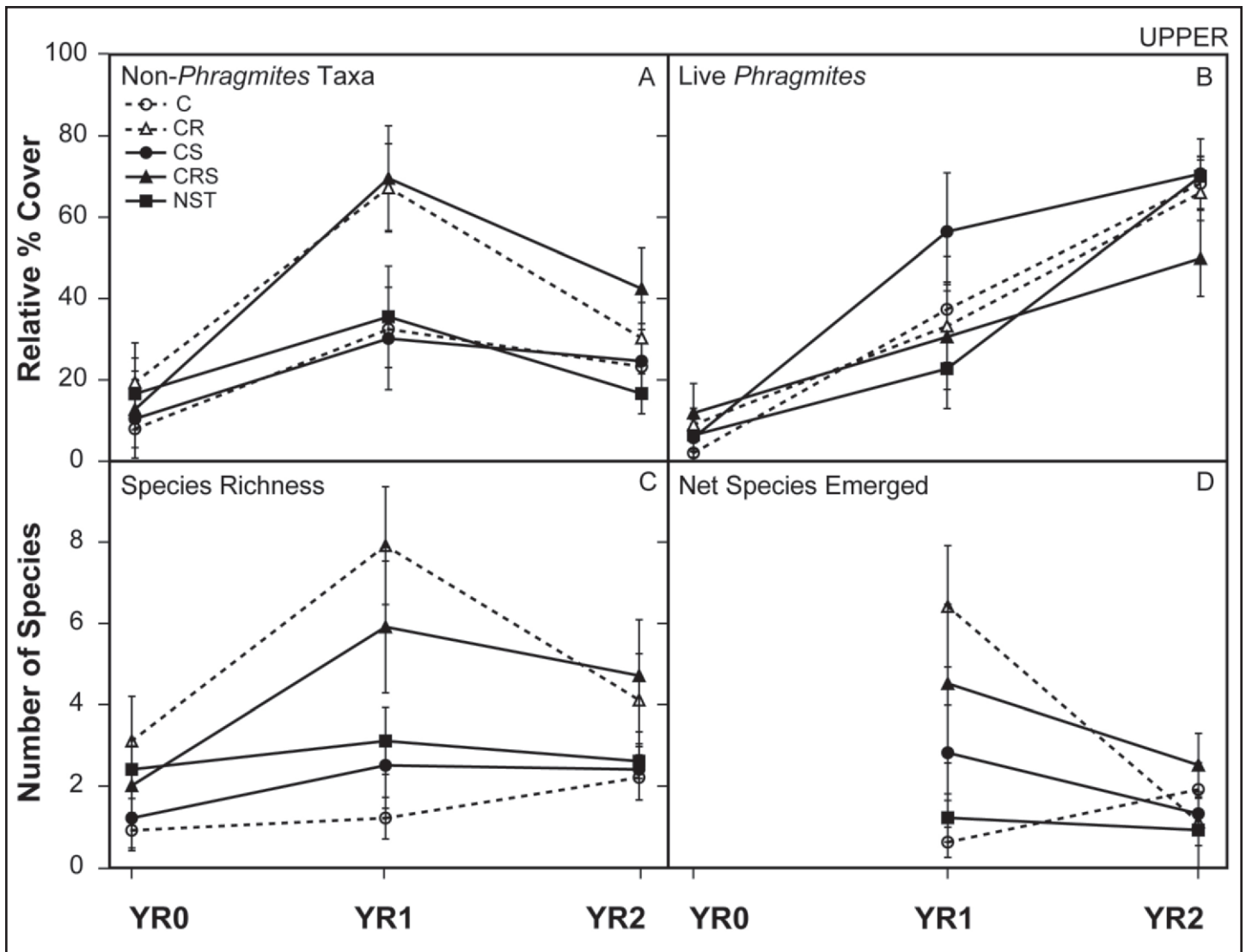
Figure 5. Means plots of effectiveness indicators at the upper topographic zone (YR0 = pre-treatment condition, YR1 = two months after treatments, YR2 = fourteen months after treatments). Error bars represent SEM.

very little *Phragmites* prior to treatments, and *Phragmites* is less successful at establishing under sustained flooding conditions (Armstrong et al. 1999; Amsberry et al. 2000; Welch et al. 2006). However, once established in shallow areas, rhizomes can spread to deeper zones (Cross and Fleming 1989; Amsberry et al. 2000), which can explain the presence of *Phragmites* in deep areas of this study. Nevertheless, persistent flooding conditions in the lower zone likely overpowered treatment effects by limiting *Phragmites* expansion and establishment of other species.

Soils and Seedbank

The presence of viable *Phragmites* seeds observed in the greenhouse seedbank study supports findings by Harris and Marshall (1960) and more recent findings by Campbell (2007) and LeBlanc et al. (2007), who documented the ability of *Phragmites* to establish from seed in freshwater wetlands. Our results suggest that *Phragmites* plants will continue to emerge from the seedbank as long as adult plants are in close proximity to provide a source. Therefore, continued management is necessary, but promoting species establishment may provide ecologically mediated control (Amsberry et al. 2000).

