DISTURBANCE-MEDIATED COMPETITION AND THE SPREAD OF *PHRAGMITES AUSTRALIS* IN A COASTAL MARSH

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Abstract. In recent decades the grass *Phragmites australis* has been aggressively invading coastal, tidal marshes of North America, and in many areas it is now considered a nuisance species. While *P. australis* has historically been restricted to the relatively benign upper border of brackish and salt marshes, it has been expanding seaward into more physiologically stressful regions. Here we test a leading hypothesis that the spread of *P. australis* is due to anthropogenic modification of coastal marshes. We did a field experiment along natural borders between stands of *P. australis* and the other dominant grasses and rushes (i.e., matrix vegetation) in a brackish marsh in Rhode Island, USA. We applied a pulse disturbance in one year by removing or not removing neighboring matrix vegetation and adding three levels of nutrients (specifically nitrogen) in a factorial design, and then we monitored the aboveground performance of *P. australis* and the matrix vegetation. Both disturbances increased the density, height, and biomass of shoots of *P. australis*, and the effects of fertilization were more pronounced where matrix vegetation was removed. Clearing competing matrix vegetation also increased the distance that shoots expanded and their reproductive output, both indicators of the potential for *P. australis* to spread within and among local marshes. In contrast, the biomass of the matrix vegetation decreased with increasing severity of disturbance. Disturbance increased the total aboveground production of plants in the marsh as matrix vegetation was displaced by *P. australis*. A greenhouse experiment showed that, with increasing nutrient levels, *P. australis* allocates proportionally more of its biomass to aboveground structures used for spread than to belowground structures used for nutrient acquisition. Therefore, disturbances that enrich nutrients or remove competitors promote the spread of *P. australis* by reducing belowground competition for nutrients between *P. australis* and the matrix vegetation, thus allowing *P. australis*, the largest plant in the marsh, to expand and displace the matrix vegetation. Reducing nutrient load and maintaining buffers of matrix vegetation along the terrestrial–marsh ecotone will, therefore, be important methods of control for this nuisance species.

Key words: above- and belowground competition; coastal marsh, (New England, USA); disturbance; estuaries; eutrophication; grasses; human impacts; invasive and nuisance species; marsh conservation; nutrients; Phragmites australis; *plant-competition theory.*

INTRODUCTION

Humans are increasingly modifying coastal landscapes. Urban and agricultural development along the terrestrial border of estuaries has increased nutrient load and physically impacted species of plants within coastal, tidal marshes (Adam 1990, Valiela et al. 1997, Vitousek et al. 1997). Such disturbances can alter the relative abundance of species and their interspecific interactions, leading to dramatic changes in the production and assemblage structure of plants within marshes (Boyer and Zedler 1998, Zedler 2000, Pennings and Bertness 2001, Zedler et al. 2001, Bertness et al. 2002). Theory predicts that competitive interactions among plants may be mediated by disturbances that affect the availability of limiting resources such

as nutrients or light (Tilman 1982, 1988). Physical disturbance may increase the availability of resources indirectly by removing competing species that share common resources, and disturbances such as nutrient enrichment may directly enhance resource availability (e.g., Turkington et al. 1993, Wilson and Tilman 1993). Under conditions of elevated resource availability, species of plants may expand their distribution because they can now withstand more stressful abiotic conditions or outcompete species that were superior competitors when resources were limiting.

Interspecific competition and tolerance to abiotic stress are important factors influencing the zonation of the dominant plants in coastal, salt marshes of southern New England, USA (Bertness and Ellison 1987, Bertness 1991*a, b*). Fertilization experiments by Levine et al. (1998) and Emery et al. (2001) have shown that the competitive hierarchy among these dominant species may be reversed when nutrient limitation is removed, particularly nitrogen, which is an important limiting nutrient of coastal marshes (Valiela and Teal 1974, Val-

iela et al. 1985). While these studies predict that increased nutrient load may alter the assemblage structure of plants in coastal salt marshes of southern New England, they fail to consider the dynamics of a common and increasingly dominant member of the marsh plant assemblage, the grass *Phragmites australis*, which over the past century has been aggressively invading coastal marshes of North America (see reviews in Marks et al. 1994, Tiner 1997, Chambers et al. 1999, Meyerson et al. 2000). *Phragmites australis* (often called ''common reed'' and hereafter referred as *Phragmites*) has been a minor component of the assemblage of plants along the relatively benign upper border of freshwater and brackish marshes for several thousands of years (Niering et al. 1977, Clark 1986, Orson et al. 1987). Now, however, it has been expanding seaward into more physiologically stressful regions of the low marsh and along the upper border of salt marshes, sometimes into areas in which it was historically absent. There is great concern that the continued spread of *Phragmites* will reduce local and regional plant diversity, change the composition and diversity of the fauna associated with these plants, and alter ecosystem function, particularly nitrogen cycling, within coastal marshes (Chambers 1997, Chambers et al. 1999, Windham and Lathrop 1999, Keller 2000, Meyerson et al. 2000, Warren et al. 2001). Indeed, in some areas of North America, *Phragmites* is currently regarded as a nuisance or noxious weed and has displaced native marsh plants, forming vast monocultures (see reviews cited above; but see Osterdorp [1989] and van der Putten [1997] for concern over the decline of *Phragmites australis* in Europe).

A leading explanation for the recent spread of *Phragmites* is that anthropogenic modification of coastal marshes has produced environmental conditions conducive to its establishment, growth, and expansion (Niering and Warren 1980, Mook and van der Toorn 1982, Roman et al. 1984, Hellings and Gallagher 1992, Burdick et al. 2001), although there is also evidence indicating that the invasion of *Phragmites* may be due to the recent introduction of a nonnative genotype that can tolerate a broader range of environmental conditions (Saltonstall 2002). Three main changes to environmental conditions along the upper border of coastal marshes have been implicated as favorable to the spread of *Phragmites*: increased freshwater input, increased nutrient load, and increased clearing of vegetation. Observations indicate that *Phragmites* thrives in physically disturbed areas, but grows poorly under low-nutrient conditions (Haslam 1972, Niering and Warren 1980, Roman et al. 1984, Phillips 1987, Gervais et al. 1993). Therefore, when not disturbed the spread of *Phragmites* may be limited by belowground competition for nutrients with the other dominant marsh plants, whereas under disturbance conditions *Phragmites* may flourish because it is released from com-

petition and critical nutrient resources are no longer limiting.

We hypothesized that the combined disturbances of increased nutrients and the clearing of competing marsh vegetation provides an environment that facilitates the spread of *Phragmites*, even under harsh abiotic conditions. We tested this hypothesis by examining how the availability of nutrient resources (particularly nitrogen) mediates competition between *Phragmites* and the other dominant grasses and rushes in a brackish marsh in Rhode Island, USA. Here we report the results of a field experiment where we applied a pulse disturbance (removal of neighboring species of marsh vegetation and the addition of nutrients in a factorial design) along natural borders between stands of *Phragmites* and the other marsh vegetation, and then monitored the aboveground performance of all species after the disturbance was removed. To gain insight into the mechanism by which *Phragmites* competes with the other species of marsh plants under different nutrient conditions, we did an experiment in the greenhouse examining the above- and belowground response of individual *Phragmites* plants to increasing levels of nutrients. By determining how disturbance mediates competition between *Phragmites* and the other dominant plants in the marsh, strategies for managing the invasion and control of *Phragmites* can be developed.

METHODS

Location studied

The study was done from May 1997 to October 1998 at a coastal, brackish marsh along the Barrington River, Seekonk, Rhode Island, USA (41°46′ N, 71°19′ W). The marsh is located in a suburban area and is bordered by farms, residential buildings, paved roadways, and forest. The marsh is relatively narrow (<100 m at its widest), but extends hundreds of meters along the river and its tributaries, which is typical of coastal marshes in the region. Plants occupying the marsh are typical of coastal, brackish and salt marshes in southern New England, with the marsh dominated by clonal, perennial species arranged in zones across an elevation gradient (Miller and Egler 1950, Redfield 1972, Nixon and Oviatt 1973, Niering and Warren 1980, Bertness and Ellison 1987). The grass *Spartina alterniflora* dominates the low marsh and riverbanks. The high marsh is occupied by the grass *S. patens* on its seaward side and by the rush *Juncus gerardi* on its landward side, with the grass *Distichlis spicata* distributed throughout (hereafter these three species are referred to collectively as ''matrix vegetation''). The highest elevations of the marsh, which include the upper border of the high marsh and the levees of the river, are dominated by stands (10s to 100s m^2 in area) of *Phragmites*, but the shrub *Iva frutescens* occupies these areas in some places. *Phragmites* covers <10% of the marsh, but it is currently spreading. Other common plants in the high

marsh include *Aster tenuifolius*, *Atriplex patula* var. *hastata*, *Salicornia europaea*, *Scirpus* spp., and *Solidago sempervirens*. We have recorded water salinities along the river ranging from 2 to 30 g/kg and soil porewater salinities at the soil surface in quadrats along the highest elevations of the marsh (see *Field experiment*, below) ranging from 4 to 32 g/kg (average values for each of three dates during the growing season were 11 ± 0.5, 24 ± 0.4, and 24 ± 0.8 g/kg [mean ± 1 SE], $n = 36$ soil porewater salinity samples; T. E. Minchinton, *unpublished data*). Tides are semi-diurnal with a maximal range of $\sim$2.4 m.

Phragmites australis

Phragmites is a clonal grass with annual shoots and perennial rhizomes that often forms monospecific stands in coastal, tidal marshes. Growth and expansion of *Phragmites* is primarily vegetative and not by seed, where rhizomes extend horizontally and give rise to new shoots. In coastal, tidal marshes of southern New England, new shoots of *Phragmites* emerge mainly in spring (April through May), grow rapidly over the next one or two months, and attain a maximal height (typically 1–4 m) by August (Buck 1995, Tiner 1997, Meyerson et al. 2000). Shoots develop terminal inflorescences from late summer to early autumn (August through September), and seeds mature until late autumn. Shoots that emerge in the spring senesce in the autumn (as does the matrix vegetation), but typically remain upright for several years (often called ''standing dead''). From the end of the growing season and throughout autumn *Phragmites* shunts resources from senescing shoots to its rhizomes, which extend horizontally and give rise to vertical rhizomes with buds lying beneath the soil surface, thus setting the patterns of emergence for shoots in the following spring (Haslam 1969).

