

Mechanisms of exclusion of native coastal marsh plants by an invasive grass

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Summary

1 Determining the mechanisms by which invasive species exclude natives is critical for conserving and restoring native populations in impacted habitats. In recent decades the grass *Phragmites australis* has been aggressively invading coastal marshes of North America, with monocultures often replacing diverse assemblages of plants.

2 Our objective was to quantify how *P. australis* modifies the abiotic (soil and light conditions) and biotic (litter and shoots) environment and to determine the mechanisms by which it excludes two common forbs, the annual chenopod *Atriplex patula* var. *hastata* and the perennial aster *Solidago sempervirens*, from the highest tidal elevations of a brackish marsh in southern New England, USA.

3 In a 3-year field experiment we added seeds of both forb species to stands of *P. australis*, where we manipulated shoots and litter in an orthogonal design, and to uninvaded marsh areas dominated by the rush *Juncus gerardi*, where we manipulated the shoots of the marsh vegetation. In general, seedling establishment and the number of plants surviving until the end of the growing season were substantially greater in areas not invaded by *P. australis*, and both shoots and litter limited the abundance of forbs within stands.

4 Forbs surviving within stands of *P. australis* grew larger and produced more seeds than those in uninvaded areas, indicating that changes to the soil resulting from invasion do not preclude the survival of established forbs. This was confirmed by a glasshouse study where the performance of forbs in soil collected from within stands of *P. australis* was better than in soil from areas dominated by *J. gerardi*.

5 Similar to many invasive grasses in terrestrial communities, *P. australis* excludes native forbs through competition, modifying the biotic environment of the marsh at both the ground (litter) and above-ground (shoots) levels. Our results suggest that successful invaders, such as *P. australis*, are likely to be the ones that can engineer habitats in multiple ways and limit populations of native species across several critical stages of their life history.

Key-words: brackish and salt marsh plants, competition, dispersal limitation and seed supply, ecosystem engineer, invasive species, litter, *Phragmites australis*, recruitment limitation, sedimentation, seedling establishment

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Introduction

The increasing spread of invasive species is dramatically changing ecological communities across coastal

estuarine and marine landscapes (Carlton 1989; Ruiz *et al.* 2000; Bertness *et al.* 2002; Grosholz 2002). Investigations quantifying the patterns of spread and impacts of species invasions have revealed that invaders may alter the abiotic and biotic environment, ecological interactions among species and the functioning of ecosystems, frequently resulting in the exclusion of native species (D'Antonio & Vitousek 1992; Mack *et al.* 2000; Minchinton & Bertness 2003). Less well-understood are the mechanisms by which invaders exclude native populations and the stage of life history at which these mechanisms limit the demographic

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processes of the native species (Byers *et al.* 2002). Experimental studies to determine the nature of ecological interactions between invasive and native species are necessary for conserving and restoring native species in impacted habitats (Parker *et al.* 1999; Byers & Goldwasser 2001).

Some of the best insights into the manner by which invasive species exclude natives come from studies in terrestrial grassland communities (e.g. Kolb *et al.* 2002; Corbin & D'Antonio 2004; Milton 2004). Changes to environmental conditions often give invasive grasses in particular an advantage that leads to the exclusion of natives through competition for key limiting above- and below-ground resources such as nutrients, space and light (Daehler 2003; Levine *et al.* 2003; Vilà & Weiner 2004). Grasses have the potential to be similarly invasive in coastal estuaries (e.g. Kuhn & Zedler 1997; Minchinton 2002a,b; Minchinton & Bertness 2003; Davis *et al.* 2004), but relatively little is known about how they exclude native plants in the intertidal landscape or whether the mechanisms of exclusion are similar to those in terrestrial communities.