Managing for certain life-history traits might be important as well, depending on site hydrology and seedbank characteristics. A viable seedbank increases the level of emergence of annual plants (Table 4) but probably has less influence on species richness or relative dominance of non-*Phragmites* taxa, which encompass multiple life-history traits (Tables 4, 6). The effect of the seedbank on net species emerged suggests that it contributed to restoration success, particularly in drier areas where wetland soils were at a higher elevation (Table 3). Plants that grew from the wetland seedbank primarily were mudflat annuals (Table 1), but emergent perennials were more abundant at intermediate water depths at the site. Therefore, augmenting
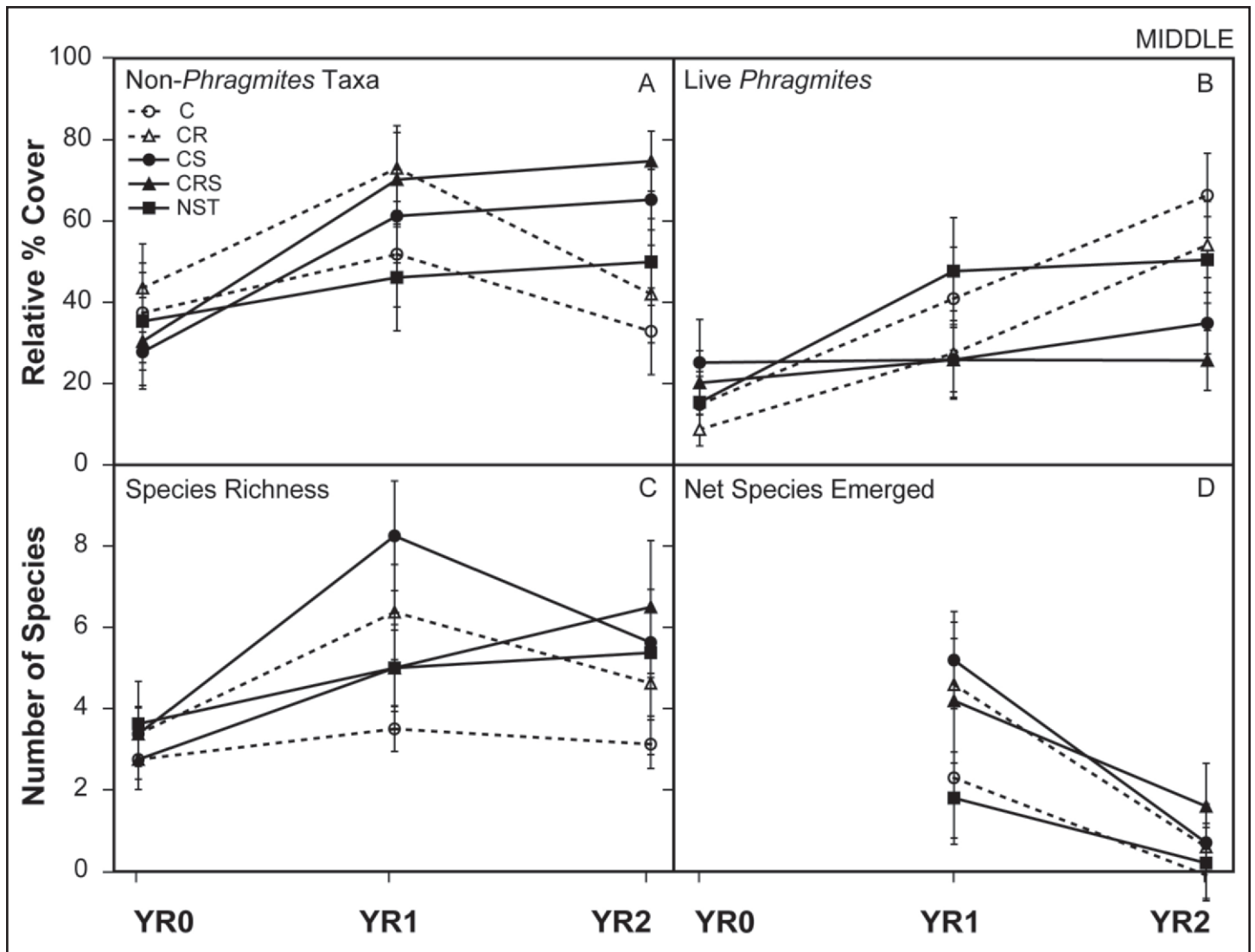
Figure 6. Means plots of each effectiveness indicator at the middle topographic zone (YR0 = pre-treatment condition, YR1 = two months after treatments, YR2 = fourteen months after treatments). Error bars represent SEM.

the seedbank with invasion-resistant native perennials also might be needed for optimal restoration success (Perry and Galatowitsch 2003; Simmons 2005).

Even if there are benefits to diversity in the year following secondary treatments, those results cannot guarantee that species richness will be maintained. The diversity of seedlings that emerge is tied to the seed-bank, but the survivorship of mature plants is determined by environmental conditions (Seabloom and van der Valk 2003), one of which is whether live *Phragmites* comes back. The correlation of a strong seedbank with more live *Phragmites* in Year 2 (Table 6) is coincidental, as the seedbank study was not influenced by *Phragmites* in the

field. However, to maintain species richness in the field, continued management is nec-essary so that *Phragmites* does not overtop the newly emerged species; augmenting the seedbank also might help maintain diversity (Perry and Galatowitsch 2003; Simmons 2005). Furthermore, ensuring that another invasive species, such as *P. arundincea*, does not take over in place of *Phragmites* is also important.

