Species composition and inter-annual dynamics of a freshwater tidal plant community following removal of the invasive grass, *Phragmites australis*

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Abstract

We document the regeneration of native freshwater wetland plant assemblages following removal of the common reed, *Phragmites australis* (Cav.) Trin. ex Steudel from two sites at Chapman Pond, East Haddam, Connecticut, USA. We gathered field data on composition of the vegetation 1 year *before* and for each of the 3 years *after* the removal in fall 1995/spring 1996 of *Phragmites* by two slightly different methods (hand-removal and herbiciding in one area, mowing/mulching and herbiciding in another). An area where *Phragmites* was left intact was similarly monitored. Our goals for this monitoring were: (1) to document plant species composition and richness before and after *Phragmites* removal and (2) to examine temporal and spatial variability in patterns of plant recruitment. *Phragmites* declined in both density and extent in both plots where removal treatments were applied. Richness, evenness, and density of non-*Phragmites* species increased steadily from 1996 to 1997 in all removal and intact plots. However, the species composition of the removal plots was richer than that of the intact plot, and more closely resembled that of comparable, uninvaded freshwater tidal wetlands. Rates of recovery of species richness in the removal plots declined from 1997 to 1998, potentially reflecting saturation of available colonization space, or the return of *Phragmites*. *Phragmites* has expanded its range in both of the removal plots since 1997. A model of its colonization indicates that *Phragmites* occupies space through localized proliferation of dense rhizomes rather than diffusely foraging with long tillers. Vigilance in monitoring is needed to document the spread of invasives, to evaluate the multi-faceted ecological effects of eradication efforts on both the invader and the regenerating community, and develop strategies for preventing re-invasion.

Introduction

This study documents the regeneration of native freshwater wetland plant assemblages following removal of the common reed, *Phragmites australis* (Cav.) Trin. ex Steudel. *Phragmites* is becoming a widespread dominant plant of freshwater to mesohaline marshes throughout the eastern United States (Chambers et al., in press). Although *Phragmites* has been present in North American wetlands for thousands, if not millions, of years (Niering et al. 1977; Orson et al. 1987), this species appears to have accelerated its colonization of wetlands in the past century (Marks et al. 1994; Prisloe and Barrett 1998). Its rapid recent expansion in the United States may be explained by multiple factors, including widespread alteration of hydrologic flows, disturbance of wetland sediments through ditching and reclamation, increases in nutrient inputs that favor its competitive ability, and/or the introduction of novel genetic variants that are competitively superior to native vegetation (reviewed by Chambers et al. 1999).

Phragmites poses a concern particularly where it forms extensive, mono-specific stands and threatens to dominate wetlands that support rich assemblages of native plant and animal species. In these situations, *Phragmites* competitively depresses the growth and diversity of native plant species and may displace them altogether, leading to declines in overall richness of native plant taxa (Stalter and Baden 1994; Windham 1995; Meyerson et al., in press). In order to protect and restore wetland communities, especially those that harbor species of conservation significance, many agencies are beginning to undertake small- and large-scale efforts to control *Phragmites*.

Despite these burgeoning efforts to eradicate *Phragmites* from several sites around North America, little published, quantitative information is available on the recovery of native communities following its removal. The few studies we encountered in an exhaustive literature search document the effect of removal treatments on population densities and mortality of *Phragmites* itself (Bongiorno et al. 1984; Boone et al. 1987; Randall and Lapin 1995), or on other trophic levels (e.g., Ditlhogo et al. 1992), but do not follow regeneration and community assembly of native wetland species. Cowie et al. (1992) found that cutting and burning of reeds in Norfolk, UK, promoted floristic diversity and richness of marsh plants. Interestingly, reed densities were higher and reed stature lower in the managed plots, which begs the hypothesis that *Phragmites* dominates competitively due to its stem height and capacity to attenuate light rather than its density and ability to capture soil resources.

We may also derive lessons by observing changes in plant species composition of native wetlands where *Phragmites* is declining without intervention. For example, *Phragmites* clones vary widely in their longevity (Haslam 1971) and the reed is disappearing from portions of its former range in Britain, with concomitant declines in reed-associated fauna (Bibby and Lunn 1982; Boar et al. 1989; Hartog et al. 1989; Ostendorp 1989). Again, however, research largely focuses on the status of *Phragmites* or associated rare consumer species exclusively, and data on regeneration of native plant communities are lacking. It is difficult to measure the success of restoration attempts without reference to comparative data on vegetation community composition. Unfortunately, many reports from restoration and monitoring projects do not appear in the published literature where they might otherwise be more widely accessible.

Quantitative studies documenting community succession and patterns of *Phragmites* re-growth are critically needed, particularly in plant communities that harbor rare species. Ideally, these studies should follow community recovery over multiple growing seasons, because species composition, especially in complex assemblages, is likely to vary over time. Working at the Chapman Pond Preserve, which encompasses a freshwater tidal marsh, staff and volunteers with the Connecticut Field Office of The Nature Conservancy (TNC) have gathered field data on the composition of the vegetation 1 year *before* and for each of the 3 years *after* the removal, by two different methods, of *Phragmites*. An area where *Phragmites* was left intact has been similarly monitored. Our goals for this monitoring were to document plant species composition and patterns of species richness and dominance both before and after *Phragmites* removal, and to examine temporal and spatial variability in patterns of plant recruitment and community structure over several years.

Site description and methods

The site

Located in East Haddam, Connecticut, Chapman Pond is an approximately 24-ha freshwater embayment of the Connecticut River (Figure 1). The pond receives freshwater inputs from tidal fluctuations in the river and from upland terrestrial sources through 3 perennial streams. Tidal amplitude is approximately 0.75 m, but standing water levels on the marsh vary with rainfall and river stage. Fringing the open pond is an extensive freshwater tidal marsh of approximately 53 ha, a natural community type that is the focus of substantial conservation effort by The Nature Conservancy and other partners within the Tidelands of the lower Connecticut River. We studied vegetation composition of the emergent freshwater marsh comprising this tidal wetland matrix. This marsh encompasses one of the largest remaining stands of wild rice (*Zizania aquatica*) in the lower Connecticut River, and four state-listed rare plant species and several rare insect species are also recorded from the marsh.