Over the past century the grass *Phragmites australis* (often called common reed and hereafter referred to as *Phragmites*) has been aggressively invading coastal marshes of North America, displacing the diverse assemblage of native plants and often forming vast monocultures (see reviews in Marks *et al.* 1994; Tiner 1997; Chambers *et al.* 1999; Meyerson *et al.* 2000; but see Ostendorp 1989 for concern over the decline of *Phragmites* in Europe). In southern New England, USA, *Phragmites* has been a minor component of the assemblage of plants along the terrestrial border of freshwater and brackish marshes for several thousands of years (Niering *et al.* 1977; Clark 1986; Orson *et al.* 1987). It is now spreading into coastal marshes from which it has historically been absent, as well as to more seaward locations within brackish and salt marshes where abiotic conditions are supposedly physiologically stressful (Amsberry *et al.* 2000). This has been attributed to the recent cryptic invasion by a non-native genotype of *Phragmites* that apparently has a much broader tolerance of environmental conditions (Saltonstall 2002, 2003). Concurrently, anthropogenic modification of coastal marshes, particularly the clearing of vegetation along the terrestrial-marsh ecotone and increased nutrient load, appears to be accelerating the spread of *Phragmites* (Bertness *et al.* 2002; Minchinton & Bertness 2003; Silliman & Bertness 2004).

Correlative surveys in southern New England have revealed that marshes dominated by *Phragmites* have fewer species of plants than those without *Phragmites* (Keller 2000; Meyerson *et al.* 2000; Silliman & Bertness 2004). There is little experimental evidence, however, substantiating a causal relationship between the invasion of *Phragmites* and the decline in the abundance and diversity of native marsh plants (but see Burdick & Konisky 2003; Minchinton & Bertness 2003). Much of the plant diversity in coastal brackish and salt marshes

of southern New England is due to a suite of halophytic forbs that typically co-occur with *Phragmites* along the terrestrial border of the marsh (Tiner 1987; Brewer *et al.* 1997; Rand 2000). *Phragmites* is typically the largest plant in these marshes and therefore it is simple to assume that it excludes the smaller forbs through shading. Occasionally, however, adult forbs are found within undisturbed stands of *Phragmites*, indicating that some species may grow under the canopy of *Phragmites*, and suggesting that the mechanisms of exclusion may be more complicated. Indeed, as *Phragmites* spreads, it not only creates a canopy over the other marsh plants, but it also engineers the habitat by increasing the accumulation of plant litter on the substratum and altering the physico-chemical conditions of the soil (e.g. Windham & Lathrop 1999; Meyerson *et al.* 2000). Through these abiotic and biotic modifications to the marsh, *Phragmites* may exclude native forbs at different stages of their life history by limiting demographic processes (i.e. dispersal and supply of seeds, establishment of seedlings, survival and reproductive output of adults) necessary for sustaining local populations.

Here we present the results of investigations designed to reveal the mechanisms by which *Phragmites* excludes native halophytic forbs in a coastal brackish marsh in Massachusetts, USA. We chose two species of common and abundant forbs with different life histories, the annual chenopod *Atriplex patula* var. *hastata* (hereafter referred to as *Atriplex*) and the perennial aster *Solidago sempervirens* (hereafter referred to as *Solidago*). First, we did a quantitative field survey to test the hypothesis that the abundance of seeds, seedlings and adults of *Atriplex* and *Solidago* is negatively related to the abundance of *Phragmites*. We then tested hypotheses about how changes to abiotic and biotic conditions due to the presence of *Phragmites* might limit the abundance of these forbs at different stages of their life history. A field experiment over three growing seasons tested whether shoots and litter of *Phragmites*, or their combination, limit the establishment, survival and reproductive output of the forbs. We supplied seeds of both forb species to areas in the marsh not invaded by *Phragmites* and also within manipulated stands of *Phragmites*. A glass-house study tested the hypothesis that the composition of the soil, *per se*, limits establishment and survival, by placing seeds of both forb species onto blocks of soil collected from within stands of *Phragmites* and from uninvaded areas in the marsh.

Materials and methods

LOCATION AND PLANTS STUDIED

The study was carried out between May 1998 and September 2000 in a brackish tidal marsh at the Adolph Rotundo Wildlife Preserve along the Palmer River in Rehoboth, Massachusetts, USA (41°47' N, 71°16' W) (Amsberry *et al.* 2000). The marsh is in a developed area, crossed by two highways, and bordered by forest,