Field experiment

Experimental design.—The experiment was done at the highest tidal elevations of the marsh where isolated stands of *Phragmites* along the upper border of the high marsh and the levees of the river are expanding into the lower tidal elevations of the marsh. From late May to early June 1997, after the springtime emergence of *Phragmites*, 36 quadrats separated by at least 2 m and with roughly equal densities of newly emerged shoots were distributed across seven stands of *Phragmites*. Four stands were clustered on one side of the marsh and three on the other side. The two groups of stands extended along 100-m sections of the marsh and were separated by 300 m and a tidal creek and causeway that extended partially through the middle of the marsh. To account for unknown variation due to the spatial separation of the two groups of stands, we took a cautious approach and considered each group as separate sites and located half the quadrats (i.e., 18 quadrats) at each site. Quadrats (6 m²) straddled the natural bor-

der along the edge of the stand where *Phragmites* is spreading into the lower elevations of the marsh dominated by matrix vegetation. One half of the quadrat was located within the stand (2 m along the natural border and 1.5 m into the stand) and the other half in the matrix vegetation (2 m along the natural border and 1.5 m into the matrix vegetation). The half of the quadrat within the stand contained a mixture of *Phragmites* shoots and matrix vegetation and was used to estimate growth of *Phragmites* within the stand, whereas the other half of the quadrat contained matrix vegetation with only an occasional *Phragmites* shoot and was used to estimate expansion of *Phragmites* into the lower elevations of the marsh. In each quadrat, at least two and usually all three of the species comprising the matrix vegetation were present, with other common plants occurring sporadically.

Two disturbance treatments (removal or no removal of matrix vegetation, three levels of nutrient addition) in a factorial design were randomly allocated to the 18 quadrats at each site, producing three replicates of each of the six treatment combinations per site. Treatments were applied as a discrete pulse from early August to late September 1997, after which quadrats were no longer manipulated. This pulse disturbance simulated reality, such as the discrete application of fertilizers to lawns, golf courses, or crops and the periodic clearing and mowing of marsh vegetation. Disturbances of this type often occur at the end of the growing season in late summer and early autumn when rhizomes are storing nutrients for growth and expansion in the following spring.

Matrix vegetation was removed by cutting it with grass clippers to a height of about 2 cm, and other species of plants that were occasionally present were also removed. Marsh turf that regrew was continually cut at two-week intervals. Nutrients were added in the form of granular, commercial 29:3:4 N:P:K fertilizer (Scotts Turf Builder Lawn Fertilizer with timed-release nitrogen [The Scotts Company, Marysville, Ohio, USA]) comprised of 29% N (0.5% ammoniacal N, 15.6% urea, 12.4% water-soluble organic N, and 0.5% water-insoluble N), 3% phosphorus (3% phosphoric acid) and 4% potassium (4% soluble potash). Three levels of nutrient addition, 0 g/m², 30 g/m², or 60 g/m², were applied four times at roughly two-week intervals by spreading the fertilizer evenly across the soil surface. Nutrients were added at times of neap tides so that leaching and dilution would be minimized. There was no evidence of burning of vegetation following nutrient addition. This amount and frequency of nutrient addition was selected to give specific levels of N addition, 0 $g \cdot m^{-2} \cdot yr^{-1}$, 35 $g \cdot m^{-2} \cdot yr^{-1}$, and 70 $g \cdot m^{-2} \cdot yr^{-1}$. These levels of nitrogen addition are at the lower limit of those applied annually to golf courses in the region (see Valiela et al. 1997) and are within the range used in similar studies examining the effects

of N addition on salt-marsh plants (see Boyer and Zedler 1998).

Sampling times and response variables.—To determine the immediate response of *Phragmites* to the disturbance treatments, quadrats were sampled at the end of the growing season, late September 1997. Only shoots that emerged after the treatments had been applied were sampled. To provide baseline levels against which to compare growth and expansion in 1998, shoots of *Phragmites* and tillers of the matrix vegetation that emerged throughout the growing season in 1997 were sampled in control quadrats (i.e., no removal of matrix vegetation, no addition of nutrients) at this time. Quadrats were sampled again in late September 1998 to determine how the pulse disturbance applied during 1997 influenced the performance of *Phragmites* and the matrix vegetation during the next growing season. Only live shoots and tillers were sampled, not standing-dead shoots of *Phragmites* or dead matrix vegetation.

The performance of *Phragmites* was quantified by measuring response variables relating to its size, morphology, leaf display, reproductive output, and expansion. In 1997 and 1998 the densities and heights of 20 shoots were counted in both the growth and expansion halves of the quadrat. The dry biomass of these shoots was estimated by multiplying shoot density and mean biomass per shoot. Biomass for each of the 20 shoots was determined using regression equations relating the heights of shoots to their dry biomass. Regression equations were obtained, one for each site, by collecting shoots ranging in height from 5 to 254 cm (with about 5 shoots in each 10-cm height category) and then determining their biomass in grams after drying them in an oven to a constant mass at 60°C and weighing them (site 1, ln biomass = 1.63[ln height] − 5.87; site 2, ln biomass = 1.87[ln height] − 6.86; T. E. Minchinton, *unpublished data*). The maximal distance that *Phragmites* expanded into the lower elevations of the marsh was estimated in 1997 by measuring the distance between the two shoots that extended farthest into the marsh before and after treatment application, and in 1998 by measuring the distance between the two shoots that extended farthest into the marsh in 1997 and 1998.

Additional variables relating to the morphology of individual *Phragmites* shoots were quantified in 1998 for 20 shoots haphazardly selected throughout the quadrat. The numbers of nodes and leaves of each shoot were counted. Mean internode length for each shoot was calculated by dividing shoot height by the number of internodes. The areas of individual leaves (leaf blades only, not sheaths) were estimated by measuring the maximal lengths and widths of two leaves (exclusive of the top and bottom leaves) haphazardly selected from each shoot, and calculating their areas (one side only) by assuming that leaves are shaped like a rectangle (for the half of the leaf closest to the stem) with a distal triangle (for the second half of the leaf). Leaf

area per shoot was estimated by multiplying the mean area per leaf by the number of leaves per shoot. Reproductive output of *Phragmites* was quantified in each quadrat by counting the number of shoots with inflorescences and calculating the percentage of shoots with inflorescences.

In 1997 and 1998, response variables indicating the performance of each species comprising the matrix vegetation (*J. gerardi*, *S. patens*, *D. spicata*) were also measured. Two samples (15 × 15 cm) of the matrix vegetation were collected from the half of the quadrat within the stand of *Phragmites*. For each species in each sample, the number of tillers was counted, the height of five tillers was measured, and the biomass was determined after drying them in an oven to a constant mass at 60°C and weighing them. Because each species was not present in every quadrat, data for the three species were pooled and analyzed collectively as matrix vegetation.

Statistical analyses.—The relevant hypothesis to be tested by this experiment is that the performance of *Phragmites* (and the matrix vegetation) in response to nutrient addition is dependent on the presence or removal of competing matrix vegetation (i.e., there is an interaction between the two disturbance treatments in their effect on the response variables). This was done using a two-factor analysis of variance (ANOVA) with nutrients and matrix vegetation considered as fixed effects. Results from the two sites were qualitatively the same, and our initial cautious approach to consider groups of stands on opposite sides of the marsh as separate sites in the design was unwarranted. Consequently, to increase statistical power of the analysis to detect differences due to disturbance treatments, we pooled the data across sites. Such pooling requires that we ignore error variation that might have occurred had we randomly allocated treatments to all quadrats at both sites rather than restricting the random allocation of treatments to quadrats at each site. The consistency of the response of *Phragmites* and matrix vegetation to treatment manipulations between sites indicates that this variance is likely to be small relative to other sources of error and, therefore, pooling is justified. All dependent variables were transformed to their natural logarithms, except for proportion data, which were transformed to the arcsine of their square roots.

Greenhouse experiment

Experimental design.—An experiment was set up in the greenhouse to determine how nutrients, in the absence of competitors and under benign abiotic conditions, influence changes in the size, morphology, leaf display, and biomass allocation of *Phragmites*. This experiment was done to help interpret the results of the field experiment, particularly by determining the relative allocation to above- and belowground structures, which is impossible to assess in the field for such a large plant as *Phragmites* without considerable destruc-

tion to the marsh. Seeds were collected from multiple stands within the marsh, sprinkled across the surface of commercial potting soil in large plastic trays, covered with a fine layer of soil, and watered daily with tap water. Seedlings appeared within two weeks and were individually transplanted into 2-L pots with commercial potting soil and watered daily with tap water. After one week, 30 hardy plants of roughly the same size (single shoot, 9.4 ± 0.48 cm, [mean ± 1 SE], n = 30 plants) were selected and equal numbers (n = 6) were randomly assigned to one of five levels of nutrient addition—0 g/m², 30 g/m², 60 g/m², 120 g/m², or 240 g/m²—of the same fertilizer used in the field experiment. Nutrients were applied only once and in the same manner as in the field experiment, giving nitrogen levels of about 0 g·m⁻²·yr⁻¹, 9 g·m⁻²·yr⁻¹, 17 g·m⁻²·yr⁻¹, 35 g·m⁻²·yr⁻¹, and 70 g·m⁻²·yr⁻¹, respectively, which spanned the range used in the field experiment. Plants were watered daily with tap water and maintained under ambient light and temperature conditions. Pots were randomly arranged in an array so that treatments were intermixed and their positions were re-randomized every three or four days. The experiment began on 1 August 1997 and ended on 1 September 1997, at which time plants had more than doubled in size.