Nutrient management has the potential to sustain plant diversity as well. Studies have shown that nitrogen addition has a delete-rious effect on diversity (e.g., Pratt 1984; Tilman 1984, 1987; Goldberg and Miller 1990) and favors *Phragmites* (Rickey and Anderson 2004; Saltonstall and Stevenson

2007). Many Great Lakes coastal wetlands have high nitrogen input, which can affect severely the biological community (Chow-Fraser et al. 1998). Ascertaining the effect of nitrogen was outside the scope of this study, as nitrogen cycles are complicated within ecosystems dominated by *Phrag-mites* (Windham and Meyerson 2003), and nitrogen flux rates are more descriptive of nutrient dynamics than simple measure-ment of concentration. Although nitrogen concentration had no observable effect in this study, increasing other soil nutrients, including phosphorus, positively affected species emergence and non-*Phragmites* dominance and negatively affected live *Phragmites* cover, suggesting that nutrient management may be beneficial.

Implications for Phragmites Control

Our primary objective was to promote species establishment and enhance growth of native flora. Decreasing *Phragmites* cover can lead to a more diverse community through interspecific competition (Amsberry et al. 2000); therefore, we examined effects of treatments on *Phragmites* in addition to species establishment in this study.

Cutting, raking, and spraying in combination were most effective at limiting *Phragmites* growth overall, but the effectiveness was apparent only after the plants had overwintered (Figures 5, 6; Tables 5, 6). Herbicides, when applied in late summer, have a deleterious effect on plant growth the following spring (Avers et al. 2007). Therefore, effects of secondary treatments on live *Phragmites* were not observed immediately following treatments.

Whereas managing for optimal species richness depends on water level, controlling for *Phragmites* alone is less dependent across water levels encountered in this study. *Phragmites* spreads vegetatively into deeper water (Cross and Flemming 1989; Amsberry et al. 2000) and is tolerant of fluctuating water levels (Chambers et al. 2003; Pagter et al. 2005; White et al. 2007). As such, degree of hydrologic inundation did not affect treatments for live *Phragmites* differentially in our study (Table 6).

Implications for Species Establishment

To promote a diverse plant community, early attention to *Phragmites* control is important (Kowalski and Wilcox 1999; Wilcox and Whillans 1999; Saltonstall and Stevenson 2007). Keeping *Phragmites* cover thin helps maintain diversity (Chambers et al. 1999; Keller 2000; Turner and Warren 2003; Minchinton et al. 2006). Thin stands of *Phragmites* may be managed for species richness with cutting and spraying. Thick stands require cutting and raking. Although litter can be removed by burning as well, it can assist *Phragmites* expansion by increasing flowering stems in the year following burning (Cowie et al. 1992; Marks et al. 1994). In any case, cutting alone is not an effective way to promote species establishment and maintain a diverse plant community, as litter has a deleterious effect on species establishment and diversity (van der Valk 1986).

For large aerial expanses of *Phragmites* stands, maximizing treatment effectiveness is important. Harvesting in early summer leads to the greatest reduction in biomass the following year (Asaeda et al. 2006). Litter removal in early summer increases emergence of wetland species (Figures 5, 6) and reduces *Phragmites* stand growth, as stems are cut before plants allocate resources to rhizome storage (Buttler 1992; Karunaratne et al. 2004; Asaeda et al. 2006). In areas of saturated soil where *Phragmites* expansion is occurring, litter removal is not as critical for species establishment (Table 3). Rather, natural water transport by wave action of cut stems away from the area of restoration can be utilized. However, limiting transport of fertile seeds to new wetland areas by cutting in June before *Phragmites* goes to seed is an important consideration. Target spraying of live *Phragmites* each year at the end of the growing season has the greatest impact on *Phragmites* (Seddon 1981; Buhler and Burnside 1983; Prasad 1984) and the least impact on other plants (Ailstock et al. 2001), thereby leading to an optimal increase in wetland species in the following year (Figures 5, 6). For large-scale restoration, a Marsh Master (Coast Machinery, Inc., Baton Rouge, LA) or similar high-flotation vehicle can be used to apply these treatments more efficiently.

Total *Phragmites* eradication may be an unrealistic goal in wetlands (Marks et al. 1994). Despite this, promoting native species establishment and richness, through management, is achievable. Welch et al. (2006) observed increased diversity with both reduced and increased *Phragmites* abundance, suggesting that greater species richness can be achieved despite the level of *Phragmites* dominance, provided that *Phragmites* does not limit light availability (Haslam 1972; Güsewell and Edwards 1999) or ecologically engineer the site (Minchinton et al. 2006). If the goal is to maintain diversity rather than eradicate *Phragmites*, cutting or cutting and litter removal may be sufficient for a few years following aerial spray and initial CRS treatment. However, further research is needed to determine if intermittent control for increasing species richness would be as effective as long-term intermittent control for *Phragmites* following short-term continuous control (Turner and Warren 2003). High-cost aerial spray may not be necessary every year if these secondary treatments are used in conjunction with spraying.

The results of this study suggest that secondary treatments can help maintain a more diverse plant community in areas treated for *Phragmites*. Used in conjunction with other options such as nutrient management and augmenting the seedbank with invasive-resistant perennials, these secondary treatments could help the overall solution to *Phragmites* dominance. However, a longer term study is needed to determine whether the secondary efforts will have lasting effects. Repetition of secondary treatments on a short time scale might be necessary. Nonetheless, it is a good alternative or supplement to annual aerial spray, which may reduce live *Phragmites* cover but has a minimal effect on species diversity.