farms and residential and commercial buildings. The marsh is intersected by tidal creeks and has been ditched at regular intervals from land to sea. The plants in the marsh are typical of brackish and salt marshes of southern New England, with characteristic bands of perennial turf-forming grasses and rushes along a gradient of elevation (e.g. Niering & Warren 1980; Bertness & Ellison 1987; see Tiner 1987 for taxonomic authorities). The banks of tidal creeks and the low marsh are dominated by the grass *Spartina alterniflora*. The high marsh is occupied by a dense matrix of grasses and rushes, including the grass *Spartina patens* and the rush *Juncus gerardi* along its lower and upper borders, respectively, with the grass *Distichlis spicata* interspersed throughout (hereafter these three species are collectively referred to as marsh turf). Within this matrix, particularly at the highest elevations of the marsh, is a relatively diverse assemblage of halophytic forbs (Tiner 1987; Rand 2000). The highest elevations of the marsh, which comprise the terrestrial border of the high marsh and the levees of tidal creeks, are also dominated by *Phragmites*, and the shrub *Iva frutescens* is occasionally present.

Phragmites is a clonal grass with annual shoots and perennial rhizomes, which spreads vegetatively to form monospecific stands. Two study sites were chosen where large, solitary stands of *Phragmites* along the levee of tidal creeks were spreading into the high marsh dominated by marsh turf (primarily *J. gerardi*, but *S. patens* and *D. spicata* were occasionally present) and a suite of forbs. Stands extended tens of metres along each tidal creek (site 1, 150 m; site 2, 100 m) and tens of metres into the marsh (site 1, 36 m; site 2, 24 m). Observations indicate that both stands are at least a decade old (see Minchinton & Bertness 2003) and comprised of the non-native strain of *Phragmites* (see Saltonstall 2002). The two species of forbs selected, *Atriplex* and *Solidago*, are common and abundant in areas of the high marsh dominated by *J. gerardi* (Tiner 1987; Rand 2000). *Atriplex* is an annual chenopod with seeds that are typically dispersed by water and *Solidago* is a perennial aster with wind-dispersed seeds that can also float in water.

PATTERNS OF ABUNDANCE OF FORBS, MARSH TURF AND *PHRAGMITES*

To quantify the observed patterns of decreasing abundance of marsh turf and forbs with increasing abundance of *Phragmites*, surveys were done at each site along a transect from the high marsh, dominated by *J. gerardi* and forbs, to the levee of the tidal creek dominated by *Phragmites*. The transect was divided into the high marsh adjacent to the edge of the *Phragmites* stand and dominated by *J. gerardi* (zone 1, hereafter referred to as the *Juncus* zone), the edge of the *Phragmites* stand adjacent to the *Juncus* zone (zone 2) and the levee of the tidal creek dominated by *Phragmites* (zone 5, hereafter referred to as the *Phragmites*

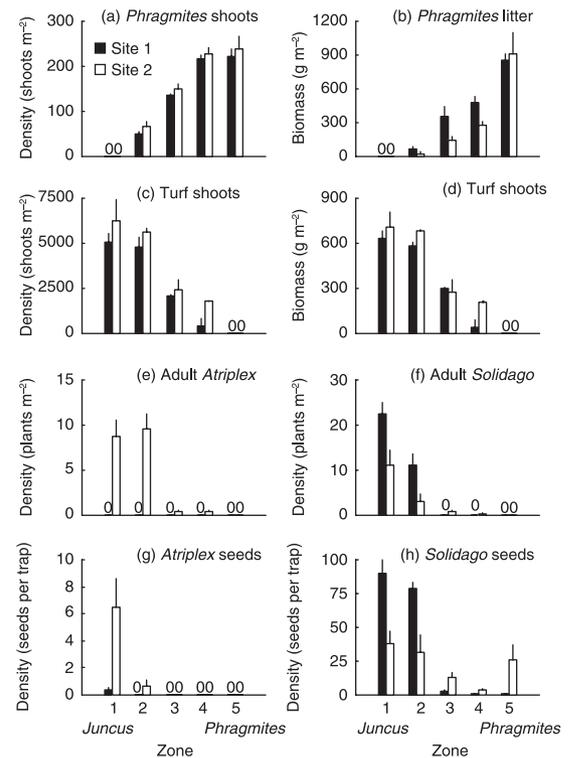


Fig. 1 Mean (\pm SE) (a) density of *Phragmites* shoots, (b) biomass of *Phragmites* litter, (c) density of shoots of marsh turf, (d) biomass of shoots of marsh turf, (e) density of adult *Atriplex* (none found in quadrats at site 1), (f) density of adult *Solidago*, (g) density of *Atriplex* seeds, and (h) density of *Solidago* seeds from the *Juncus* zone (zone 1) to the *Phragmites* zone (zone 5).