Response variables.—Several response variables indicating the performance of *Phragmites* were measured at the end of the experiment, including the number of shoots, the height of each shoot, the number of leaves on each shoot, the area of individual leaves (leaf blades only, not sheaths), and the length of rhizomes. Shoot length was calculated as the sum of the heights of all shoots. The areas of individual leaves were measured as described previously (see *Field experiment: sampling times and response variables*). Leaf area of each plant was calculated by multiplying mean area per leaf by the total number of leaves. Plants were then harvested and above- (stems with leaf sheaths and leaf blades separately) and belowground (roots and rhizomes separately) dry biomass was determined by drying the plants in an oven to a constant mass at 60°C and weighing them. Additional response variables for each plant were derived from these primary measurements: specific leaf area (SLA = leaf area/leaf mass), leaf area ratio (LAR = leaf area/total plant biomass), specific rhizome length (SRL = rhizome length/rhizome biomass), stem mass ratio or fraction (SMR = stem biomass/total plant biomass), leaf mass ratio (LMR = leaf biomass/total plant biomass), root mass ratio (RTMR = root biomass/total plant biomass), and rhizome mass ratio (RHMR = rhizome biomass/total plant biomass).

Statistical analyses.—There are two relevant hypotheses to be tested by this experiment. The first is simply that plant performance varies with nutrient addition, and this was tested using a one-factor analysis of variance (ANOVA). Initial size was not included as a covariate because plants were selected to be roughly the same initial size. Significant differences in the performance of *Phragmites* with nutrient addition may, however, be due to the effects of allometry as the plant size changes with nutrient addition or to the effects of nutrient addition itself independent of plant size (Poorter and Nagel 2000). Therefore, the second hypothesis was that plant performance varies with nutrient addition independent of plant size, and this was tested using one-factor analysis of covariance (ANCOVA), with total plant biomass at the end of the experiment as the covariate accounting for potential allometric effects resulting from differences in plant size. Testing both hypotheses is important as they lead to different insights about the mechanisms that govern the response of *Phragmites* to fertilization. The covariate and all dependent variables were transformed to their natural logarithms, except for the proportion data, which were transformed to the arcsine of their square roots.

RESULTS

Field experiment

Response of Phragmites *in 1997.*—There was a rapid and dramatic response of *Phragmites* to the disturbance of clipping matrix vegetation and fertilization (Fig. 1). Only two weeks after the first treatment application, new shoots began to emerge. Removing matrix vegetation or adding nutrients increased both the densities and heights of shoots growing within the stand and those expanding into the marsh (all significant effects except for nutrients on the density of shoots expanding into the marsh; Fig. 1, Table 1). Shoots within the stand were of similar heights to those expanding into the marsh, but ~4 times as many shoots emerged from within the stand (Fig. 1). Under the most severe disturbance treatment (matrix vegetation removed, highest level of nutrients), the density of newly emerged shoots (~30 shoots/m²) was almost equal to the number that had emerged throughout the entire growing season in control quadrats (~41 shoots/m²) (Fig. 1 and see dashed line in Fig. 2).

The effect of nutrients on the biomass of new shoots emerging within the stand or expanding into the marsh was dependent on the presence of matrix vegetation (Fig. 1, significant interaction in Table 1). There was no effect of nutrients in the presence of matrix vegetation, where only the buds of new shoots pierced the soil surface, and these contributed little biomass (Fig. 1). In contrast, fertilization where matrix vegetation had been cleared significantly increased the biomass of *Phragmites*, as shoots grew relatively tall and produced leaves (the largest shoot was 71 cm with nine leaves) (Fig. 1). Shoots expanded at least 3 times and significantly farther where matrix vegetation had been removed than where it was naturally present (Fig. 1, Table 1). Nutrient addition did not significantly influence expansion, but shoots under the most severe disturbance treatment expanded twice as far as those in any
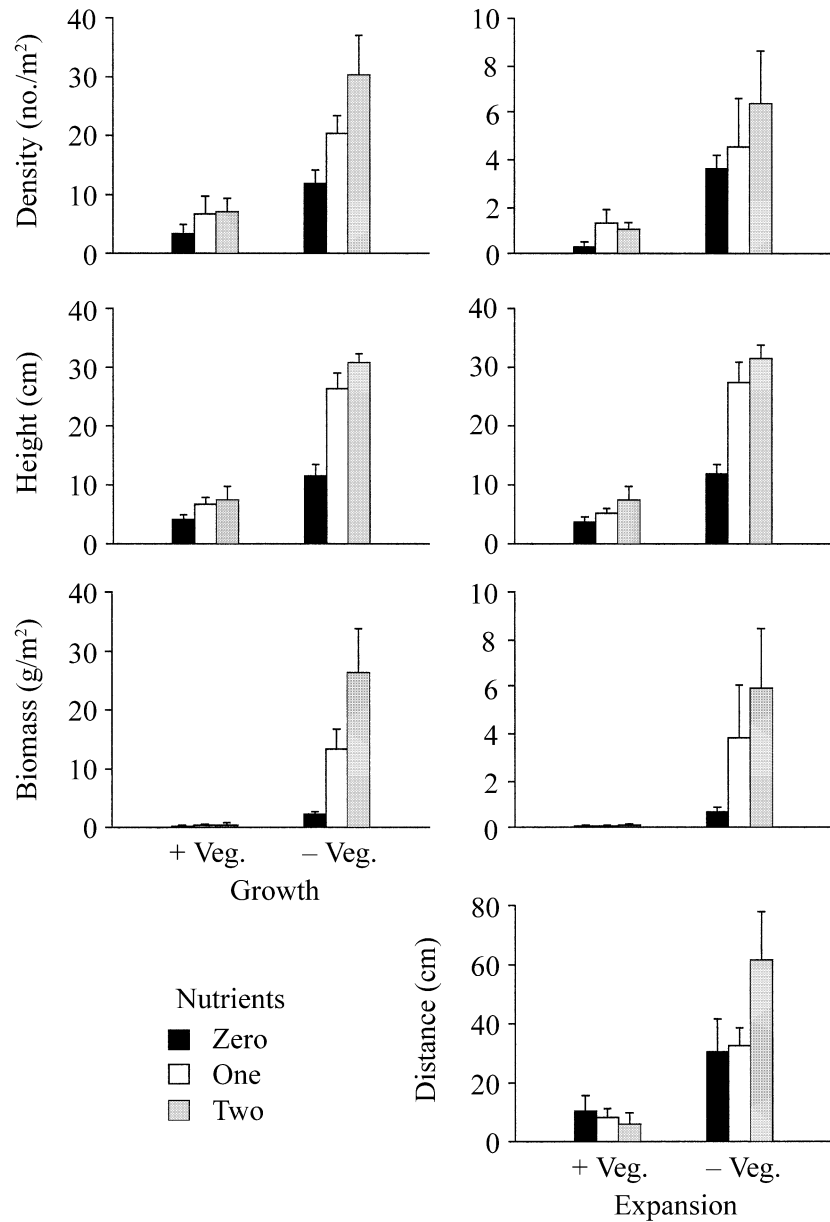
FIG. 1. *Phragmites* shoot density, height, and biomass, and expansion distance of *Phragmites* emerging within the stand (i.e., growth) and expanding into the marsh (i.e., expansion) in the presence (+Veg.) or absence (−Veg.) of matrix vegetation at each of three levels of nutrient addition (zero = 0 g $N \cdot m^{-2} \cdot yr^{-1}$, one = 35 g $N \cdot m^{-2} \cdot yr^{-1}$, and two = 70 g $N \cdot m^{-2} \cdot yr^{-1}$) in 1997. Data are for plants that emerged after the application of the disturbance treatments, presented as means + 1 SE.

other treatment, and almost as far as those that had been growing throughout the growing season in control quadrats (Fig. 1 and dashed line in Fig. 2, Table 1).

Response of Phragmites *in 1998.*—The disturbances applied at the end of the growing season of 1997 had a strong influence on the growth and expansion of *Phragmites* during 1998. Many of the effects on *Phragmites* in 1998 were qualitatively similar to those immediately following the application of treatments in 1997, but their magnitudes were reduced (compare Figs. 1 and 2). Removal of matrix vegetation in 1997

produced a significant increase and a doubling of the density of shoots emerging within the stand and expanding into the marsh by the end of the growing season of 1998 (Fig. 2, Table 2). Fertilization, in contrast, did not affect the density of shoots, although there was a general trend for shoot density to be greater where more nutrients had been added (except for shoots expanding into the marsh where matrix vegetation had been removed; Fig. 2, Table 2). In control quadrats, about the same number of shoots emerged in 1998 as in 1997, whereas shoots in areas subjected to the most

TABLE 1. Results of two-factor analyses of variance for the effect of matrix vegetation (Veg.; present or removed, df = 1, 30), nutrient addition (Nut.; three levels, df = 2, 30), and their interaction (df = 2, 30) on *Phragmites* shoot density, height, and biomass, and expansion distance of *Phragmites* emerging within the stand (i.e., growth) and expanding into the marsh (i.e., expansion) in 1997 (see data in Fig. 1).

Variable	Vegetation		Nutrients		Veg. × Nut.		Residual
	MS	*F*	MS	*F*	MS	*F*	MS
Growth							
Density	13.87	48.0***	1.70	5.9**	0.04	0.1 NS	0.29
Height	15.45	92.3***	1.90	11.3***	0.35	2.1 NS	0.17
Biomass	36.21	190.4***	4.46	23.5***	2.70	14.2***	0.19
Expansion							
Density	9.48	34.8***	0.40	1.5 NS	0.20	0.7 NS	0.27
Height	16.40	115.5***	1.46	10.3***	0.21	1.4 NS	0.14
Biomass	10.04	39.4***	1.21	4.8*	0.92	3.6*	0.25
Distance	32.83	18.3***	0.19	0.1 NS	0.42	0.2 NS	1.80

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; NS = not significant.

severe disturbance treatment had more than double the density of shoots as control quadrats (Fig. 2). In contrast to its substantial effect on the density of shoots, clearing matrix vegetation did not affect the heights of shoots (Fig. 2, Table 2). Nutrient addition, in contrast, produced significantly taller shoots within the stand, but, as for the density of shoots, this was not evident for shoots expanding into the marsh where matrix vegetation had been removed (Fig. 2, Table 2). In all treatments, including controls, shoots were 30–80% taller in 1998 than in control quadrats in 1997 (Fig. 2).