Martha Carlson holds a master's degree

in aquatic ecology from the University of Michigan School of Natural Resources and Environment (SNRE) in Ann Arbor, MI, where she is a doctoral candidate. Concurrently, she is a scientist in training at the U.S. Geological Survey – Great Lakes Science Center. Her research examines interactions between hydrology and vegetation, impacts of climate change, and implications for management of Great Lakes coastal wetlands.

Kurt Kowalski is a research ecologist at the U.S. Geological Survey – Great Lakes Science Center and a Ph.D. Candidate at the University of Michigan School of Natural Resources and Environment. His research efforts focus on the ecology, restoration, and management of Great Lakes coastal wetlands.

Douglas Wilcox retired from the U.S. Geological Survey and is now the Empire Innovation Professor of Wetland Science at SUNY-Brockport in his native western New York State. His research on Great Lakes wetlands focuses on management issues related to water-level fluctuations, water-level regulation, and climate change, as well as wetland restoration methodologies.

LITERATURE CITED

Ailstock, M.S., C.M. Norman, and P.J. Bushmann. 2001. Common reed *Phragmites australis*: control and effects upon biodiversity in freshwater nontidal wetlands. Restoration Ecology 9:49-59.

Aldworth, J., and W.P. Hoffman. 2002. Split-plot model with covariate: a cautionary tale. The American Statistician 56:284-289.

Amsberry, L., M.A. Baker, P.J. Ewanchuk, and M.D. Bertness. 2000. Clonal integration and the expansion of *Phragmites australis*. Ecological Applications 10:1110 – 1118.

Armstrong, J., F. Afreen-Zobayed, S. Blyth, and W. Armstrong. 1999. *Phragmites australis*: effects of shoot submergence on seedling growth and survival and radial oxygen loss from roots. Aquatic Botany 64:275-290.

Asaeda, T., L. Rajapakse, J. Manatunge, and N. Sahara. 2006. The effect of summer harvesting of *Phragmites australis* on growth characteristics and rhizome resource storage. Hydrobiologia 553:327-335.

Avers, B., R. Fahlsing, E. Kafcas, J. Schafer, T. Collin, L. Esman, E. Finnell, A. Lounds, R. Terry, J. Hazelman, J. Hudgins, K. Getsinger, and D. Scheun. 2007. A guide to the control and management of invasive *Phragmites*. Michigan Department of Environmental Quality, Lansing.

Barry, M.J., R. Bowers, and F.A. de Szalay. 2004. Effects of hydrology, herbivory and sediment disturbance on plant recruitment in a Lake Erie coastal wetland. American Midland Naturalist 15:217-232.

Bennington, C.C., and W.V. Thayne. 2005. Use and misuse of mixed model analysis of variance in ecological studies. Ecology 75:717-722.

Bonate, P.L. 2000. Analysis of Pretest-Posttest Designs. Chapman and Hall/CRC Press, Boca Raton, Fla.

Bray, R.H., and L.T. Kurtz. 1945. Determination of total, organic, and available forms of phosphorus in soils. Soil Science 59:39-45.

Buhler, D.D., and O.C. Burnside. 1983. Effects of spray components on glyphosate toxicity to annual grasses. Weed Science 31:124-130.

Buttler, A. 1992. Permanent plot research in wet meadows and cutting experiment. Vegetatio 103:113-124.

Campbell, A.L. 2007. Sexual reproduction in the non-native common reed, *Phragmites australis* (Cav.) Trin ex. Steudel: seed production, dormancy and germination. M.S. thesis, The Ohio State University, Columbus.

Chambers, R.M., L.A. Meyerson, and K. Saltonstall. 1999. Expansion of *Phragmites australis* into tidal wetlands of North America. Aquatic Botany 64:261-273.

Chambers, R.M., D.T. Osgood, D.J. Bart, and F. Montalto. 2003. *Phragmites australis* invasion and expansion in tidal wetlands: interactions among salinity, sulfide, and hydrology. Estuaries 26:398-406.

Chow-Fraser, P., V. Lougheed, V. Le Thiec, B. Crosbie, L. Simser, and J. Lord. 1998. Long-term response of the biotic community to fluctuating water levels and changes in water quality in Cootes Paradise Marsh, a degraded coastal wetland of Lake Ontario. Wetlands Ecology and Management 6:19-42.

Cowie, N.R., W.J. Sutherland, M.K.M. Ditlhogo, and R. James. 1992. The effects of conservation management of reed beds. II. The flora and litter disappearance. Journal of Applied Ecology 29:277-284.

Cross, D.H., and K.L. Fleming. 1989. Control of *Phragmites* or common reed. Waterfowl Management Handbook Leaflet 13.4.12, U.S. Fish and Wildlife Service, Washington, D.C.

Curtis, J.T, and R.P. McIntosh. 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. Ecology 32:476-496.

Federer, W.T., and M.P. Meredith. 2005. Covariance analysis for split-plot and split-block designs. The American Statistician 46:155-162.

Findlay, S., P. Groffman, and S. Dye. 2003. Effects of *Phragmites australis* removal on marsh nutrient cycling. Wetlands Ecology and Management 11:157-163.

Flora of North America Editorial Committee (eds.). 1993+. Flora of North America North of Mexico. 12+ vols. New York and Oxford. Available online <http://www.efloras.org>. Accessed 11 November 2007.