zone): the area remaining between zone 2 and zone 5 was divided into two equal zones (3 and 4). Therefore, zone 1 had the greatest density of *Juncus* and no *Phragmites*, zones 2–4 had progressively less *Juncus* and more *Phragmites*, and zone 5 had no *Juncus* and the greatest density of *Phragmites* (see Fig. 1a–d). Each zone extended 50 m alongshore and was 6 m wide (except that zones 3 and 4 at site 1 were 12 m wide because of the greater width of the stand at that site), and the central 3-m band within each zone was sampled.

In June 1998, the abundance of *Phragmites* litter (dead shoots and leaves on the substratum) and marsh turf was estimated separately by collecting the above-ground plant material from each of four randomly located quadrats (15 cm \times 15 cm) in each zone. The shoots of each species of marsh turf were counted, and then these samples and those for *Phragmites* litter were dried to a constant mass at 50 °C and weighed. The numbers of recently recruited seedlings of *Atriplex* and *Solidago* were also counted in these quadrats. At the end of the first growing season (September 1998) when most plants are reproductive, the density of *Phragmites* shoots (live and dead), adult *Atriplex* and adult *Solidago* was measured in five randomly located quadrats (1 m \times 1 m) in each zone. The number of species of plants was also counted in each zone.

PATTERNS OF SEED SUPPLY OF FORBS

To quantify patterns of seed dispersal of forbs in relation to the abundance of *Phragmites*, 10 seed traps were randomly placed in each of the five zones at each site (see Rand 2000). The traps consisted of two, circular plastic plates (surface area about 314 cm² per plate), placed back-to-back and held together with cable ties. The outer surfaces of the plates were covered with a thin layer of Tanglefoot™ insect trap coating. Traps were attached to wire stakes and positioned 10 cm above and perpendicular to the marsh substratum so that both seeds dispersed by wind at low tide and those dispersed by water at high tide were caught. Traps were placed in the marsh in August 1998 before *Atriplex* and *Solidago* had gone to seed and collected 3 months later in November 1998 after seeds had dispersed. Seeds were identified and counted in the laboratory under a dissecting microscope. For each species, a two-factor analysis of variance (ANOVA) was used to determine differences in seed supply (transformed to natural logarithms) among zones (five zones) and between sites.

INFLUENCE OF SOIL, SHOOTS AND LITTER OF
PHRAGMITES

We determined whether *Phragmites* limits the abundance of forbs after the arrival of seeds by examining effects on the establishment, survival and growth of *Atriplex* and *Solidago* and the reproductive output of *Atriplex*.

The influence of soil

Ten blocks of soil (10 cm × 10 cm × 10 cm) were extracted from the *Phragmites* and *Juncus* zones at each site, giving a total of 40 blocks of soil. Blocks were placed individually in plastic pots in the glasshouse at Brown University, and above-ground vegetation was clipped to the level of the soil. Fifty *Atriplex* or 250 *Solidago* seeds collected from the marsh in the previous year were added to each of 20 pots, giving five replicate pots per zone per site for each species. Different numbers of seeds were used because germination success was expected to be different for each species. The pots were randomly arranged in an array and their positions were re-randomized at least once per week. Plants were maintained at ambient light and temperature and watered daily with fresh water. By removing the physico-chemical (e.g. salinity, flooding, light) and biological (e.g. above-ground vegetation) differences that would be present between zones in the field, variation specifically due to below-ground differences in the composition of the soil (including root matter) could be studied. Note that, because we did not manipulate *Phragmites*, differences in the soil between the *Phragmites* and *Juncus* zones may be due to factors other than the presence of *Phragmites* (although *Phragmites* is known to

modify its soil environment; see Windham & Lathrop 1999; Meyerson *et al.* 2000); nevertheless, comparing the performance of forbs on these soils tests whether soil properties can, by themselves, exclude forbs from the *Phragmites* zone.