Phragmites australis is first visible (in aerial photographs) at the north-west margin of Chapman Pond in 1965; it was not visible in photographs from 1934 and 1951 (Prisloe and Barrett 1998). Total coverage of *Phragmites* has increased in area from 0.42 to 1.44 ha
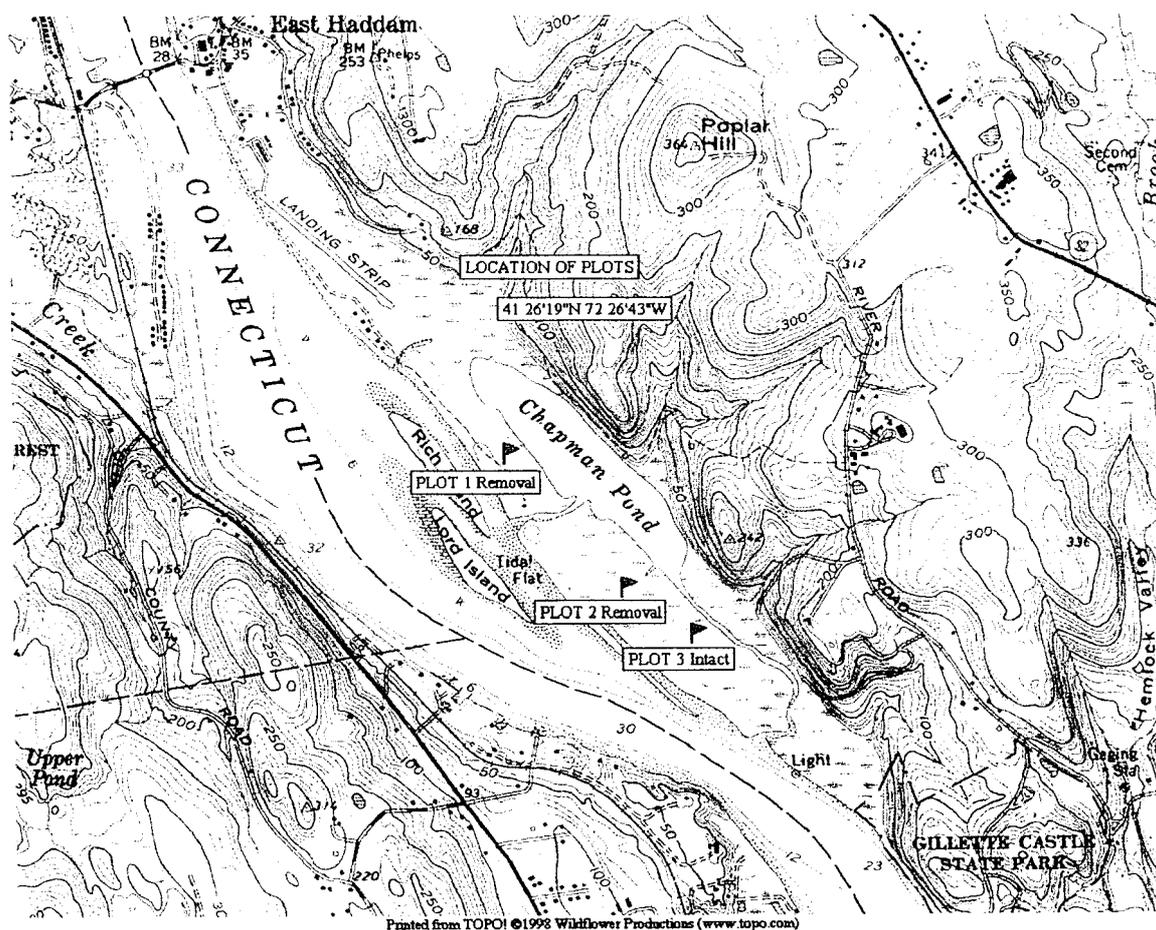
Figure 1. Map of Chapman Pond, East Haddam, Connecticut, showing locations of the two *Phragmites* removal plots and the intact plot.

(203%) from 1968 to 1994, according to estimates by Prisloe and Barrett (1998) using geographic information systems. Three distinct stands of *Phragmites* currently occupy the site; it is unknown if these are genetically distinct clones. The northern stand (containing removal plot 1) occurs on soft clay and peat substrate bordered by swamp forest (principally *Salix nigra* and *Acer rubrum*) at the upland, and intertidal herbaceous vegetation (primarily *Pontederia cordata*, *Sagittaria latifolia* and *Leersia oryzoides*) at its pond-ward margin. The middle stand (containing removal plot 2) occurs on more resistant peat in which the large grasses *Zizania aquatica, Typha latifolia,* and *Leersia oryzoides* are the predominant plant species present. The southern stand (containing intact plot 3) is a dense, mono-dominant stand of *Phragmites* bordering a community of herbaceous vegetation that resembles the profile of the middle stand, on similar substrate.

Phragmites *removal*

Perceiving that *Phragmites* directly threatened species of the native wetland, The Nature Conservancy had been conducting periodic small-scale cutting of the pond-ward perimeter of the northern *Phragmites* stand since 1986. This cutting had slowed but not stopped the eastern expansion of this *Phragmites* stand. In August, 1995, The Nature Conservancy and the Connecticut Department of Environmental Protection initiated herbicide treatments in the northern and the middle *Phragmites* stands. A 1% solution of Rodeo (Monsanto, Inc.; active herbicidal compound glyphosate) was applied to standing *Phragmites* stems using a hand-held sprayer. In the northern stand (hereafter referred to as plot 1), herbicide was sprayed at the pond-ward margin from a boat. In the middle stand (hereafter referred to as plot 2), herbicide was sprayed from a low-ground-pressure

amphibious vehicle. Following herbicide application late in the growing season, each stand was mulched in place during the subsequent spring. Plot 1 was subjected to hand-cutting, and whole, felled stems were left in place. Plot 2 was mowed using a Seppi mower, which shreds the plant material into fine pieces. Thus, each stand received slightly different removal treatments occurring on a comparable spatial scale. Each treatment removed on the order of 0.4 ha of *Phragmites* (Paul Capotosto, CT DEP, personal communication), but left a portion of the original *Phragmites* stand in place. An entire *Phragmites* stand was left intact in the southern sector of Chapman Pond (hereafter referred to as plot 3), and monitored similarly to the removal plots.