Differences in the biomass of *Phragmites* reflected the densities and heights of shoots. There was a significant effect of the removal of matrix vegetation on the biomass of shoots emerging within the stand and expanding into the marsh (Fig. 2, Table 2). Nutrient addition increased the biomass of *Phragmites*, but this was only significant within the stand because, again, shoots expanding into the marsh where matrix vegetation had been cleared followed the opposite trend (Fig. 2, Table 2). The biomass of *Phragmites* in control quadrats almost doubled in 1998 compared to 1997, indicating that even under ambient conditions *Phragmites* is expanding (Fig. 2). Under the most severe disturbance treatment, the biomass of *Phragmites* at the end of the growing season of 1998 was an order of magnitude greater than under ambient conditions at the end of the previous year (Fig. 2). In two of the three treatments where matrix vegetation had been removed, the biomass of *Phragmites* that expanded into the marsh in 1998 was greater than in the control treatment within the stand in 1997, representing a dramatic expansion of the stand into the lower elevations of the marsh in only one growing season. As in the previous year, the distance that shoots expanded into the marsh was influenced by the removal of matrix vegetation, but not by the addition of nutrients (Fig. 2, Table 2). For both years combined, under the most severe disturbance treatment shoots expanded, on average, 148

cm into the marsh, with the maximal expansion distance in one quadrat of 217 cm.

The effects of clearing matrix vegetation and adding nutrients on the internode length of shoots were generally the same as those on their heights, indicating that the increase in shoot height with fertilization reflects a significant lengthening of the internode rather than a greater number of nodes (Fig. 3, Table 3). Given this similarity in the number of nodes per shoot, it is not surprising that the number of leaves per shoot was not significantly different among treatments (Fig. 3, Table 3). In contrast to their numbers, however, the surface areas of individual leaves were significantly larger in the presence of matrix vegetation than where it had been removed in the previous year, and leaf area was positively related to the level of fertilization (primarily because leaves were longer) (Fig. 3, Table 3). Consequently, differences among treatments in leaf area per shoot reflected the surface areas of individual leaves and not their numbers (Fig. 3, Table 3).

Disturbances applied in 1997 also affected the reproductive output of *Phragmites* in 1998. Removal of matrix vegetation generated about twice as many and significantly greater densities of inflorescences compared to quadrats with natural vegetation (Fig. 3, Table 3). Inflorescences were roughly the same size in all treatments, suggesting that this doubling in number represents a doubling in seed production. When expressed as a percentage of shoot density, however, this difference disappeared, indicating that reproductive output was related to the increased density of shoots due to the removal of matrix vegetation. In contrast, fertilization had no influence on the production of inflorescences (Fig. 3, Table 3).

Response of matrix vegetation in 1998.—The production of matrix vegetation in 1998 was also influenced by the disturbances applied at the end of the growing season of 1997, but in contrast to *Phragmites*, the abundance of matrix vegetation declined with in-
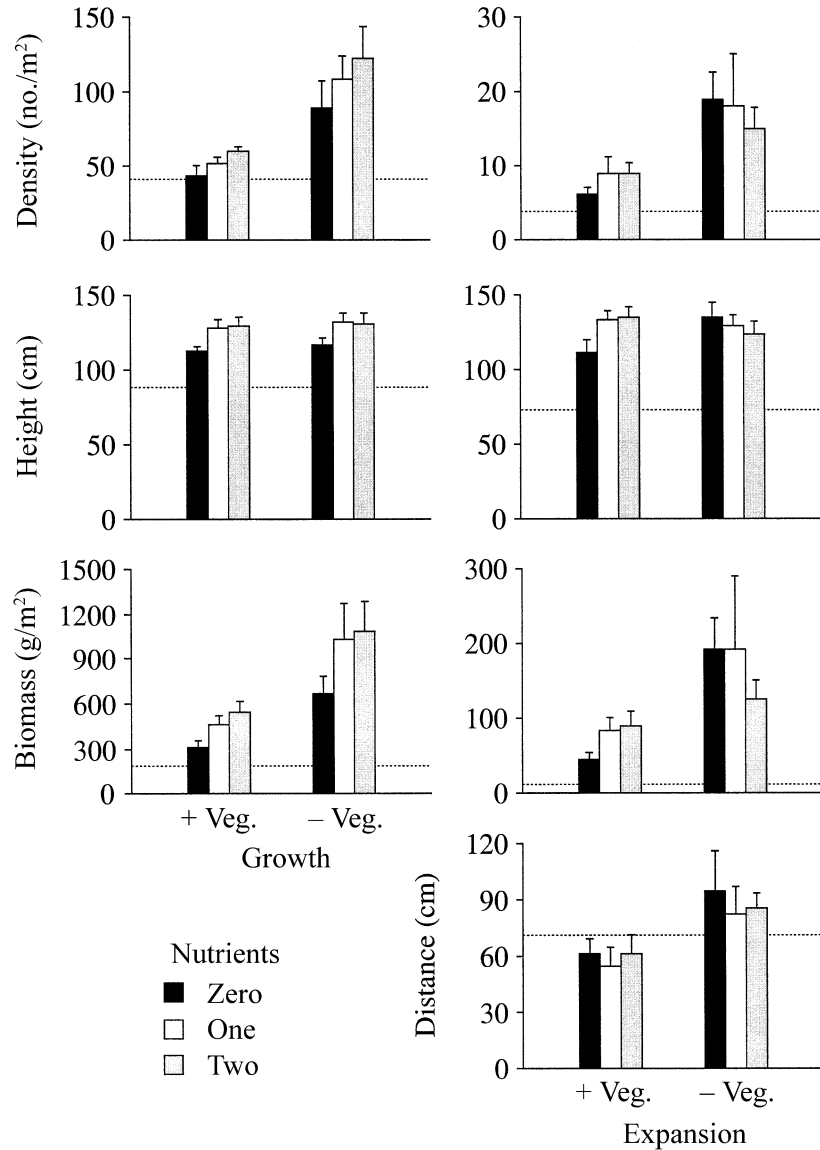
FIG. 2. *Phragmites* shoot density, height, and biomass, and expansion distance of *Phragmites* emerging within the stand (i.e., growth) and expanding into the marsh (i.e., expansion) in the presence (+Veg.) or absence (−Veg.) of matrix vegetation at each of three levels of nutrient addition (zero = 0 g N·m^{-2}·yr^{-1}, one = 35 g N·m^{-2}·yr^{-1}, and two = 70 g N·m^{-2}·yr^{-1}) in 1998. Data are means + 1 SE. Dotted lines indicate mean levels in control quadrats in 1997.

creasing severity of disturbance. Removal of matrix vegetation did not affect the density of tillers that emerged in the subsequent year, but tillers were significantly shorter where matrix vegetation had been cleared (Fig. 4, Table 4). Fertilization, in contrast, significantly reduced the density of tillers, but increased their heights (Fig. 4, Table 4). The biomass of the matrix vegetation reflected changes in the densities of tillers more than their heights. Fertilization in 1997 significantly reduced the biomass of the matrix vegetation in 1998 and, except in control quadrats, the biomass was also substantially reduced where matrix vegetation had been cleared in the previous year (Fig. 4, Table 4).

Under all treatments conditions, matrix vegetation was taller, less dense, and had a considerably smaller biomass in 1998 than in control quadrats in 1997 (Fig. 4). Moreover, matrix vegetation covered the entire substratum in all quadrats in 1997, but by the end of 1998 there were patches of bare soil in all treatments. The percentage of bare soil was significantly greater where matrix vegetation had been cleared in the previous year, and there was a nonsignificant trend where matrix vegetation was removed for more bare soil with increasing nutrient addition (Fig. 4, Table 4). Although each species comprising the matrix vegetation was not represented in all quadrats (and thus could not be analyzed

TABLE 2. Results of two-factor analyses of variance for the effect of matrix vegetation (Veg.; present or removed, df = 1, 30), nutrient addition (Nut.; three levels, df = 2, 30), and their interaction (df = 2, 30) on *Phragmites* shoot density, height, and biomass, and expansion distance of *Phragmites* emerging within the stand (i.e., growth) and expanding into the marsh (i.e., expansion) in 1998 (see data in Fig. 2).