The study was carried out from August to December 1998, and the establishment and mortality of plants was calculated as the percentage of seeds that established and the percentage of established plants that died, respectively. After 3 months, most of the *Atriplex* plants had flowered and set seed, and at this time plants were recorded as producing seeds or not, harvested, dried to a constant mass at 50 °C and weighed. An additional month was allowed for *Solidago* seedlings to grow larger and, after 4 months, *Solidago* were similarly harvested and weighed. For each species, a two-factor ANOVA was used to determine the effect of zone (*Juncus* or *Phragmites* zone) and site on the establishment, survival, density and biomass of *Atriplex* and *Solidago* grown in the glasshouse and on the percentage of *Atriplex* plants with seeds.

The influence of shoots and litter

The presence or absence of *Phragmites* shoots and *Phragmites* litter was manipulated in an orthogonal design in the *Phragmites* zone. Similarly, the presence or absence of shoots of the species comprising the marsh turf (primarily *Juncus*) was manipulated in the *Juncus* zone, where *Atriplex* and *Solidago* are normally found. Litter was not present in the *Juncus* zone and therefore the influence of this factor was not examined in the *Juncus* zone, resulting in differences in experimental design between zones. Ten plots were randomly located in each of the *Phragmites* (2 m × 3 m) and *Juncus* (0.5 m × 1.5 m) zones at each site and separated by at least 3 m. Half of these plots were randomly selected in each zone and the shoots of *Phragmites* or marsh turf were clipped as close to the substratum as possible (1–2 cm) using hedge clippers, and the other five plots were left as uncut controls. Shoots that regrew were clipped at regular intervals during the growing season.

Cages into which *Atriplex* and *Solidago* seeds would be added were placed into the middle of each plot and spaced 50 cm apart. Two replicate cages (both without litter) were added to each plot in the *Juncus* zone and four arranged in a square (two with litter and two without litter) to each plot in the *Phragmites* zone, giving a total of 40 cages in the *Phragmites* zone and 20 cages in the *Juncus* zone at each site. *Phragmites* litter naturally covers much of the substratum in the *Phragmites* zone, but in varying amounts, so the litter was removed from all cages and a standardized amount based on the means of survey estimates (17.7 g dry biomass/225 cm² or 24.6 g per cage) was added to two randomly selected cages in each plot in the *Phragmites* zone.

Cages were cylindrical (26 cm tall, 314 cm² area) and made of galvanized hardware cloth (1.3 cm mesh size) lined with row crop cover cloth, which allowed water

and light to enter the cages, but did not allow seeds in or out. Inevitably, the availability of light within the cages was diminished by about 28% by the cloth (authors' unpublished data), but the cloth was only in place for 6 weeks as seedlings established, all replicates had cloth, and it is impossible to manipulate these seeds without such cages. Each cage was divided in half with a wall of hardware cloth lined with row crop cover cloth so that *Atriplex* seeds could be added to one side and *Solidago* seeds to the other. The tops of cages were covered with lids made of white polyester organza fabric attached with elastic bands. This prevented seeds from escaping and allowed seedlings to be counted without removing the cage.

Using seeds collected from the marsh in the previous year, 100 *Atriplex* and 500 *Solidago* seeds were added to their respective halves of each cage in June 1998, and then the establishment of seedlings was monitored about every 2 weeks. Six weeks after adding the seeds, establishment had ceased and therefore the dividing walls and row cover cloth lining the cages were removed. The wire skeleton of the cages remained in place to exclude litter until plants were harvested at the end of the growing season. After *Atriplex* had set seed at the end of the growing season (September 1998), plants of both species were harvested. *Atriplex* were counted, the percentage with seeds was noted, the number of seeds per plant was counted, and then the plants were dried to a constant mass at 50 °C and weighed. *Solidago* were counted, harvested, dried and weighed as described for *Atriplex*, but no seeds were available for counting because *Solidago* is a perennial and did not become reproductive in its first year.