Vegetation monitoring

In 1995, prior to initiating concerted removal efforts, data were collected on plant species composition in the three stands of *Phragmites*. Vegetation sampling methods were similar in each of the plots, with baseline and transect length sensitive to the shape and total area of the *Phragmites* or removal zone. A permanent 100 m baseline was established through each *Phragmites* stand, and points for up to 10 perpendicular line transects, extending into the area occupied by the current *Phragmites* stand, were chosen randomly along the baseline (Figure 2). Up to 10 1 × 1 m quadrats were then randomly arrayed along each transect line to a maximum distance of 60 m away from the baseline (total $N = 50$ quadrats/plot). Within each quadrat, numbers of all live standing stems of all plant species
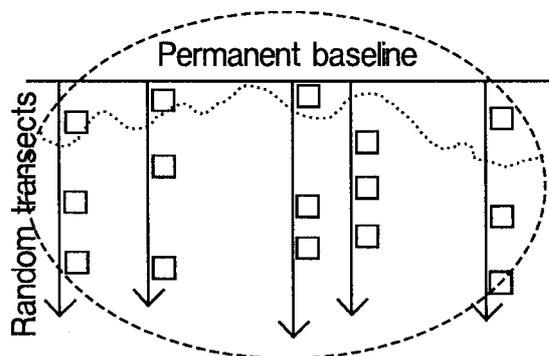
Figure 2. Diagram illustrating basic design of random quadrat sampling. Small squares signify 1 × 1 m quadrats. Transect lines passed through the edge of the remaining *Phragmites* stand in removal areas, represented by the dotted line. Transects were laid within in the intact *Phragmites* stand, represented by the dashed line.

were counted. When densities of ramets per quadrat exceeded 200, we estimated the number of stems per square meter by censusing 0.5 × 0.5 m subquadrats. Stem counts were used in preference to visual estimates of percent cover due to the diversity of morphologies present in each quadrat and the fact that most quadrats showed near 100% cover and considerable vertical overlap of plants. Sampling took place each year (1995–1998) in late summer, and the same data were recorded at each date (transect placement varied randomly). Following *Phragmites* removal in 1996, each permanent baseline in plots 1 and 2 occupied the edge of the remaining stand and permanent transects extended out into the removal area. Inspection of grids displaying the distribution of the randomly-placed quadrats within each plot from 1995–1998 indicates that we achieved comparable spatial coverage of the same area from year to year.

As the foregoing description makes clear, these sampling regimes were not strictly replicated because the original design precluded the use of multiple treatment replicates due to a number of constraints on cost and personnel. Because of this pseudoreplication (*sensu* Hurlbert 1984), apparent differences in response attributable to differences in treatment type cannot be distinguished from *a priori* inter-site differences. While strong inferences cannot be made about the precise relationship between treatment type and patterns of community regeneration and *Phragmites* re-growth, the pre- and post-treatment data do speak to treatment efficacy, and the long-term post-treatment data on community ecology are informative.

We tested the null hypotheses that: (1) vegetation structure, including species richness, composition, and dominance patterns would not differ among intact and removal areas; and (2) structure would not differ before and after *Phragmites* removal. Data were analyzed using Systat version 7.0 and StatXact version 3.0 for Windows. Data were transformed as necessary to conform to assumptions of analysis of variance, and ANOVA with Scheffé post-hoc multiple-comparisons testing was used; otherwise, non-parametric tests were employed to distinguish treatment effects.

Results

Effects of removal on Phragmites australis

Density of live stems of *Phragmites australis* were similar in all three plots prior to initiation of removal
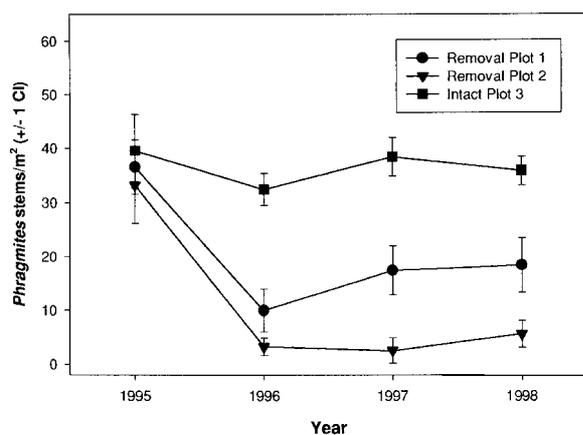
Figure 3. Trends in the density (per square meter) of live *Phragmites* stems in the intact plot 3 and removal plots 1 and 2. Points are means; error bars indicate 95% confidence intervals on the mean.

treatments in 1995, and remained at between 35 and 45 stems/m² between 1995 and 1998 in the intact plot 3. In contrast, the density of *Phragmites* stems declined significantly in both removal plots 1 and 2 between 1995 and 1996 (Mann–Whitney U-test, $P < 0.0001$ for each plot). In 1996, plots 1 and 2 did not differ significantly; treatments had reduced *Phragmites* densities to similarly low levels. In subsequent years, the mean density of *Phragmites* stems/m² remained significantly lower in the removal plots 1 and 2 than in the intact plot 3 (Figure 3). However, removal plot 2 exhibited significantly lower mean densities of *Phragmites* than removal plot 1 in 1997 (Kruskal–Wallis test statistic $\chi_2^2 = 22.92$, $P < 0.0001$) and in 1998 ($\chi_2^2 = 12.07$, $P < 0.0001$).