	Vegetation		Nutrients		Veg. × Nut.		Residual
Variable	MS	F	MS	F	MS	F	MS
Growth							
Density	4.141	33.4***	0.357	2.9 NS	0.001	<0.1 NS	0.124
Height	0.004	0.3 NS	0.058	5.5**	<0.001	<0.1 NS	0.011
Biomass	4.659	24.5***	1.004	5.3*	0.005	<0.1 NS	0.190
Expansion							
Density	3.497	11.7**	0.028	0.1 NS	0.173	0.6 NS	0.299
Height	0.003	0.1 NS	0.019	0.9 NS	0.068	3.1 NS	0.022
Biomass	4.529	7.7**	0.146	0.2 NS	0.757	1.3 NS	0.586
Expansion	1.407	7.9**	0.057	0.3 NS	0.003	<0.1 NS	0.179

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; NS = not significant.
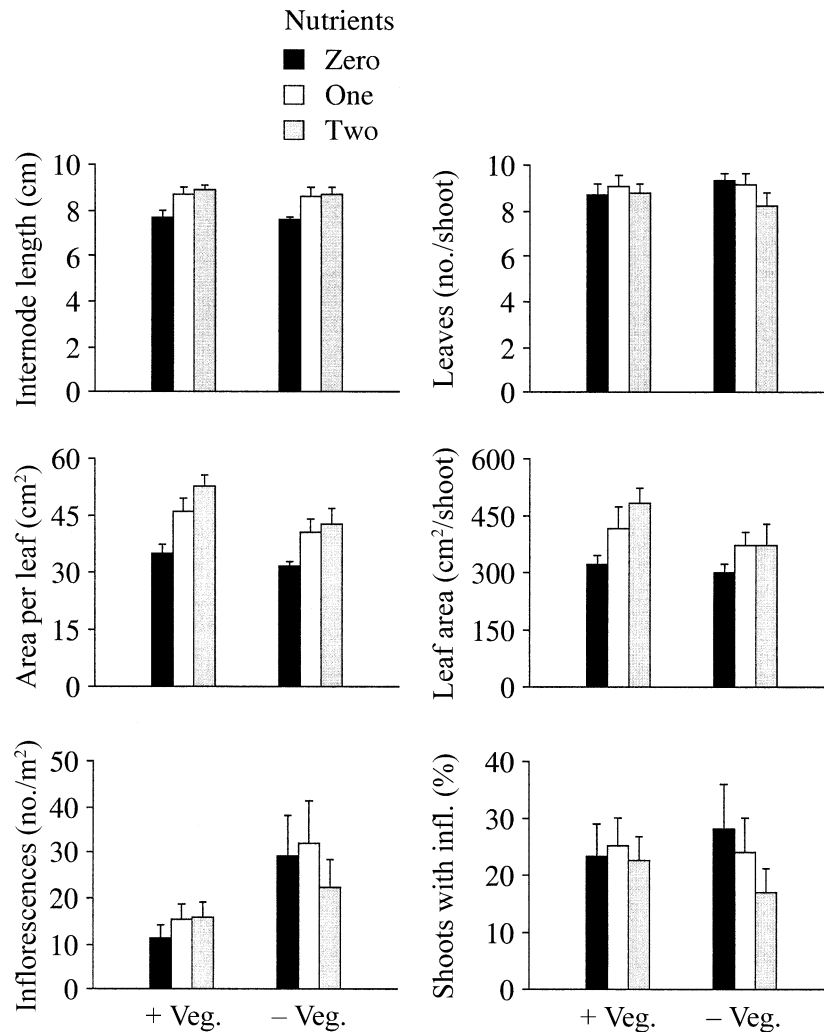

FIG. 3. Internode length, number of leaves per shoot, area per leaf, leaf area per shoot, inflorescence density, and percentage of shoots with inflorescences for shoots of *Phragmites* throughout the quadrat in the presence (+Veg.) or absence (−Veg.) of matrix vegetation at each of three levels of nutrient addition (zero = 0 g N·m^{-2}·yr^{-1}, one = 35 g N·m^{-2}·yr^{-1}, and two = 70 g N·m^{-2}·yr^{-1}) in 1998. Data are means + 1 SE.

TABLE 3.   Results of two-factor analyses of variance for the effect of matrix vegetation (Veg.; present or removed, df = 1, 30), nutrient addition (Nut.; three levels, df = 2, 30), and their interaction (df = 2, 30) on various estimates of performance for shoots of *Phragmites* throughout the quadrat in 1998 (see data in Fig. 3).

Shoot variable	Vegetation		Nutrients		Veg. × Nut.		Residual
	MS	F	MS	F	MS	F	MS
Internode length	0.001	0.3 NS	0.071	17.1***	<0.001	0.1 NS	0.004
No. leaves per shoot	<0.001	<0.1 NS	0.019	1.2 NS	0.017	1.1 NS	0.016
Area per leaf	0.204	6.2*	0.362	11.2***	0.015	0.4 NS	0.032
Leaf area per shoot	0.219	3.2 NS	0.245	3.6*	0.054	0.8 NS	0.068
Inflorescence density	2.932	6.2*	0.172	0.4 NS	0.296	0.6 NS	0.471
Percentage shoots with inflorescences	0.003	0.1 NS	0.016	0.6 NS	0.012	0.5 NS	0.025

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; NS = not significant.

separately), *Juncus gerardi*, *Spartina patens*, and *Distichlis spicata* responded in the same way to the treatment manipulations.

Total plant production.—Total plant biomass (*Phragmites* and matrix vegetation combined) within the stand in 1998 was positively related to the severity of the disturbance applied in 1997 (Fig. 5). Total plant biomass was greater where matrix vegetation had been removed and nutrients had been added, although the latter was not significant (two-factor ANOVA: vegetation, $F_{1,30} = 15.4$, $P < 0.001$; nutrients, $F_{2,30} = 0.9$, $P > 0.40$). The relative contribution of *Phragmites* and matrix vegetation to total plant biomass followed opposite trends. Aboveground biomass increased with the severity of the disturbance for *Phragmites*, whereas it

decreased for the matrix vegetation, indicating that *Phragmites* was displacing the matrix vegetation under disturbance conditions.

Greenhouse experiment

The addition of nutrients influenced the above- and belowground size, morphology, and biomass allocation of individual plants grown in pots in the greenhouse (Fig. 6), producing many of the same changes observed when *Phragmites* was fertilized in the field. Many of the performance variables exhibited a curvilinear response to fertilization, with the largest increases or decreases at the lower nutrient levels followed by a gradual levelling off at higher nutrient levels (Fig. 6). Total plant biomass and the number of shoots were
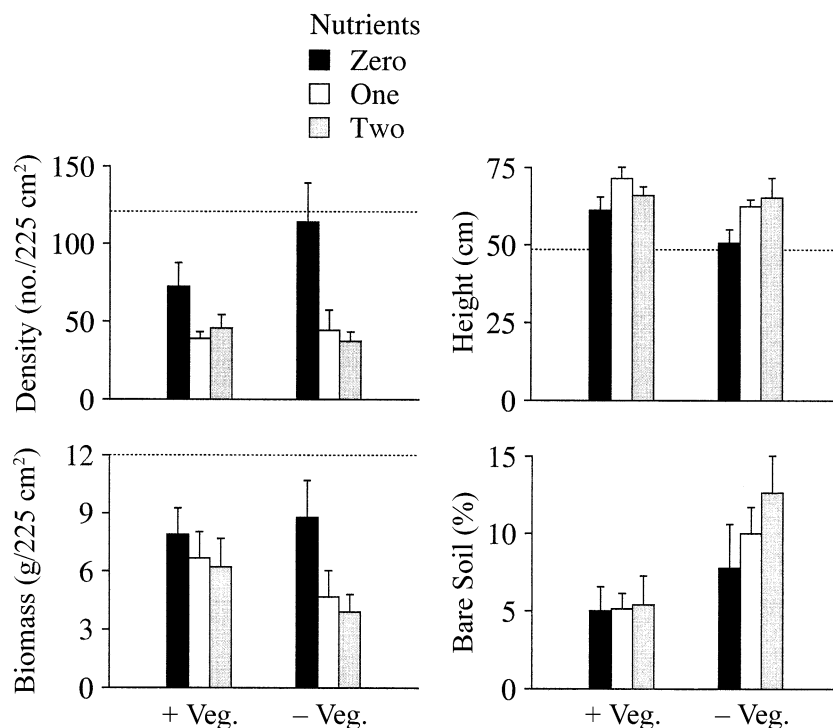

FIG. 4.   Density, height, and biomass of tillers of matrix vegetation and the percentage of bare soil within the stand of *Phragmites* in the presence (+Veg.) or absence (−Veg.) of matrix vegetation at each of three levels of nutrient addition (zero = 0 g N·m^{-2}·yr^{-1}, one = 35 g N·m^{-2}·yr^{-1}, and two = 70 g N·m^{-2}·yr^{-1}) in 1998. Data are means + 1 SE. Dotted lines indicate mean levels in control quadrats in 1997 (including 0% bare soil not shown on graph).

TABLE 4. Results of two-factor analyses of variance for the effect of matrix vegetation (Veg.; present or removed, df = 1, 30), nutrient addition (Nut.; three levels, df = 2, 30), and their interaction (df = 2, 30) on tiller density, height, and biomass of matrix vegetation and percentage of bare soil within the stand of *Phragmites* in 1998 (see data in Fig. 4).

	Vegetation		Nutrients		Veg. × Nut.		Residual
Variable	MS	F	MS	F	MS	F	MS
Density	0.036	0.1 NS	2.329	8.1**	0.302	1.0 NS	0.289
Height	0.133	5.2*	0.120	4.7*	0.017	0.7 NS	0.026
Biomass	0.724	2.4 NS	1.050	3.4*	0.267	0.9 NS	0.307
Bare soil	0.071	5.4*	0.015	1.1 NS	0.010	0.8 NS	0.013

* $P < 0.05$; ** $P < 0.01$; NS = not significant.

positively and significantly related to nutrient addition (Fig. 6, Table 5). Shoot length followed a similar, although nonsignificant trend, whereas the heights of individual shoots were significantly reduced by fertilization (Fig. 6, Table 5). Consequently, there was a shift with increasing nutrient level from fewer, taller shoots to more, shorter ones. There was also a nonsignificant trend for rhizome length to increase with fertilization, but specific rhizome length (SRL) was independent of nutrient addition (Fig. 6, Table 5). The number of leaves per shoot was not affected by fertilization, but because shoot density significantly increased with nutrient addition so did the total number of leaves (Fig. 6, Table 5). Similarly, the surface area of individual leaves, leaf area, specific leaf area (SLA), and leaf area ratio (LAR) were all positively related to nutrient addition, although for SLA this trend was not significant (Fig. 6, Table 5). Biomass allocation in response to nutrient addition varied with plant structure. Allocation to leaves (i.e., leaf mass ratio [LMR]) was positively and significantly related to nutrient addition, whereas allocation to stems (SMR) was not affected by nutrients (Fig. 6, Table 5). Allocation to belowground structures was opposite to that for aboveground structures, with root mass ratio (RTMR) negatively affected by the addition of nutrients and allocation to rhizomes (rhizome
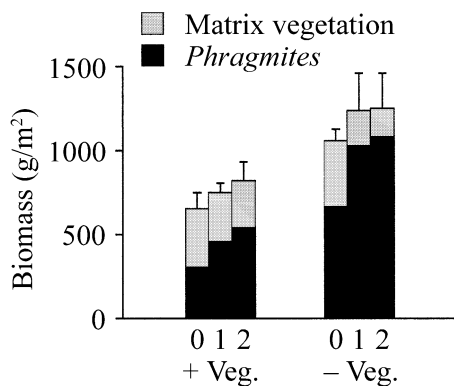

FIG. 5. Biomass of *Phragmites* and matrix vegetation within the stand of *Phragmites* in the presence (+Veg.) or absence (−Veg.) of matrix vegetation at each of three levels of nutrient addition (0 = 0 g N·m^{-2}·yr^{-1}, 1 = 35 g N·m^{-2}·yr^{-1}, and 2 = 70 g N·m^{-2}·yr^{-1}) in 1998. Data are means + 1 SE.

mass ratio [RHMR]) following a similar, although nonsignificant trend (Fig. 6, Table 5). Therefore, there was proportionally greater allocation to aboveground biomass with increasing nutrient addition.