Throughout the growing season in 1998, *Atriplex* seeds that had been added at the beginning of the experiment could be seen on the soil within the cages and, in spring 1999, a new cohort of seedlings of both *Atriplex* and *Solidago* emerged within the exact area of the cages. It was clear that these seedlings came from seeds that had been added in the previous year (and not from naturally dispersed seeds or seeds of experimental plants) because these species of forbs exhibit extremely localized dispersal and seedlings are rare except near the parental plant (see Rand 2000), seedlings of these species were never found during surveys in this study, and experimental plants had been harvested before their seeds had dispersed. Therefore, to determine whether similar results would be obtained for this second cohort, manipulations of shoots and litter were implemented again and continued until the end of the growing season of 1999. The only difference from the previous year was that cages used to exclude litter were not lined with row cover cloth because we were not concerned about escaping seeds. Establishment and survival were monitored and, at the end of the growing season (September 1999), plants were harvested and data collected as in the previous year. We again checked for seeds and new seedlings in spring and at the end of the growing season of 2000, but none was found.

Ultimately, relatively few seedlings established or survived in some treatments (see Results). Therefore, to increase the power of statistical tests, data from both cohorts were pooled across years, which was appropriate because differences among treatments were qualitatively similar in 1998 and 1999. For each replicate, data were combined across years by summing the number of plants that established (or survived) in each of the two years. Establishment of plants was calculated as the percentage of the number of seeds added in June 1998 that established, and survival as the percentage of established plants that survived to be harvested at the end of the growing season.

Because of the necessary differences in the experimental design between zones (due to the absence of litter in the *Juncus* zone), two separate analyses were done to test for the effect of shoots and litter of *Phragmites* on the establishment and survival of forbs. In the first, a four-factor, nested ANOVA was used to determine the effect of litter (present or removed), shoots (present or removed), plots (nested within the factors for the effects of shoots and sites), and sites in the *Phragmites* zone. In the second, litter was excluded as a factor, and a three-factor ANOVA was used to determine the effect of shoots (present or removed; for shoots of *Phragmites* in the *Phragmites* zone and for shoots of marsh turf in the *Juncus* zone), zone (*Juncus* or *Phragmites*), and site. For this second analysis, the average values for the two cages in each plot were used as replicates.

Environmental conditions

Relevant abiotic factors that might limit the performance of forbs were measured in the presence and absence of shoots within each zone at each site, including edaphic conditions (salinity, redox potential, moisture and grain size), sedimentation rate, availability of light and relative tidal height. These measurements were taken to help explain the results by determining how the abiotic environment varied spatially across the marsh and with experimental manipulations of the vegetation. Soil porewater salinity was measured in each plot during neap tides on several occasions during the growing seasons of 1998 and 1999 and, due to the similarity of the relative differences among treatments across dates, only those from August 1998 are presented. Salinity was determined by extracting pore water from the top 2 cm of a small core of soil and measuring it using a hand-held NaCl refractometer with a precision of $\pm 1 \text{ g kg}^{-1}$. Soil redox potential, an indicator of soil oxygen availability, and soil moisture were measured in each plot about 1 week after a spring tide in October 1998. Soil oxygen availability was estimated by removing a core (1 cm diameter \times 5 cm long) of soil, inserting a platinum redox electrode (filled with 4 mol L⁻¹ KCL saturated with Ag/AgCl reference solution) into the hole, and measuring the redox potential using a portable meter (Orion pH ISE meter, model

230 A). Soil moisture was estimated by removing two cores (1.5 cm diameter \times 6 cm long) of soil from each plot, wrapping them in aluminium foil to retain the water, and then weighing them before and after drying to a constant mass at 50 °C. Soil moisture was calculated as the percentage difference between the wet and dry weights. The same cores were used to compare soil grain sizes and these were pooled across plots (about 33 and 51 g dry biomass per sample in the *Juncus* and *Phragmites* zones, respectively) and wet sieved to determine percentage composition of the following grain size classes: macro-organic (> 2 mm), very coarse sand (1–2 mm), coarse sand (0.5–1 mm), medium sand (0.25–0.5 mm), fine sand (0.125–0.25 mm), very fine sand (0.063–0.125 mm), and silt and clay (< 0.063 mm).