Three-dimensional plots show the temporal and spatial dynamics of *Phragmites* decline and re-growth in the removal plots 1 and 2 (Figure 4). It was possible to visualize through these graphs the gradual increase in stem density occurring from the edges of the remaining stand. In plot 1, *Phragmites* stems recruited in a wave running parallel to the eastern edge of the remaining stand, toward the shore of Chapman Pond. In contrast, *Phragmites* stems began to increase in density at two edges running perpendicular to the unherbicided edge of plot 2.

Because quadrats were not placed at the same positions each year, it was problematic to estimate linear rates of *Phragmites* colonization into new space. We modeled the recruitment dynamics of *Phragmites* in plot 1 using a 3-parameter logistic non-linear

regression model [equation: $y = a/(1 + (x/x_0)^b)$, where a (y asymptote) and b (slope) and x_0 (position of inflection point) are estimated parameters, y is stem density, and x is distance in meters from baseline]. Figure 5 illustrates the curves fitted to sampling points; models explained between 24% and 54% of the variance in stem density. Density and extent of *Phragmites* remained similar between 1996 and 1997. However, stem density at points near the baseline increased in 1998, and the position of the leading edge of the stand (indicated by the inflection point declining from the asymptote) shifted almost 5 m between 1997 and 1998. This model demonstrates that *Phragmites* colonization occurred less through the recruitment of new, exploratory tillers foraging into open space than through the build-up of a dense phalanx (*sensu* Lovett-Doust 1981) of stems just behind the advancing front.

The re-colonization of *Phragmites* was also apparent in an increase in relative importance. In 1995, 100% of quadrats surveyed in plots 1 and 2 contained some *Phragmites* (density > 0 stems/m²). In 1996, removal treatments had reduced this occurrence to 36% of quadrats in plot 1 and 40% of quadrats in plot 2. In 1998, 64% of randomly surveyed quadrats in plot 1 and 45% of the quadrats in plot 2 contained *Phragmites*.

Regeneration of other wetland plant species following Phragmites removal

Prior to the removal treatments, the mean density of stems of species other than *Phragmites* was low in all plots (Figure 6). Plots initially exhibited different mean non-*Phragmites* stem densities (Kruskal–Wallis test statistic $\chi_2^2 = 36.547$, $P < 0.0001$), with plot 3 showing the highest number of stems per square meter. In the year just following removal, non-*Phragmites* stem densities remained low in all plots; removal plots 1 and 2 did not differ. In 1997, by contrast, the density of non-*Phragmites* stems increased significantly in both removal plots 1 (Mann–Whitney $U = 611.5$, $P < 0.0001$) and 2 (Mann–Whitney $U = 261.0$, $P < 0.0001$), attaining similar values in both plots. In 1998, non-*Phragmites* stem densities continued to climb; however, removal plot 2 showed significantly higher mean densities than removal plot 1 (Mann–Whitney $U = 787.0$, $P = 0.002$).

To assess the putative impacts of *Phragmites* on other plant species, we evaluated whether *Phragmites* stem densities were correlated with the density of stems of non-*Phragmites* species. Due to a large number

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Dynamics of *Phragmites* in Removal Plot 1
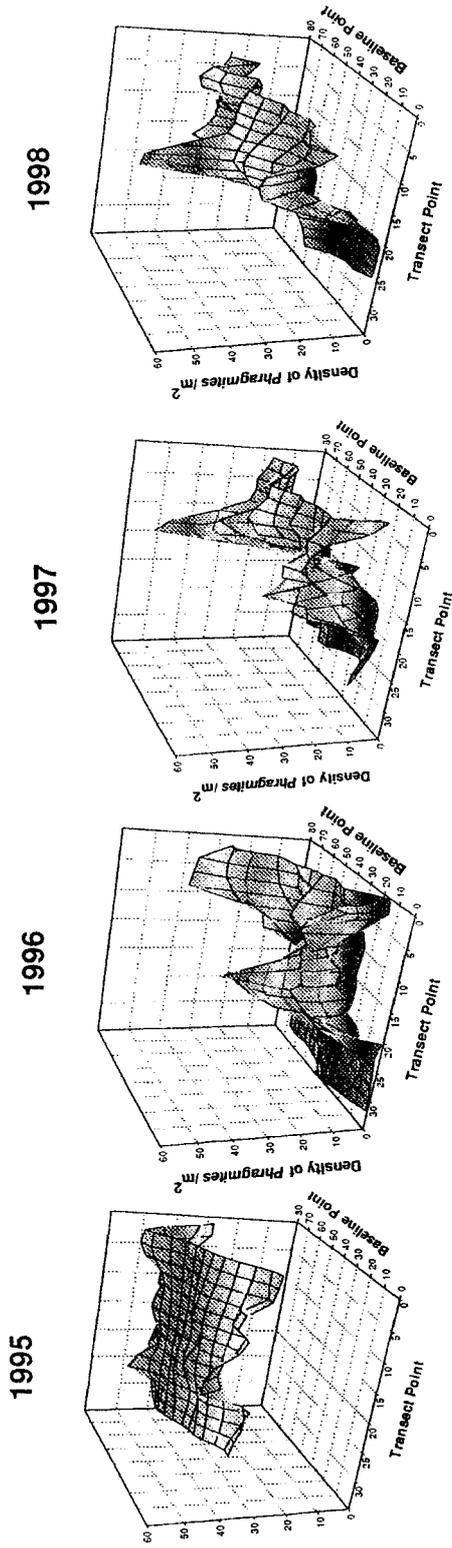
Dynamics of *Phragmites* in Removal Plot 2
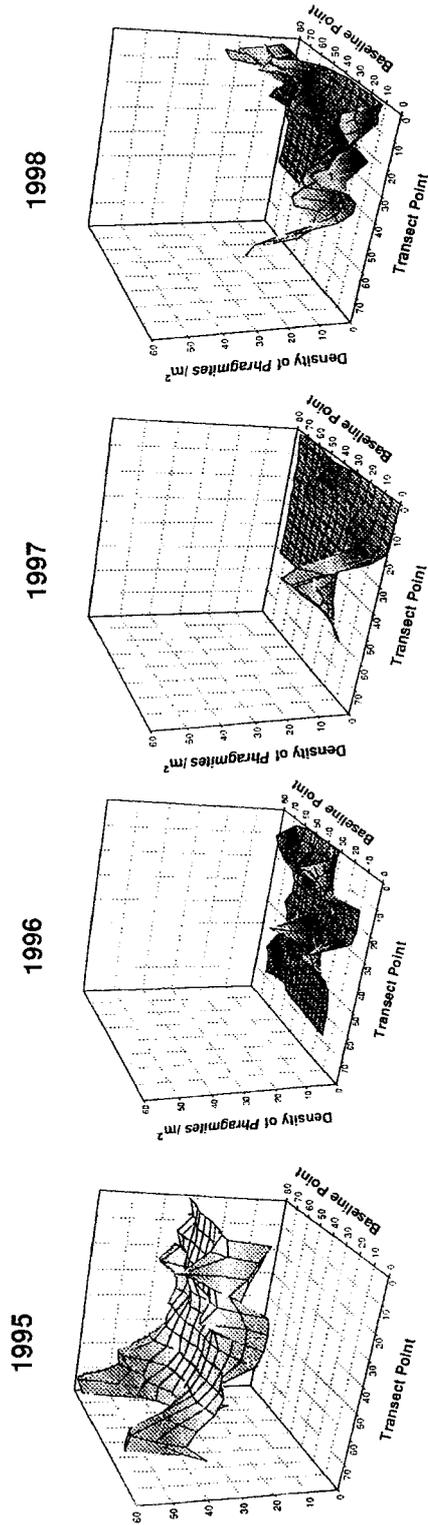
Figure 4. Dynamics of *Phragmites* stem densities (per square meter) in the removal plots 1 and 2 between 1995 and 1998. Graphs show the decrease in density of living stems following herbicide application and physical stem removal in 1996, and the gradual increase in *Phragmites* densities at the edges of the stands through which the transects passed. Recall that the permanent baseline ran through and parallel to the 'leading' edge of each *Phragmites* stand. Transect and baseline coordinates are given in meters from the permanent baseline marker established in 1995.