Goldberg, D.E., and T.E. Miller. 1990. Effects of different resource additions on species diversity in an annual plant community. Ecology 71:213-225.

Güsewell, S., and P. Edwards. 1999. Shading by *Phragmites australis*: a threat for species-rich fen meadows? Applied Vegetation Science 2:61-70.

Güsewell, S., C. Le Nédic, and A. Buttler. 2000. Dynamics of common reed (*Phragmites australis*) in Swiss fens with different management. Wetlands Ecology and Management 8:375-389.

Hara, T., J. van der Toorn, and J.H. Mook. 1993. Growth dynamics and size structure of shoots of *Phragmites australis*, a clonal plant. Journal of Ecology 81:47-60.

Harris, S.W., and W.H. Marshall. 1960. Experimental germination of seed and establishment of seedlings of *Phragmites communis*. Ecology 41:395.

Haslam, S.M. 1972. Biological flora of the British Isles: *Phragmites communis* Trin. Journal of Ecology 60:585-610.

Hellings, S.E., and J.L. Gallagher. 1992. The effects of salinity and flooding on *Phragmites australis*. Journal of Applied Ecology 29:41-49.

Hudon, C., P. Gagnon, and M. Jean. 2005. Hydrological factors controlling the spread of common reed (*Phragmites australis*) in the St. Lawrence River (Quebec, Canada). Ecoscience 12:347-357.

Hurlbert, S.H. 1971. The nonconcept of species diversity: a critique and alternative parameters. Ecology 52:577-586.

Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54:187-211.

Husak, S. 1978. Control of reed and reed mace stands by cutting. Pp. 404-408 *in* D. Dykyjova and J. Kvet, eds., Pond Littoral Ecosystems: Structure and Functioning.

Springer, Berlin.

Karunaratne, S., T. Asaeda, and K. Yutani. 2004. Age-specific seasonal storage dynamics of *Phragmites australis* rhizomes: a preliminary study. Wetlands Ecology and Management 12:343-351.

Keddy, P.A., and A.A. Reznicek. 1986. Great Lakes vegetation dynamics: the role of fluctuating water levels and buried seeds. Journal of Great Lakes Research 12:25-36.

Keller, B.E.M. 2000. Plant diversity in *Lythrum*, *Phragmites*, and *Typha* marshes, Massachusetts, U.S.A. Wetlands Ecology and Management 8:391-401.

Kercher, S.M., and J.B. Zedler. 2004. Flood tolerance in wetland angiosperms: a comparison of invasive and noninvasive species. Aquatic Botany 80:89-102.

Kowalski, K.P., and D.A. Wilcox. 1999. Use of historical and geospatial data to guide the restoration of a Lake Erie coastal marsh. Wetlands 19:858-868.

Kowalski, K.P., D.A. Wilcox, and M.J. Wiley. 2006. Final report: coastal wetland habitat restoration and exploration. Report to U.S. Environmental Protection Agency, Great Lakes National Program Office, Chicago.

League, M.T., E.P. Colbert, D.M. Seliskar, and J.L. Gallagher. 2006. Rhizome growth dynamics of native and exotic haplotypes of *Phragmites australis* (common reed). Estuaries and Coasts 29:269-276.

LeBlanc, M.-C., C. Lavoie, S. de Blois, J. Labbé, and F. Belzile. 2007. Which factors explain the invasion of a large lake of southern Quebec (Canada) by the exotic genotype of common reed (*Phragmites australis*)? Society of Wetland Scientists 2007 International Meeting Abstracts. Society of Wetland Scientists, Sacramento, Calif.

Littell, R.C., G.A. Milliken, W.W. Stroup, and R.D. Wolfinger. 1996. SAS® System for Mixed Models. SAS Institute, Cary, N.C.

Maceina, M.J., P.W. Bettoli, and D.R. DeVries. 1994. Use of split-plot analysis of variance design for repeated-measures fishery data. Fisheries 19:14-20.

Marks, M., B. Lapin, and J. Randall. 1994. *Phragmites australis* (*P. communis*): threats, management and monitoring. Natural Areas Journal 14:285-294.

Miao, S.L., and F.H. Sklar. 1998. Biomass and nutrient allocation of sawgrass and cattail along a nutrient gradient in the Florida Everglades. Wetlands Ecology and Management 5:245-263.

Minchinton, T.E., J.C. Simpson, and M.D. Bertness. 2006. Mechanisms of exclusion of native coastal marsh plants by an invasive grass. Journal of Ecology 94:342-354.

Monteiro, A., I. Moreira, and E. Sousa. 1999. Effect of prior common reed (*Phragmites australis*) cutting on herbicide efficacy. Hydrobiologia 415:305-308.

Moreira, I., A. Monteiro, and E. Sousa. 1999. Chemical control of common reed (*Phragmites australis*) by foliar herbicides under different spray conditions. Hydrobiologia 415:299-304.

Newman, J.A., J. Bergelson, and A. Grafen. 1997. Blocking factors and hypothesis tests in ecology: is your statistics text wrong? Ecology 78:1312-1320.

Newman, S., J. Schuette, J.B. Grace, K. Rutchey, T. Fontaine, K.R. Reddy, and M. Peitrucha. 1998. Factors influencing cattail abundance in the northern Everglades. Aquatic Botany 60:265-280.