When analysis of covariance was run for each of the variables using total plant biomass as a covariate to account for allometric effects, only one result was different (Table 5). There was no longer a significant increase in the surface area of individual leaves with nutrient addition, suggesting that these differences were due to changes in plant size rather than to the nutrients themselves. Therefore, fertilization has important effects on the morphology and biomass allocation of *Phragmites* that are not simply due to allometry as the plant grows. For two variables, RTMR and RHMR, there was a significant interaction between the effect of nutrients and the covariate, suggesting that the relationship between each of these variables and total plant biomass changes with nutrient level (Table 5).

DISCUSSION

Our results demonstrate that disturbance can dramatically increase the spread of *Phragmites*, resulting in a change in the relative abundance of the dominant species of plants occupying the highest elevations of the high marsh. Initial dominance by matrix vegetation (*Juncus gerardi*, *Spartina patens*, and *Distichlis spicata*) was ceded to *Phragmites* after less than two growing seasons. Removing competing matrix vegetation doubled the growth of *Phragmites* and increased its expansion and reproductive output, thus enhancing the potential for *Phragmites* to spread within and among marshes. Nutrient enrichment further enhanced the aboveground production of *Phragmites*, producing a shift in allocation of biomass from structures for nutrient acquisition to structures for growth and expansion. By mediating competition between *Phragmites* and the species comprising the matrix vegetation, disturbance promotes the spread of *Phragmites* within coastal marshes of southern, New England (USA).

Disturbance and the spread of Phragmites

Phragmites expanded rapidly soon after the disturbances were applied; the growth and expansion of
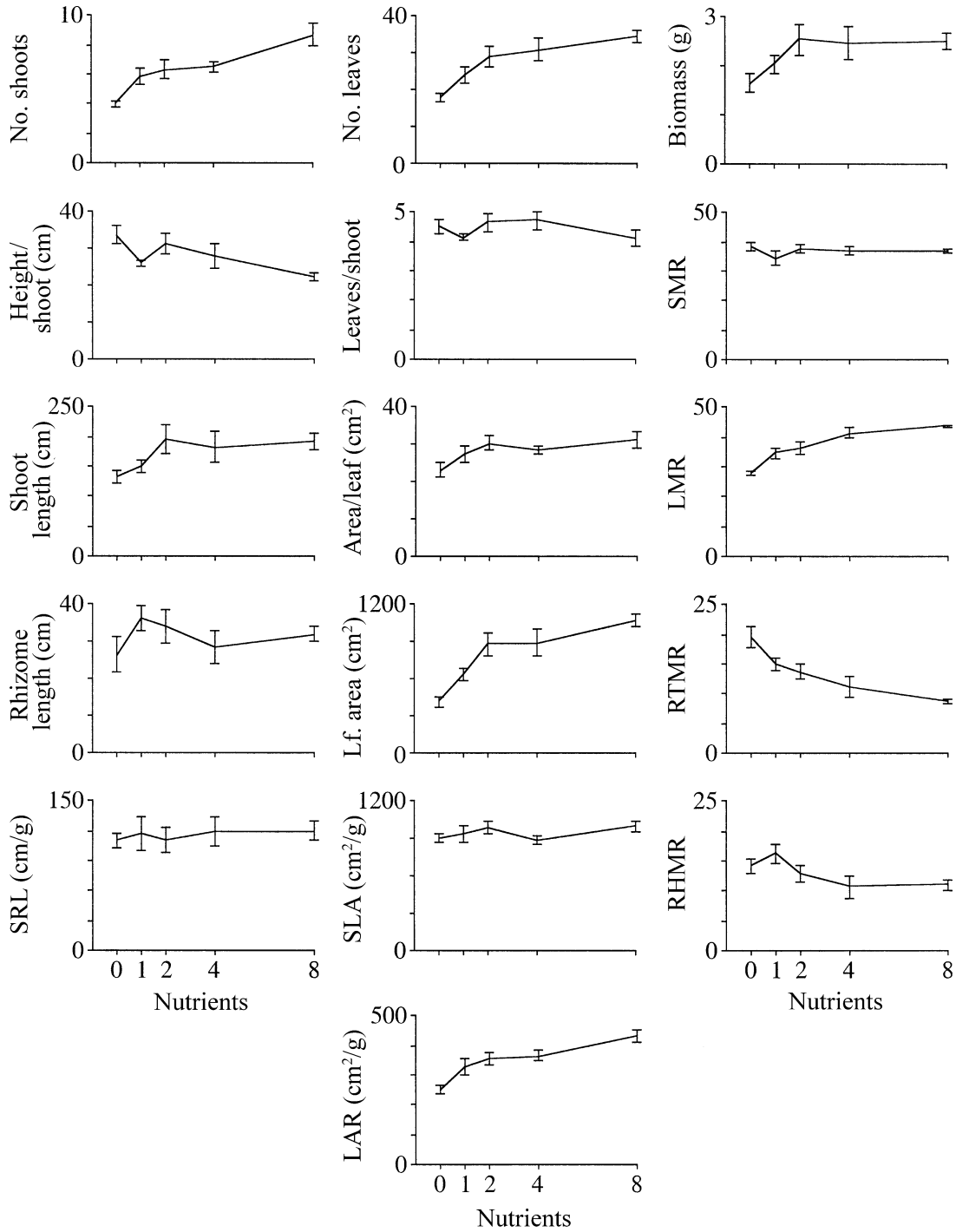
FIG. 6. Estimates of variables representing the size, morphology, and biomass allocation of individual *Phragmites* plants in response to five levels of nutrient addition (0 = 0 g N·m^{-2}·yr^{-1}, 1 = 9 g N·m^{-2}·yr^{-1}, 2 = 17 g N·m^{-2}·yr^{-1}, 4 = 35 g N·m^{-2}·yr^{-1}, and 8 = 70 g N·m^{-2}·yr^{-1}) over one month in the greenhouse. SLR = specific rhizome length; SLA = specific leaf area; LAR = leaf area ratio; SMR = stem mass ratio; LMR = leaf mass ratio; RTMR = root mass ratio; RHMR = rhizome mass ratio. Data are means ± 1 SE.

TABLE 5. Results of one-factor analyses of variance (ANOVA, df of F ratio = 4, 25) and one-factor analyses of covariance (ANCOVA) for the effect of nutrients on various estimates of *Phragmites* performance.

	ANOVA		ANCOVA†					
	Nutrients		Nutrients		Biomass		Nut. × Bio.	
Variable	F	P	F	P	F	P	F	P
Size								
Biomass	2.8	*	...	...	...	...	...	...
Shoot length	2.5	NS	0.4	NS	32.0	***	0.8	NS
Morphology								
Number of shoots	12.0	***	7.6	***	0.7	NS	0.1	NS
Height per shoot	3.6	*	15.8	***	36.9	***	2.3	NS
Rhizome length	1.0	NS	0.8	NS	0.3	NS	2.6	NS
Specific rhizome length, SRL	0.1	NS	1.8	NS	16.7	***	1.2	NS
Leaves per shoot	1.2	NS	2.8	NS	12.7	**	2.1	NS
Number of leaves	9.8	***	5.2	**	12.0	**	0.7	NS
Area per leaf	3.1	*	0.9	NS	6.8	*	0.8	NS
Leaf area	15.3	***	14.3	***	52.4	***	1.3	NS
Specific leaf area, SLA	1.1	NS	1.3	NS	0.9	NS	2.1	NS
Leaf area ratio, LAR	10.0	***	14.2	***	7.8	**	1.3	NS
Biomass allocation								
Stem mass ratio, SMR	0.9	NS	1.2	NS	2.2	NS	1.3	NS
Leaf mass ratio, LMR	17.7	***	26.0	***	10.7	**	2.8	NS
Root mass ratio, RTMR	7.7	***	...	...	...	...	5.4	**
Rhizome mass ratio, RHMR	2.4	NS	...	...	...	...	4.7	**

  * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; NS = not significant.

  † Total plant biomass is the covariate in the ANCOVA. For the ANCOVA, where the nutrient × biomass interaction was significant (df of F ratio = 4, 20) in the original model with nutrients, biomass, and nutrients × biomass, the analysis was ended because the slopes were not homogeneous. Where the nutrients × biomass was not significant in the original model, this term was dropped and results presented for nutrients (df of F ratio = 4, 24) and biomass (df of F ratio = 1, 24) are for a second model fitted with only these two factors.

shoots under the most severe disturbance was almost equal to that for the entire growing season under ambient conditions. The emergence and growth of such large densities of shoots at the end of the growing season is atypical for *Phragmites* under ambient conditions, and demonstrates that *Phragmites* is extremely flexible, and capable of taking advantage of favorable environmental conditions whenever they arise. It is unlikely, however, that the spread of *Phragmites* in the following year was a direct response to the pulse of disturbance applied in the previous year, because the clipped matrix vegetation regrew in the following spring and nutrients added at the end of the summer are unlikely to be still available (Otto 1997). More likely, *Phragmites* "stored" the additional nutrient resources acquired under disturbance conditions, which were then manifested in growth during next season. Indeed, at the end of the summer and throughout autumn, *Phragmites* is known to shunt resources from its senescing shoots to its rhizomes, which extend to give rise to vertical rhizomes with buds lying beneath the soil surface (Haslam 1969). The late-season expansion likely established a new baseline from which *Phragmites* spread during the next growing season. Therefore, there can be a temporal uncoupling between a disturbance and the response by *Phragmites*, which may make it difficult for managers to determine causal links between human impacts and patterns of spread of *Phragmites*, at least over short time scales.