Sedimentation rates were measured in each plot from September to December 1998. In each plot, we placed two sediment traps, consisting of 50 mL centrifuge tubes, into the ground so that their tops were level with the soil, thus recording sedimentation that would be experienced by seedlings. Tube openings were covered with nylon screen (about 1 mm mesh size) to prevent macro-invertebrates and large debris from entering. After 90 days we withdrew the sediment traps, and the sediment was dried to a constant mass at 50 °C and weighed. The availability of light was quantified between 11.00 and 14.00 on a cloudless day in August 1998 using a light meter (LI-COR solar monitor, model 1776). Two instantaneous measurements ($\mu\text{E m}^{-2} \text{ s}^{-1}$) were taken under and immediately above the litter in each plot, and these were expressed relative to measurements in the open marsh, which were unobstructed by marsh vegetation or litter. Light measurements were only done at site 2, but given the similarities in the densities of shoots and abundance of litter between sites, results should be similar at site 1. We determined the relative differences in elevation among zones and between sites by measuring water depth during spring high tides at 10 random locations within each zone at each site several times during the study. A three-factor ANOVA was used to determine the effect of shoots (present or removed, for shoots of *Phragmites* in the *Phragmites* zone and for shoots of marsh turf in the *Juncus* zone), zone (*Juncus* or *Phragmites* zone) and site on soil salinity, soil redox potential, soil moisture and sedimentation rate. Grain size distributions and light availability were not analysed statistically.

STATISTICAL ANALYSES

For all statistical analyses, site and plot were considered random factors and zone, shoots and litter were considered fixed factors. Where appropriate, data were transformed to their natural logarithms or to the arcsine of their square roots before analysis. Student-Newman-Keuls (SNK) multiple comparisons tests were used to locate significant differences among treatment means when there were significant interactions in

the ANOVA (at $P < 0.05$ for both SNK tests and ANOVA), and the results of these tests are simply described in the text.

Results

PATTERNS OF ABUNDANCE OF FORBS, MARSH TURF AND *PHRAGMITES*

There was a gradual and substantial increase in the density of *Phragmites* shoots from the *Juncus* zone in the high marsh to the *Phragmites* zone at the edge of the tidal creek (Fig. 1a). As shoot density increased, so did the biomass of *Phragmites* litter on the substratum, with a particularly pronounced increase in the *Phragmites* zone (Fig. 1b). In contrast, the density and biomass of shoots of marsh turf ($> 75\%$ *Juncus* by dry biomass, but *S. patens* and *D. spicata* were also present) decreased gradually from the *Juncus* to the *Phragmites* zone (Fig. 1c,d). The density of adult *Atriplex* (which was present but not recorded in quadrats at site 1) and adult *Solidago* declined more abruptly, with few individuals extending more than 6 m into the stand of *Phragmites* (Fig. 1e,f). Moreover, no seedlings of *Atriplex* or *Solidago* were found in any of the quadrats sampled. The number of species of plants declined from the *Juncus* to the *Phragmites* zone at both sites, with none of the 10 species recorded in the *Juncus* zone (*Atriplex*, *D. spicata*, *I. frutescens*, *Juncus*, *Potentilla anserina*, *Scirpus* spp., *Solidago*, *S. patens*, *Typha angustifolia*, *Triglochin maritimum*) present in the *Phragmites* zone.

PATTERNS OF SEED SUPPLY OF FORBS

An order of magnitude more *Solidago* seeds were trapped than *Atriplex* seeds, but seed supply for both species roughly paralleled the abundance of adults and declined precipitously from the *Juncus* zone to the *Phragmites* zone (Fig. 1g,h). For both species, differences in seed supply between sites varied among zones (*Atriplex*, $F_{4,90} = 8.2$, $P < 0.001$; *Solidago*, $F_{4,90} = 15.8$, $P < 0.001$; results for interaction between zone and site in ANOVA). In the *Juncus* zone, significantly fewer *Atriplex* seeds were caught at site 1, where adults were uncommon, than at site 2, and no *Atriplex* seeds were trapped beyond zone 2, which extended only 6 m into the stand of *Phragmites* (Fig. 1g, SNK tests). Densities of *Solidago* seeds in zones 1 and 2 were significantly greater at site 1 than at site 2, reflecting adult abundances, whereas densities of seeds of *Solidago* in other zones were significantly greater at site 2 than at site 1 (Fig. 1h, SNK tests). The spike in the density of *Solidago* seeds in the *Phragmites* zone at site 2 (Fig. 1h) probably occurred through the supply of seeds from plants located only a few metres away on the other side of the tidal creek. This result is important because it attests to the efficacy of the traps, with large numbers of seeds caught even in areas with great densities of *Phragmites* shoots.