Olsen, S.R., C.V. Cole, F.S. Watanabe, and L.A. Dean. 1954. Estimation of available phosphorus in soils by extraction with sodium bicarbonate. Department of Agriculture Circular 939, U.S. Department of Agriculture, Washington, D.C.

Pagter, M., C. Baragto, and H. Brix. 2005. Tolerance and physiological responses of *Phragmites australis* to water deficit. Aquatic Botany 81:285-299.

Perry, L.G., and S.M. Galatowitsch. 2003. A test of two annual cover crops for controlling *Phalaris arundinacea* invasion in restored sedge meadow wetlands. Restoration Ecology 11:297-307.

Prasad, R. 1984. Impact of glyphosate on macrophytes. Plant Physiology 75:139.

Pratt, C.R. 1984. Response of *Solidago graminifolia* and *S.juncea* to nitrogen fertilization applications: changes in biomass allocation and implications for community structure. Bulletin of the Torrey Botanical Club 111:469-478.

Reed, Jr., Porter B. 1988. National list of plant species that occur in wetlands: national summary. Biological Report 88 (24), U.S. Fish and Wildlife Service, Washington, D.C.

Rickey, M.A., and R.C. Anderson. 2004. Effects of nitrogen addition on the invasive grass *Phragmites australis* and a native competitor *Spartina pectinata*. Journal of Applied Ecology 41:888-896.

Rolletschek, H., A. Rolletschek, R. Hartzendorf, and J.-G. Kohl. 2000. Physiological consequences of mowing and burning of *Phragmites australis* stands for rhizome ventilation and amino acid metabolism. Wetlands Ecology and Management 8:425-433.

Saltonstall, K. 2002. Cryptic invasion by a non-native genotype of the common reed, *Phragmites australis*, into North America. Proceedings of the National Academy of Science 99:2445-2449.

Saltonstall, K. 2003. Genetic variation among North American populations of *Phragmites australis*: implications for management. Estuaries 26:445-452.

Saltonstall, K., and J.C. Stevenson. 2007. The effect of nutrients on seedling growth of native and introduced *Phragmites australis*. Aquatic Botany 86:331-336.

Seabloom, E.W., and A.G. van der Valk. 2003. Plant diversity, composition, and invasion of restored and natural prairie pothole wetlands: implications for restoration. Wetland 23:1-12.

Seddon, J.C. 1981. The control of aquatic weeds with the isopropylamine salt of N-phosphonomethyl glycine. Proceedings of the Conference on Aquatic Weeds and Their Control. Christ Church, Oxford, England, 7-8 April 1981. Association of Applied Biologist, Wellesbourne, Warwick, England.

Simmons, M.T. 2005. Bullying the bullies: the selective control of an exotic, invasive annual (*Rapistrum rugosum*) by oversowing with a competitive native species (*Gaillardia pulchella*). Restoration Ecology 13:609-615.

Smith, S.M. 2005. Manual control of *Phragmites australis* in freshwater ponds of Cape Cod National Seashore, Massachusetts, USA. Journal of Aquatic Plant Management 43:50-53.

Spence, D.H.N. 1982. The zonation of plants in freshwater lakes. Advanced Ecological Research 12:37-124.

Stalter, R., and Baden, J. 1994. A twenty-year comparison of vegetation of three abandoned rice fields, Georgetown County, South Carolina. Castanea 59:69-77.

Tilman, D. 1984. Plant dominance along an experimental nutrient gradient. Ecology 65:1445-1 453.

Tilman, D. 1987. Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. Ecological Monographs 57:189-214.

Turner, R.E., and R.S. Warren. 2003. Valuation of continuous and intermittent *Phragmites* control. Estuaries 26:618-623.

[USDA] United States Department of Agriculture. 2007. The PLANTS Database. National Plant Data Center, Baton Rouge, LA. Available online <http://plants.usda.gov>. Accessed 21 May 2007.

van der Valk, A.G. 1986. The impact of litter and annual plants on recruitment from the seed bank of a lacustrine wetland. Aquatic Botany 24:13-26.

Vestergaard, P. 1994. Response to mowing of coastal brackish meadow plant communities along an elevational gradient. Nordic Journal

Rates, patterns, and impacts of *Phragmites australis* expansion and effects of experimental *Phragmites* control on vegetation, macroinvertebrates, and fish with tidelands of the lower Connecticut River. Estuaries 24:90-107.

Welch, B.A., C.B. Davis, and R.J. Gates. 2006. Dominant environmental factors in wetland plant communities invaded by *Phragmites australis* in East Harbor, Ohio, USA. Wetlands Ecology and Management 14:511-525.

White, S.D., B.M. Deegan, and G.G. Ganf. 2007. The influence of water level fluctuations on the potential for convective flow in the emergent macrophytes *Typha domingensis* and *Phragmites australis*. Aquatic Botany 86:369-376.

Wilcox, D.A., and J.E. Meeker. 1991. Disturbance effects on aquatic vegetation in regulated and unregulated lakes in northern Minnesota. Canadian Journal of Botany 69:1542-1551.

Wilcox, D.A., and S.J. Nichols. 2008. The effects of water-level fluctuations on vegetation in a Lake Huron wetland. Wetlands 28:487-501.

Wilcox, D.A., and T. Whillans. 1999. Techniques for restoration of disturbed coastal wetlands of the Great Lakes. Wetlands 19:835-857.