Figure 6. Temporal trends in the density (per square meter) of live stems of all plant species other than *Phragmites* in the intact plot 3 and removal plots 1 and 2. Points are means; error bars indicate 95% confidence intervals.
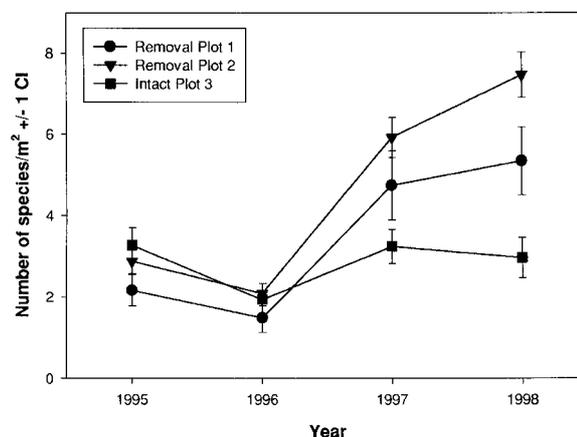
Figure 7. Trends in the richness (per square meter) of live stems of all plant species other than *Phragmites* in the intact plot 3, and removal plots 1 and 2. Points are means; error bars indicate 95% confidence intervals.

Figure 5. Profile of *Phragmites* re-colonization of plot 1 from 1996 to 1998. Dots show the density of *Phragmites* stems as a function of distance from the permanent baseline, which was located inside the edge of the advancing *Phragmites* stand. Curves show the best-fit non-linear regression solution for a logistic equation describing the relationship between density and distance (see text), with r^2 values indicated.

of empty cells (i.e., *Phragmites* densities $= 0$), the data were converted to quintiles, and the Jonckheree–Terpstra exact test for $R \times C$ doubly-ordered contingency tables (Mehta and Patel 1995) was used to examine whether stem densities co-varied non-randomly and to explicitly address the hypothesis that the density of non-*Phragmites* stems was dependent upon the density of *Phragmites* stems. The density of non-*Phragmites* species was inversely related to

the density of *Phragmites* stems in quadrats of both removal plots, in both 1997 (Standardized $JT(x) = -4.125$, $P < 0.0001$ for plot 1; $JT(x) = -2.19$, $P = 0.017$ for plot 2) and 1998 ($JT(x) = -3.34$, $P = 0.0003$ for plot 1; $JT(x) = -3.347$, $P = 0.0002$ for plot 2).

Patterns of mean richness of non-*Phragmites* stems paralleled those of densities after the removal treatments (Figure 7). Immediately following *Phragmites* removal, mean species richness per quadrat declined significantly in both plots 1 and 2. Species richness