There was an interaction between the disturbances in their influence on the production of *Phragmites* in 1997. Where matrix vegetation was present, the biomass of *Phragmites* was not affected by fertilization, but the biomass of *Phragmites* was directly related to nutrient supply where aboveground competitors were removed. This suggests that the availability of nutrients for the growth of *Phragmites* is mediated by competition with neighboring matrix vegetation (Levine et al. 1998, Emery et al. 2001). This interactive effect subsided in 1998 after the pulse disturbance was removed. It is probable, however, that if a press disturbance with continual clearing of matrix vegetation and fertilization were applied, then the interactive effects of these multiple stressors would be manifested. Indeed, in terrestrial habitats, interactions between fertilization and disturbance are known to have significant effects on the growth and assemblage structure of plants (e.g., Hobbs and Atkins 1988, Wilson and Tilman 1991, Turkington et al. 1993). Understanding how disturbances interact to affect the spread of *Phragmites*, as well as other nuisance and invasive species, is critical for developing strategies to control this species in coastal marshes. Indeed, the simple presence of neighboring matrix vegetation reduced the production of *Phragmites* by 50%. Consequently, an important strategy for controlling, or at least reducing, the expansion of *Phragmites*, particularly in marshes subjected to nutrient enrichment, would be to maintain buffers of dense, matrix vege-

tation around existing stands of *Phragmites* and along the terrestrial–marsh ecotone.

Disturbance not only affected the size of *Phragmites*, but also its morphology. In the field *Phragmites* responded to disturbance by increasing the number of shoots that emerged, not by producing extremely tall shoots with large numbers of leaves. Under freshwater conditions in the greenhouse there were similar changes in morphology: *Phragmites* seedlings produced more shorter shoots and fewer taller shoots with increasing nutrient levels (see also Clevering 1998). Both in the field and greenhouse, increased nutrient levels also generated larger individual leaves. In contrast, proportionally less plant mass was invested into roots as nutrient levels increased. Therefore, there is a shift in biomass allocation with increasing nutrient levels from belowground structures such as roots to aboveground structures such as shoots and leaves. Similar changes in above- to belowground biomass allocation are likely to have occurred in the field, particularly where neighboring matrix vegetation competing for nutrient resources had been cleared. Such changes in biomass allocation with increasing nutrient levels have been widely documented for many plants, including *Phragmites* (Clevering 1998, Poorter and Nagel 2000), and represent a fundamental shift in energy expenditure from structures for belowground acquisition of nutrients to aboveground structures for acquisition of light.

Nutrient enrichment had no influence on the distance that *Phragmites* expanded nor on the density of inflorescences it produced, the two best indicators of the ability of *Phragmites* to spread within and among marshes. In contrast, the magnitude of both variables doubled when neighboring matrix vegetation was cleared, with the production of inflorescences linked to the density of shoots. Removing competing matrix vegetation thus promotes the expansion of stands within marshes (see also Amsberry et al. 2000) and potentially increases the supply of seeds to neighboring marshes. Again, matrix vegetation may act as a natural buffer suppressing the local spread of *Phragmites*.

Mechanisms of Phragmites *spread*

There are probably two primary mechanisms by which competing matrix vegetation reduces the growth and expansion of *Phragmites*. First, there may be strong belowground competition for nutrients, particularly nitrogen, which is typically limiting in brackish and salt marshes (Valiela and Teal 1974). In monoculture, nutrient addition can increase the biomass of the species comprising the matrix vegetation (see Emery et al. [2001], although nutrient levels were greater in their study), whereas in the presence of *Phragmites*, fertilization decreased their biomass (this study). Therefore, when fertilized, *Phragmites* appears to be using nutrients that would otherwise be available to the matrix vegetation. Although belowground competition was not directly assessed in this experiment, the increased

response of *Phragmites* to nutrient supply in the absence of matrix vegetation also provides indirect evidence for such a mechanism. Moreover, Emery et al. (2001) have demonstrated that belowground competition for nutrients is an important mechanism determining the outcome of competitive interactions and the relative abundance among species comprising the matrix vegetation in coastal marshes (see also Levine et al. 1998). Second, matrix vegetation may act as a physical barrier to the emergence and growth of shoots. Neighboring vegetation surrounding small transplants of *Phragmites* can reduce its expansion (Amsberry et al. 2000), and the emergence and growth of *Phragmites* can be suppressed by its own litter (Granéli 1989) and floating plant debris or wrack stranded in the marsh (Minchinton 2002*a*). Consequently, in the absence of competing matrix vegetation or under elevated nutrient resources, *Phragmites* is released from belowground competition for nutrients. Once released from belowground competition, *Phragmites* is likely to be a stronger aboveground competitor, even under harsh abiotic conditions. Disturbance dramatically increased the density of *Phragmites* shoots, which likely reduced the light available to the matrix vegetation beneath the canopy of *Phragmites*. In response, the production of matrix vegetation was reduced and tillers were taller, sparser, and covered less of the substratum. The species comprising the matrix vegetation were probably allocating resources towards growing taller and capturing light rather than producing more tillers to cover the substratum. *Phragmites* is larger than all the other plants in the marsh and shading may to be a primary mechanism by which it excludes competing plants from the marsh.

Phragmites *spread and marsh conservation*

Disturbance, particularly chronically elevated nutrient loads, may have long-term consequences for the structure of plant assemblages within coastal marshes. Field experiments have shown that the competitive hierarchy among the dominant grasses and rushes in marshes of southern New England may be reversed when fertilized (Levine et al. 1998, Emery et al. 2001). Under elevated nutrient conditions, the grass *Spartina alterniflora*, which is typically confined to the low marsh by superior competitors, becomes the species that is not only the most tolerant of harsh abiotic conditions, but also the best competitor. Consequently, Levine et al. (1998) predicted that *S. alterniflora* would eventually monopolize marshes under chronic nutrient enrichment (see also Emery et al. 2001). Similarly, the upper limit of *Phragmites* is set by the terrestrial border of the marsh and its lower limit by its physiological tolerance to the physical stresses associated with tidal flooding (e.g., salinity, waterlogging). Thus under ambient nutrient conditions *Phragmites* has been historically restricted to the upper border of brackish and salt marshes. Based on our results, brackish marshes sub-

jected to increased clearing of vegetation and nutrient load should result in the expansion of *Phragmites* from the higher to the lower elevations of the marsh. Under increasing nutrient load, our results demonstrate that *Phragmites* would outcompete *J. gerardi*, *S. patens*, and *D. spicata*, and that simultaneous clearing of marsh vegetation would accelerate the displacement of these species. As *Phragmites* expands seaward under increased nutrient load, *S. alterniflora* would be expanding landward according to the model of Levine et al. (1998) (see also Emery et al. 2001, Bertness et al. 2002), leading to a brackish marsh dominated by *Phragmites* and *S. alterniflora*. We predict (and currently observe) that *Phragmites*, being the larger plant, would also outcompete *S. alterniflora* (Buttery and Lambert 1965) in brackish marshes where abiotic stresses are not as severe as in salt marshes, eventually resulting in a monoculture of *Phragmites*. In salt marshes, abiotic conditions may simply be too extreme for complete dominance by *Phragmites* and, consequently, *S. alterniflora* would dominate the lower elevations of these marshes under elevated nutrient conditions, with *Phragmites* restricted to the relatively benign upper border of the marsh. Other anthropogenic disturbances that physically elevate the marsh surface (e.g., dumping of dredge spoil) or change the natural salinity regime by increasing freshwater input may, ultimately, promote dominance by *Phragmites* in salt marshes (Burdick et al. 2001).

Disturbances ultimately resulted in a greater total aboveground biomass of plants. This increase occurred because of a shift in the relative biomass of species with increasing disturbance, from dominance by matrix vegetation to dominance by *Phragmites*, which has greater per unit area biomass. Other studies have shown that not only does the aboveground plant biomass tend to be greater in marshes dominated by *Phragmites* compared to those without *Phragmites*, but so does the standing stock of nitrogen in plants (Windham and Lathrop 1999, Meyerson et al. 2000). Disturbances, including nutrient enrichment in this study, may thus alter the standing stock and cycling of N in marshes by changing their occupancy from diverse assemblages of plants to dominance by *Phragmites*. Our results also indicate that the total production of plants should increase as diverse marshes become monocultures of *Phragmites*, which is contrary to studies showing positive relationships between species richness and production of wetland plants (e.g., Englehardt and Ritchie 2001). These effects of nutrient enrichment on the relationship between species composition, production, and N cycling warrant attention because they demonstrate critical links among population, community, and ecosystem levels of organization (Vitousek 1990).

While it is clear that fertilization and removal of competitors can dramatically enhance the spread of *Phragmites* on a local scale, it remains unknown whether anthropogenic modification of the coastal landscape is the ultimate cause for the regional expansion of this species throughout marshes in southern New England. Indeed, *Phragmites* in this study was spreading even under ambient conditions, indicating that this marsh may already be impacted or some other factor is promoting the spread of *Phragmites*. The rapid growth observed in control quadrats in 1998 may be due to the extremely high levels of rainfall that occurred during the 1997–1998 El Niño event (Minchinton 2002b). Alternatively, Saltonstall (2002) has found evidence suggesting that a nonnative genotype of *Phragmites* has displaced the native type in marshes of southern New England (in Connecticut and Massachusetts in particular), and suggested that this new strain is responsible for the recent spread of *Phragmites*. It is possible that *Phragmites* in the marsh from this study in Rhode Island is the nonnative genotype. If this is true, then results here show that elevated nutrient loads and physical disturbance of the marsh vegetation will further accelerate the local spread of this invasive *Phragmites* genotype throughout coastal marshes of southern New England. Many coastal marshes in this region are small fragments <100 m wide and surrounded by developed land. Therefore the expansion of *Phragmites* at a rate of 1.5 m per year as documented here under the most severe disturbance conditions will have devastating consequences within only decades. Strategies to manage the growth and expansion of stands of *Phragmites* should focus on reducing nutrient loads and maintaining natural vegetation buffers along the terrestrial–marsh ecotone. Where *Phragmites* is already established and spreading rapidly, however, removal of the plant may be the only effective method of control.