Wilcox, D.A., K.P. Kowalski, H.L. Hoare, M.L. Carlson, and H.N. Morgan. 2008. Cattail invasion of sedge/grass meadows in Lake Ontario: photointerpretation analysis of sixteen wetlands over five decades. Journal of Great Lakes Research 34:301-323.

Windham, L. and R. Lathrop. 1999. Effects of *Phragmites australis* (common reed) invasion on above-ground biomass and soil properties in brackish tidal marsh of the Mullica River, New Jersey. Estuaries 22:927-935.

Windham, L., and L.A. Meyerson. 2003. Effects of common reed (*Phragmites australis*) expansions on nitrogen dynamics of tidal marshes of the northeastern U.S. Estuaries 26:452-464.

Woo, I., and J.B. Zedler. 2002. Can nutrients alone shift a sedge meadow towards a dominance by the invasive *Typha* × *glauca*? Wetlands 22:509-521.

Appendix. Importance values (IV), life history, wetland status, habit, and origin of the more common species (i.e., those with an IV > 0.6 in at least one sampling period) observed in the seedbank study (SB), pre-treatment field sampling (YR0), and post-treatment field sampling in Year 1 (YR 1) and Year 2 (YR2). IV was calculated as the sum of relative frequency and either relative density (SB) or relative dominance (YR0, YR1, and YR2). Nomenclature follows Flora of North America Editorial Committee (1993+).

Taxon	Life History[a]	Wetland Status[b]	Habit[c]	Origin[u]	Importance Value			
					SB	YR0	YR1	YR2
Alisma triviale Pursh	P	OBL	F/H	N	0.15	–	0.93	–
Ammannia robusta Heer & Regel	A	NI	F/H	N	24.84	–	2.17	–
Bidens cernua L.	A	OBL	F/H	N	0.75	–	7.26	–
Bidens sp. L.	A	–	F/H	N	–	1.43	–	–
Bolboschoenus fluviatilis (Torrey) Soják	P	OBL	G	N	–	1.72	3.05	4.38
Butomus umbellatus L.	P	OBL	F/H	I	–	–	0.74	0.98
Calystegia sepium (L.) R. Br.	P	FAC	V, F/H	N	–	0.60	0.15	–
Ceratophyllum demersum L.	P	OBL	F/H	N	–	–	4.46	3.20
Cirsium arvense (L.) Scopoli	P	FACU	F/H	I	–	1.72	0.16	3.19
Cyperus diandrus Torrey and *Cyperus bipartitus* Torrey	A	FACW+	G	N	4.93	–	1.60	–
Cyperus erythrorhizos Muhlenberg	A or P	OBL	G	N	11.42	–	1.26	–
Cyperus odoratus L. and *Cyperus strigosus* L.	A or P	FACW+/FACW	G	N	11.20	–	5.97	–
Cyperus spp. L.	A or P	–	G	N	6.41	0.85	0.15	–
Echinochloa crusgalli (L.) P. Beauv.	A	FACW	G	I	0.90	–	1.54	–
Echinochloa walteri (Pursh) A. Heller	A	OBL	G	N	0.92	–	1.97	2.54
Eleocharis acicularis (L.) Roemer & Schultes	A or P	OBL	G	N	38.97	11.93	14.49	–
Eleocharis erythropoda Steudel	P	OBL	G	N	0.48	3.58	2.37	0.26
Eleocharis obtusa (Willd.) Schultes	A or P	OBL	G	N	2.79	–	1.65	1.95
Eleocharis palustris (L.) Roemer & Schultes	P	OBL	G	N	–	–	1.39	0.66
Epilobium ciliatum Raf.	P	FACU	F/H	N	0.60	–	–	–
Epilobium coloratum Spreng.	P	OBL	F/H	N	–	–	0.62	–
Eragrostis hypnoides (Lam.) Britton, Sterns & Poggenb.	A	OBL	G	N	1.21	–	–	–
Eupatorium perfoliatum L.	P	FACW+	F/H	N	–	2.71	0.18	1.33
filamentous algae	–	–	–	–	–	–	–	4.49
MacMillan	A or P	OBL	F/H	N	2.14	–	1.19	0.24
Impatiens capensis Meerb.	A	FACW	F/H	N	–	–	–	0.95

Continued

[a]Life History: A = annual, B = biennial, P = perennial.

[b]Wetland indicator status (Reed 1988): OBL = obligate wetland, FACW = facultative wetland, FAC = facultative; FACU = faculative upland, NI= no indicator, + and - signs indicate tendency toward higher and lower ends of the category.

[c]Habit: F/H = forb/herb, G = graminoid, T = tree, V = vine, S = shrub, SS = subshrub.

[d]Origin: N = native, I = introduced. Habit and origin were determined according to USDA (2007).