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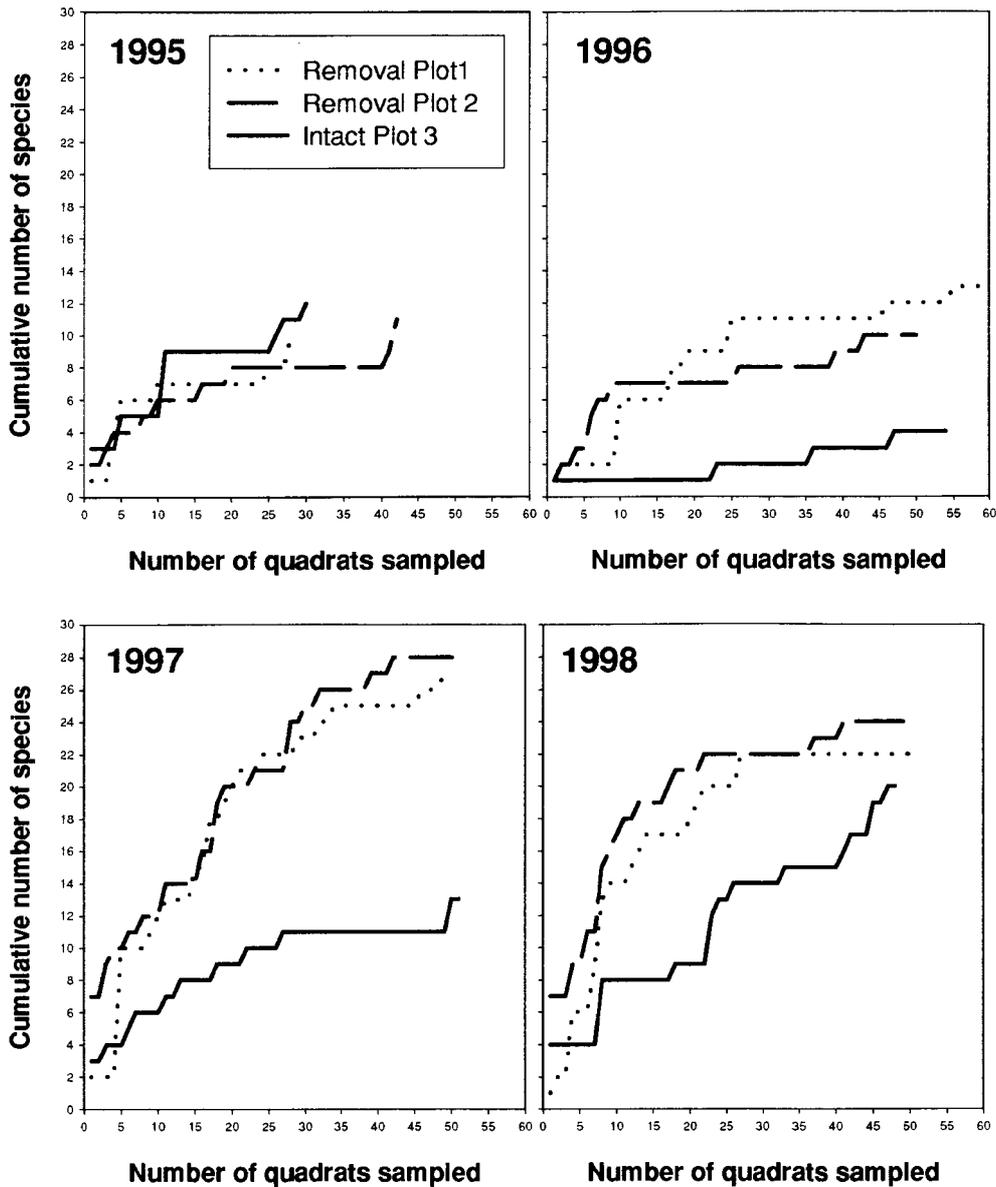
Figure 8. Species–effort curves for removal plots 1 and 2 and intact plot 3. Curves show the cumulative number of plant species identified as the number of quadrats sampled increased.

also declined significantly in intact plot 3, for reasons that are unclear. In 1997 and 1998, species richness increased in both removal plots, while remaining low in intact plot 3. Removal plot 1 consistently showed lower species richness than removal plot 2 in 1997, and this disparity increased in 1998 (Figure 7).

Cumulative species richness encountered across all quadrats in each plot was plotted as a species–effort curve for each year (Figure 8). The asymptotic form

of the curves confirmed that our sampling captured true species richness in all plots. Removal plots 1 and 2 contained qualitatively similar numbers of total species in all years, but the cumulative totals dropped between 1997 and 1998 in both plots. Total number of species found in the intact plot 3 increased from 1996 to 1998, potentially indicating recruitment of new species into the established *Phragmites* stand over time.

As species richness increased, the community composition of the marsh assemblage changed in the removal plots (Figure 9). Immediately following the removal treatments in 1996, *Phragmites*, *Peltandra virginica*, the vine *Mikania scandens*, and the fern *Onoclea sensibilis* (the latter three are typical constituents of a *Phragmites* understory) occurred most frequently in the quadrats of both areas; other vegetation remained very sparse. One and two years after removal, *Leersia oryzoides*, *Pontederia cordata*, *Bidens connata*, and *Zizania aquatica* had gained prominence in the marsh. Spearman rank correlations performed on quadrat occurrence data for species that were encountered both in 1997 and 1998 showed that ranks remained stable among years in plots 1 and 2 (Spearman's $\tau = 0.809$, $P < 0.0001$, $N = 27$). That is, a species was likely to occur at the same frequency in 1998 as in 1997. Coefficients of variation for species occurrence dropped from 2.7 to 1.3 after 1996, indicating a more even distribution of species in the removal plots. *Onoclea sensibilis* remained the dominant non-*Phragmites* species in the intact plot 3. All other species occurred at very low frequencies in plot 3, yielding a correspondingly high coefficient of variation (Figure 9).

We also explored whether the species composition was similar in both of the recovering marsh areas. Jaccard indices (ranging from 0, for dissimilar profiles, to 1, for identical compositions) were computed from information on the number of species that were shared by plots 1 and 2 in the years following *Phragmites* removal. The species composition of the regenerating assemblages was moderately similar among the two plots in 1997 (Jaccard index = 0.629) and 1998 (Jaccard index = 0.563). Plot 2 contained species in the genera *Carex, Cyperus*, and *Juncus* not present in plot 1 in both years, while *Eleocharis* spp. and *Mikania scandens* occurred uniquely in plot 1. In order to assess whether the species composition of this regenerating marsh community bore resemblance to that recorded for similar uninvaded freshwater tidal wetlands, we compiled a full list of plant species encountered and compared it to a list of species from sites in the Connecticut River tidelands given by Barrett (1994). We sampled in areas of Chapman Pond that correspond most closely with the *Polygonum*, *Hypericum*, and *Sagittaria* typologies distinguished by Barrett (1994). We identified 53 species of vascular plants, including 4 non-angiosperms (ferns and horsetails), during our surveys from 1995 to 1998 (Table 1). During reconnaissance

Table 1. List of plant species found at Chapman Pond, 1995 to 1998. Nomenclature follows Gleason and Cronquist (1991) and Barrett (1994). Taxa in boldface type were found uniquely in this study and are not listed by Barrett (1994).