Literature Cited

Adam, P. 1990. Saltmarsh ecology. Cambridge University Press, Cambridge, UK.

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.

Bertness, M. D. 1991a. Interspecific interactions among high marsh perennials in a New England salt marsh. Ecology **72**:125–137.

Bertness, M. D. 1991b. Zonation of *Spartina patens* and *Spartina alterniflora* in a New England salt marsh. Ecology **72**:135–148.

Bertness, M. D., and A. M. Ellison. 1987. Determinants of pattern in a New England salt marsh plant community. Ecological Monographs **57**:129–147.

Bertness, M. D., P. J. Ewanchuk, and B. R. Silliman. 2002. Anthropogenic modification of New England salt marsh landscapes. Proceedings of the National Academy of Sciences (USA) **99**:1395–1398.

Boyer, K. E., and J. B. Zedler. 1998. Effects of nitrogen additions on the vertical structure of a constructed cordgrass marsh. Ecological Applications **8**:692–705.

Buck, E. L. 1995. Selected environmental factors and the spread of *Phragmites australis* (common reed) in the tidelands of the Lower Connecticut River. Thesis. Connecticut College, New London, Connecticut, USA.

Burdick, D. M., R. Bauschaum, and E. Holt. 2001. Variation in soil salinity associated with expansion of *Phragmites australis* in salt marshes. Environmental and Experimental Botany **46**:247–261.

Buttery, B. R., and J. M. Lambert. 1965. Competition between *Glyceria maxima* and *Phragmites communis* in the region of Surlingham Broad. Journal of Ecology **53**:163–181.

Chambers, R. M. 1997. Porewater chemistry associated with *Phragmites* and *Spartina* in a Connecticut tidal marsh. Wetlands **17**:360–367.

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.

Clark, J. S. 1986. Late-holocene vegetation and coastal processes at a Long Island tidal marsh. Journal of Ecology **74**:561–578.

Clevering, O. A. 1998. An investigation into the effects of nitrogen on growth and morphology of stable and die-back populations of *Phragmites australis*. Aquatic Botany **60**:11–25.

Emery, N. C., P. J. Ewanchuk, and M. D. Bertness. 2001. Competition and salt-marsh plant zonation: stress tolerators may be dominant competitors. Ecology **82**:2471–2484.

Englehardt, K. A. M., and M. E. Ritchie. 2001. Effects of macrophyte species richness on wetland ecosystem functioning and services. Nature **411**:687–689.

Gervais, C., R. Trahan, D. Moreno, and A.-M. Drolet. 1993. Le *Phragmites australis* au Québec: distribution géographique, nombres chromosomiques et reproduction. Canadian Journal of Botany **71**:1386–1393.

Granéli, W. 1989. Influence of standing litter on shoot production in reed, *Phragmites australis* (Cav.) Trin. ex Steudal. Aquatic Botany **35**:99–109.

Haslam, S. M. 1969. The development and emergence of buds in *Phragmites communis* Trin. Annals of Botany **33**:289–301.

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.

Hobbs, R. J., and L. Atkins. 1988. Effect of disturbance and nutrient addition on native and introduced annuals in plant communities in the Western Australian wheatbelt. Australian Journal of Ecology **13**:171–179.

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

Levine, J. M., J. S. Brewer, and M. D. Bertness. 1998. Nutrients, competition and plant zonation in a New England salt marsh. Journal of Ecology **86**:285–292.

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

Meyerson, L. A., K. Saltonstall, L. Windham, E. Kiviat, and S. Findlay. 2000. A comparison of *Phragmites australis* in freshwater and brackish marsh environments in North America. Wetlands Ecology and Management **8**:89–103.

Miller, W. B., and F. E. Egler. 1950. Vegetation of the Wequetequock–Pawcatuck tidal marshes, Connecticut. Ecological Monographs **20**:143–172.

Minchinton, T. E. 2002*a*. Disturbance by wrack facilitates spread of *Phragmites australis* in a coastal marsh. Journal of Experimental Marine Biology and Ecology **281**:89–107.

Minchinton, T. E. 2002*b*. Precipitation during El Niño correlates with increasing spread of *Phragmites australis* in New England, USA, coastal marshes. Marine Ecology Progress Series **242**:305–309.

Mook, J. H., and J. van der Toorn. 1982. The influence of environmental factors and management on stands of *Phragmites australis*. Journal of Applied Ecology **19**:501–517.

Niering, W. A., and R. S. Warren. 1980. Vegetation patterns and processes in New England salt marshes. BioScience **30**:301–307.

Niering, W. A., R. S. Warren, and C. G. Weymouth. 1977. Our dynamic tidal marshes: vegetation changes as revealed by peat analysis. Connecticut Arboretum Bulletin 22.

Nixon, S. W., and C. A. Oviatt. 1973. Ecology of a New England salt marsh. Ecological Monographs **43**:463–498.

Orson, R. A., R. S. Warren, and W. A. Niering. 1987. Development of a tidal marsh in a New England river valley. Estuaries **10**:20–27.

Ostendorp, W. 1989. Die-back of reeds in Europe: a critical review. Aquatic Botany **35**:5–26.

Otto, S. R. 1997. Effects of N enrichment and vegetation type on microbial processes in a freshwater tidal marsh. Thesis. Brown University, Providence, Rhode Island, USA.

Pennings, S. C., and M. D. Bertness. 2001. Salt marsh communities. Pages 289–316 *in* M. D. Bertness, S. D. Gaines, and M. E. Hay, editors. Marine community ecology. Sinauer Associates, Sunderland, Massachusetts, USA.

Phillips, J. D. 1987. Shoreline processes and establishment of *Phragmites australis* in a coastal plain estuary. Vegetatio **71**:139–144.

Poorter, H., and O. Nagel. 2000. The role of biomass allocation in the growth response of plants to different levels of light, CO_2, nutrients and water: a quantitative review. Australian Journal of Plant Physiology **27**:595–607.

Redfield, A. C. 1972. Development of a New England salt marsh. Ecological Monographs **42**:201–237.

Roman, C. T., W. A. Niering, and R. S. Warren. 1984. Salt marsh vegetation change in response to tidal restriction. Environmental Management **8**:141–150.

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 Sciences (USA) **99**:2445–2449.

Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, New Jersey, USA.

Tilman, D. 1988. Plant strategies and the dynamics and structure of plant communities. Princeton University Press, Princeton, New Jersey, USA.

Tiner, R. W. 1997. Managing common reed (*Phragmites australis*) in Massachusetts: an overview of the species and control techniques. Massachusetts Wetlands Restoration and Banking Program, Boston, Massachusetts, USA.

Turkington, R., E. Klein, and C. P. Chanway. 1993. Interactive effects of nutrients and disturbance: an experimental test of plant strategy theory. Ecology **74**:863–878.

Valiela, I., G. Collins, J. Kremer, K. Lajtha, M. Geist, B. Seely, J. Brawley, and C. H. Sham. 1997. Nitrogen loading from coastal watersheds to receiving estuaries: new method and application. Ecological Applications **7**:358–380.

Valiela, I., and J. M. Teal. 1974. Nutrient limitation in salt marsh vegetation. Pages 547–563 *in* R. J. Reimold and W. H. Queen, editors. Ecology of halophytes. Academic Press, New York, New York, USA.

Valiela, I., J. M. Teal, C. Cogswell, J. Hartman, S. Allen, R. van Etten, and D. Goehringer. 1985. Some long-term consequences of sewage contamination in salt marsh ecosys-

tems. Pages 301–316 *in* P. J. Godfrey, E. R. Kaynor, S. Pelezarski, and J. Benforado, editors. Ecological considerations in wetland treatment of municipal wastewaters. Van Nostrand Reinhold, New York, New York, USA.

van der Putten, W. H. 1997. Die-back of *Phragmites australis* in European wetlands: an overview of the European research programme on reed die-back and progression (1993–1994). Aquatic Botany **59**:263–275.

Vitousek, P. M. 1990. Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. Oikos **57**:7–13.

Vitousek, P. M., J. D. Ader, R. W. Howarth, G. E. Likens, P. A. Matson, D. W. Schindler, W. H. Schlesinger, and D. G. Tilman. 1997. Human alteration of the global nitrogen cycle: sources and consequences. Ecological Applications **7**: 737–750.

Warren, R. S., P. E. Fell, J. L. Grimsby, E. L. Buck, G. C. Rilling, and R. A. Fertik. 2001. Rates, patterns, and impacts of *Phragmites australis* expansion and effects of experimental *Phragmites* control on vegetation, macroinvertebrates, and fish within tidelands of the lower Connecticut River. Estuaries **24**:90–107.

Wilson, S. D., and D. Tilman. 1991. Interactive effects of fertilization and disturbance on community structure and resource availability in an old-field plant community. Oecologia **88**:61–71.

Wilson, S. D., and D. Tilman. 1993. Plant competition and resource availability in response to disturbance and fertilization. Ecology **74**:599–611.

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

Zedler, J. B. 2000. Progress in wetland restoration ecology. Trends in Ecology and Evolution **15**:402–407.

Zedler, J. B., J. C. Callaway, and G. Sullivan. 2001. Declining biodiversity: why species matter and how their functions might be restored in Californian tidal marshes. BioScience **53**:1005–1017.