Taxon	Life History[a]	Wetland Status[b]	Habit[c]	Origin[d]	Importance Value			
					SB	YR0	YR1	YR2
Juncus canadensis J. Gay	P	OBL	G	N	–	–	–	1.70
Juncus gerardii Loiseleur–Deslongchamps	P	OBL	G	N	–	–	–	2.09
Juncus spp. L.	P	–	G	N	0.77	–	–	–
Lactuca serriola L. var. integrata	A or B	FAC	F/H	I	0.72	–	0.81	3.29
Leersia oryzoides (L.) Sw.	P	OBL	G	N	2.61	0.99	2.86	2.25
Lemna minor L.	P	OBL	F/H	N	–	4.33	3.32	4.11
Lindernia dubia (L.) Pennell	A or B	OBL	F/H	N	11.53	–	3.21	–
Ludwigia alternifolia L.	P	OBL	F/H	N	7.86	–	0.67	0.23
Ludwigia palustris (L.) Elliott	P	OBL	F/H	N	5.28	–	5.11	–
Lycopus americanus Muhl. ex W.P.C. Barton	P	OBL	F/H	N	–	0.29	0.88	0.53
Lycopus uniflorus Michx.	P	OBL	F/H	N	2.53	–	–	1.00
Lythrum salicaria L.	P	OBL	SS, F/H	I	–	2.90	–	–
Mimulus ringens L.	P	OBL	F/H	N	–	–	0.99	–
Myriophyllum sibiricum Kom.	P	NI	F/H	N	–	–	1.14	–
Najas flexilis (Willd.) Rostkovius & W. L. E. Schmidt	A	OBL	F/H	N	–	–	1.02	–
Najas minor Allioni	A	OBL	F/H	I	–	–	0.61	–
Nelumbo lutea Willd.	P	OBL	F/H	N	–	3.49	3.70	–
Panicum dichotomiflorum Michx.	A	FACW–	G	N	0.82	–	0.15	–
Penthorum sedoides L.	P	OBL	F/H	N	17.06	–	3.04	–
Phalaris arundinacea L.	P	FACW+	G	N	–	–	–	9.63
Phragmites australis (Cav.) Trin. ex Steud.	P	FACW+	SS, S, G	I	5.55	19.93	34.21	47.51
Phragmites australis, dead	–	–	–	–	–	75.42	14.63	11.46
Polygonum lapathifolium L.	A	FACW+	F/H	N	7.14	5.77	1.44	–
Polygonum pensylvanicum L.	A	FACW+	F/H	N	0.59	–	0.76	–
Polygonum persicaria L.	A or P	FACW	F/H	I	0.61	–	0.46	1.49
Polygonum punctatum Buch.–Ham. ex D. [	A or P	OBL	F/H	N	1.71	–	4.55	3.95
Polygonum spp. L.	A or P	–	F/H	–	1.87	1.54	–	–
Pontederia cordata L.	P	OBL	F/H	N	–	0.29	0.16	0.70
Potamogeton crispus L.	P	OBL	F/H	I	–	5.86	1.17	3.00
Potamogeton nodosus Poiret	P	OBL	F/H	N	–	12.76	8.49	11.89
Potamogeton pectinatus L.	P	OBL	F/H	N	–	2.10	3.12	0.71
Potamogeton sp. L.	P	–	F/H	–	–	3.26	0.45	–
							Continued	

[a]Life History: A = annual, B = biennial, P = perennial.

[b]Wetland indicator status (Reed 1988): OBL = obligate wetland, FACW = facultative wetland, FAC = facultative; FACU = faculative upland, NI= no indicator, + and - signs indicate tendency toward higher and lower ends of the category.

[c]Habit: F/H = forb/herb, G = graminoid, T = tree, V = vine, S = shrub, SS = subshrub.

[d]Origin: N = native, I = introduced. Habit and origin were determined according to USDA (2007).

Taxon	Life History[a]	Wetland Status[b]	Habit[c]	Origin[d]	Importance Value			
					SB	YR0	YR1	YR2
Potamogeton foliosus Rafinesque	P	OBL	F/H	N	–	–	0.88	0.46
Ricciocarpos natans (L.) Corda	–	–	NV	N	5.96	–	–	–
Rorippa palustris (L.) Besser	A, B, or P	OBL	F/H	N	2.87	0.57	1.47	–
Rosa palustris Marshall	P	OBL	SS	N	–	–	0.16	4.20
Sagittaria latifolia Willd.	P	OBL	F/H	N	1.97	6.06	11.65	17.60
Salix exigua Nutt.	P	FACW+	T, S	N	–	3.67	1.53	1.35
Schoenoplectus tabernaemontani (C. C. Gm	P	OBL	G	N	0.68	1.54	1.88	1.28
Scirpus cyperinus (L.) Kunth	P	OBL	G	N	–	–	0.18	0.72
Sparganium eurycarpum Engelmann	P	OBL	F/H	N	–	0.62	1.27	0.47
Spirodela polyrhiza (L.) Schleid.	P	OBL	F/H	N	–	1.64	1.99	6.44
Triadenum fraseri (Spach) Gleason	P	OBL	F/H	N	0.74	–	–	–
Trifolium pratense L.	B or P	FACU+	F/H	I	–	–	0.15	2.41
Typha angustifolia L.	P	OBL	F/H	I	7.65	16.98	20.94	24.42
Typha spp., dead	P	OBL	F/H	–	–	–	0.61	5.30
Typha ×glauca	P	OBL	F/H	–	–	–	0.34	0.82
Verbena hastata L.	B or P	FACW+	F/H	N	0.60	–	0.16	0.23

[a]Life History: A = annual, B = biennial, P = perennial.

[b]Wetland indicator status (Reed 1988): OBL = obligate wetland, FACW = facultative wetland, FAC = facultative; FACU = faculative upland, NI= no indicator, + and - signs indicate tendency toward higher and lower ends of the category.

[c]Habit: F/H = forb/herb, G = graminoid, T = tree, V = vine, S = shrub, SS = subshrub.

[d]Origin: N = native, I = introduced. Habit and origin were determined according to USDA (2007).