Acorus calamus	**Onoclea sensibilis**
Alisma subcordatum	**Osmunda regalis**
Amorpha fruticosa	**Parthenocissus quinquefolia**
Apios americana	*Peltandra virginica*
Bidens cernua	*Phragmites australis*
Bidens connata	*Pilea pumila*
Bidens laevis	*Polygonum hydropiperoides*
Boehmeria cylindrica	**Polygonum lapathifolium**
Carex lacustris	*Polygonum punctatum*
Carex stricta	*Polygonum sagittatum*
Crassula aquatica	*Pontederia cordata*
Desmodium cuspidatum	*Rorripia islandica*
Echinochloa walteri	*Rumex verticillatus*
Eleocharis palustris	*Sagittaria montevidensis*
Equisetum fluviatile	*Sagittaria latifolia*
Eupatorium perfoliatum	*Salix nigra*
Hypericum mutilum	*Scirpus fluviatilis*
Impatiens capensis	*Scirpus validus*
Iris pseudacorus	*Scutellaria laterifolia*
Leersia oryzoides	**Solidago sp.**
Limosella subulata	**Thelypteris palustris**
Lobelia cardinalis	**Toxicodendron radicans**
Ludwigia palustris	*Typha latifolia*
Lythrum salicaria	*Typha angustilfolia*
Mentha arvensis	*Verbena hastata*
Mikania scandens	*Zizania aquatica*
Mimulus alatus	

in 1993, Barrett (1994) described 56 angiosperm species (no non-angiosperms were enumerated). Forty species are shared between the two lists; that is, we found 71.4% of his listed angiosperm species regenerating in the removal plots. Jaccard indices indicated a similarity of 0.579 between the regenerating wetland at Chapman Pond and other documented freshwater tidal wetlands along the Connecticut River (Barrett 1994). Importantly, wild rice (*Zizania aquatica*), whose growth The Nature Conservancy sought to encourage by removing *Phragmites*, returned in force, especially in plot 2. Its importance rank increased from 16 in 1996, to 11 in 1997, and 5 in 1998 (Figure 9).

Discussion

We asked several questions in compiling these data on the composition of the freshwater tidal marsh at

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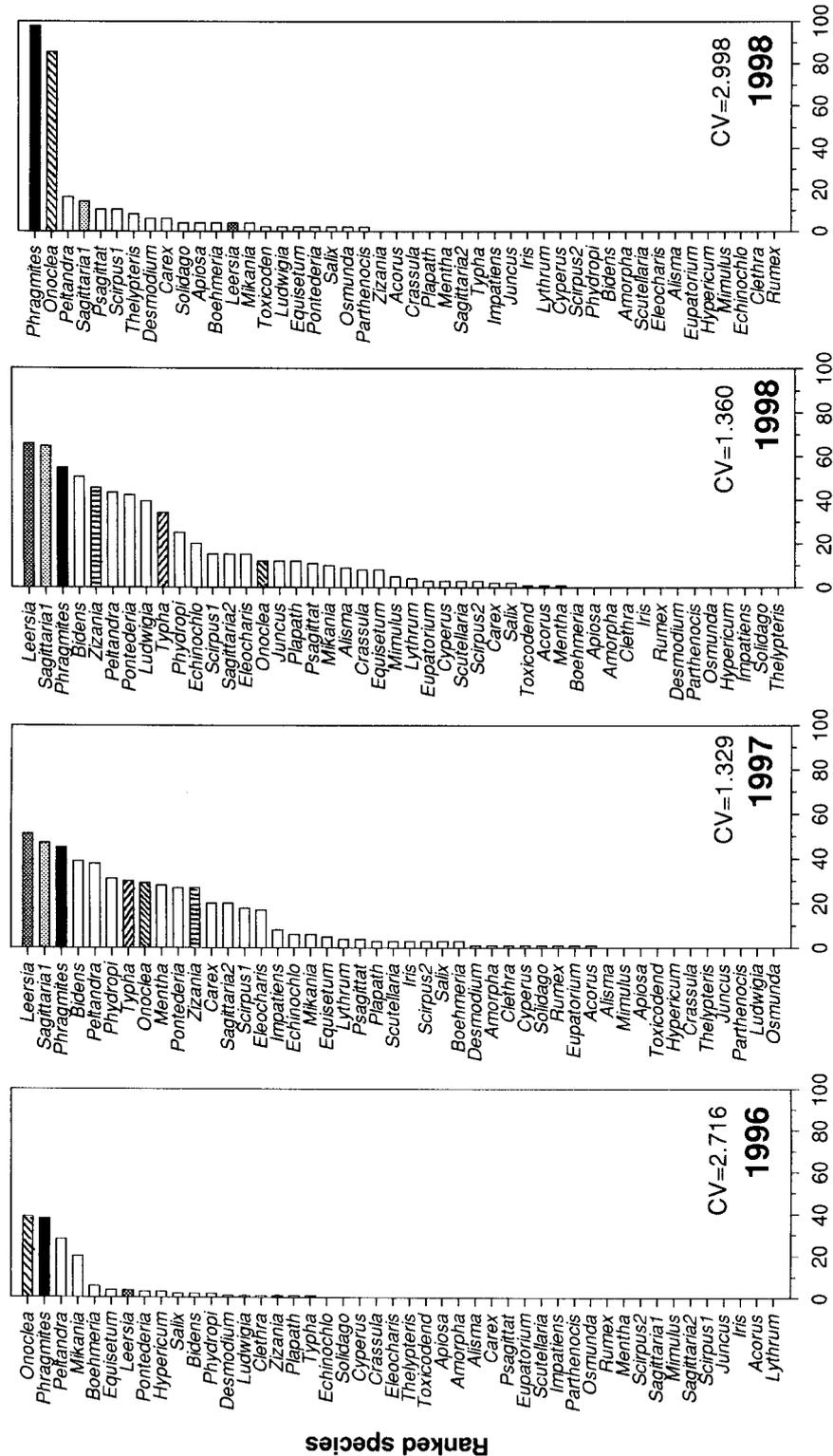
Figure 9. Temporal dynamics of species composition in the removal plots (data pooled among plots for simplicity) from 1996 to 1998. Species are ranked according to the proportion of total quadrats in which they occurred, and the coefficient of variation (an index of species evenness) is shown at the bottom of each plot. Bars corresponding to selected dominant species of interest (*Phragmites australis, Onoclea sensibilis, Zizania aquatica, Sagittaria latifolia, Typha latifolia,* and *Leersia oryzoides*) are shaded to show changes in their rank-order position among years.

Chapman Pond. First, did the removal treatments have a measurable effect on the prevalence and density of *Phragmites australis*? Second, how did the species richness and composition of the flora change in the years following *Phragmites* removal relative to the stand where *Phragmites* was left intact? Third, is *Phragmites* returning to the sites from which it was removed, and, if so, how is it impacting the non-*Phragmites* vegetation?

Herbiciding and cutting of *Phragmites* stems in late summer 1995 and spring 1996 resulted in significant, transient declines in the density and extent of the stands of reed in both plots relative to the intact plot (Figures 3 and 4). Despite slight methodological differences in the treatments, these effects were initially similar among the plots.

Species other than *Phragmites* were very sparse in all plots prior to the treatments, and remained so in the intact plot 3 throughout the sampling period. Both stem densities (Figure 6) and species richness per quadrat (Figure 7) were significantly depressed where *Phragmites* occurred, but both increased steadily after 1996. We were fortunate to be able to compare the composition of the post-removal vegetation to data recorded by Barrett (1994) in Chapman Pond and other tidal wetlands along the Connecticut River; and to demonstrate that the recovering assemblage bore substantial resemblance to uninvaded sites (Table 1).

The regeneration of a species-rich assemblage of plants in the gap created by *Phragmites* removal probably occurred, following a lag in 1996, by recruitment from a combination of seed bank sources and perennating buds that may have remained viable even under conditions of *Phragmites* dominance (van der Valk and Pederson 1989; Barrett 1994). No steps were taken following herbiciding to physically restore the site to a preferred species composition, so the regeneration that occurred reflects a lottery process of recruitment from the different source pools existing at the different plots. Despite probable differences in substrate and flooding regime (not quantified in this study), the removal plots each attained a more diverse and more even species composition relative to that observed before the treatments and to that of plot 3 (Figure 9). There was considerable year-to-year change in the composition and richness of all three assemblages, however (Figures 7 and 8), and plot 1 consistently showed fewer species than plot 2. We cannot attribute these differences to treatment effects due to the original pseudoreplicated

design; but future studies should examine fine-scale treatment effects carefully.

It is of interest that the cumulative richness of non-*Phragmites* species increased from 1995 to 1998 in the intact stand (Figure 8). Clearly, *Phragmites* did not exclude all other freshwater tidal wetland species. It is conceivable that new species were introduced into the understory as researchers created new paths into the *Phragmites* stand over the years of sampling; the effects of trampling and disturbance should be investigated in other studies. Several vine and fern species (especially the sensitive fern, *Onoclea sensibilis*) appear to colonize and persist in the understory of a *Phragmites* stand (Figure 9). These species may increasingly serve as the source bank for new recruits if a *Phragmites* stand is allowed to occupy an area for several years prior to removal, leading to the regeneration of a very different assemblage from the ones observed in this study.

Multiple years of monitoring also make it clear that *Phragmites* can re-invade sites following removal (Figure 4). The source of new *Phragmites* stems likely resides with the remnant stand, as recruitment from seed is uncommon in this species (Galinato and van der Valk 1986), and evidence for the support of new shoots by physiological integration with the parent clone is strong (Hara et al. 1993). Demography of individual *Phragmites* ramets could not be followed in this study, but a model of *Phragmites* movement constructed from plot 1, where stand expansion was particularly tractable, is revealing (Figure 5). Rather than sending out long tillers from the leading edge of the stand into uncolonized space, *Phragmites* at Chapman Pond appears to gain dominance by increasing the density of stems behind an advancing front (Figure 5). This phalanx of stems appears to advance several meters per year at this site [which is consistent with independent estimates of spatial spread (Prisloe and Barrett 1998)]. The rate of movement will likely be affected by substrate conditions and the composition of the flora with which it may compete. Such a mode of growth may reflect the normal growth pattern of the species and/or a response to herbciding or mowing. Cowie et al. (1992) found that cutting reed (without herbicide) induced an increase in stem density; however, these stems were shorter than those of untreated stands (1.4 m tall) and did not appear to suppress the growth of other vegetation. Where *Phragmites* remains tall (in excess of 3 m at Chapman Pond) as well as dense, it significantly reduces light

availability to plants in the understory (Farnsworth and Meyerson, unpublished data) and thus may depress growth and seed germination. Spatially explicit, multi-year data like those collected here can inform models of invasion and spread (Hastings 1996), and are needed to assess if and when re-treatment is necessary. This study demonstrates that a diverse freshwater tidal marsh can regenerate in the wake of *Phragmites* invasion and removal, but also cautions that monitoring and publication of data from multiple sites are needed to provide convincing measures of success and to detect re-invasion.

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