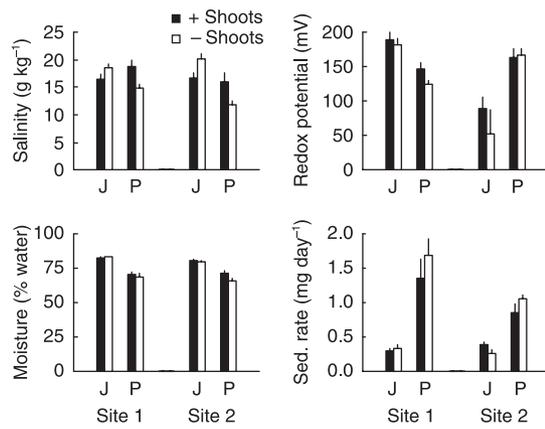


Fig. 2 Mean (\pm SE) soil porewater salinity (g salt kg^{-1} seawater), soil redox potential, percentage soil moisture and sedimentation rate in the presence or absence of shoots in the *Juncus* (J) and *Phragmites* (P) zones at each of two sites.

INFLUENCE OF SOIL, SHOOTS AND LITTER OF *PHRAGMITES*

Environmental conditions

There was on average less than a 1 cm difference in elevation between the *Juncus* zone at site 1, the *Phragmites* zone at site 1, and the *Phragmites* zone at site 2. The *Juncus* zone at site 2 was, however, 6 cm lower than these other three zones. Differences in soil porewater salinity among treatments were relatively small (Fig. 2). In the presence of shoots, salinity was similar between zones, whereas salinity in the *Juncus* zone was significantly greater than in the *Phragmites* zone where shoots had been removed (Fig. 2, Table 1, SNK results for interaction between zone and shoots). Salinity in the *Juncus* zone was significantly greater where shoots had been removed than where they were present, whereas the reverse was true in the *Phragmites* zone (Fig. 2, Table 1, SNK results for interaction between zone and shoots). Soil redox potential was significantly greater in the *Juncus* zone than in the *Phragmites* zone

at site 1, but the reverse was true at site 2, where the low tidal elevation in the *Juncus* zone corresponded with a low redox potential (Fig. 2, Table 1, SNK results for interaction between site and zone). Although soil moisture was significantly greater in the *Juncus* zone than in the *Phragmites* zone and at site 1 than at site 2, these differences among treatments were relatively small (Fig. 2, Table 1). At both sites, sediments accumulated at a significantly faster rate in the *Phragmites* zone than in the *Juncus* zone, and this difference was more pronounced at site 1 (Fig. 2, Table 1, SNK results for interaction between site and zone). There was no effect of removing shoots on soil redox potential, soil moisture or sediment accumulation (Fig. 2, Table 1). The primary difference in the composition of the soil was the macro-organic component (roots and rhizomes), whose mean across sites was about four times greater in the *Juncus* zone (18.6% of soil mass) than in the *Phragmites* zone (4.5% of soil mass) (Table 2). The availability of light in plots without shoots and litter in the *Phragmites* zone or without shoots of marsh turf in the *Juncus* zone was 91% ($91.1 \pm 2.7\%$ light; mean \pm SE, $n = 5$) and 98% ($97.9 \pm 1.3\%$ light; mean \pm SE, $n = 5$) of that measured under full sunlight in the open marsh, respectively. In contrast, the presence of shoots reduced light availability to only 2% of full sunlight in both the *Phragmites* ($1.6 \pm 0.6\%$ light; mean \pm SE, $n = 5$) and *Juncus* zones ($1.7 \pm 0.8\%$ light; mean \pm SE, $n = 5$). Similarly, litter diminished light in the *Phragmites* zone to less than 3% of that available in the open marsh, regardless of the presence ($0.4 \pm 0.3\%$ light; mean \pm SE, $n = 5$) or absence ($2.5 \pm 0.7\%$ light; mean \pm SE, $n = 5$) of shoots.

The influence of soil

In the glasshouse, seedlings of *Atriplex* and *Solidago* established and grew successfully in both *Juncus* and *Phragmites* soil. There was no significant influence of soil type on percentage establishment for either species (Fig. 3, Table 3). Mortality for both species was minimal, except for *Solidago* seedlings in *Juncus* soil from

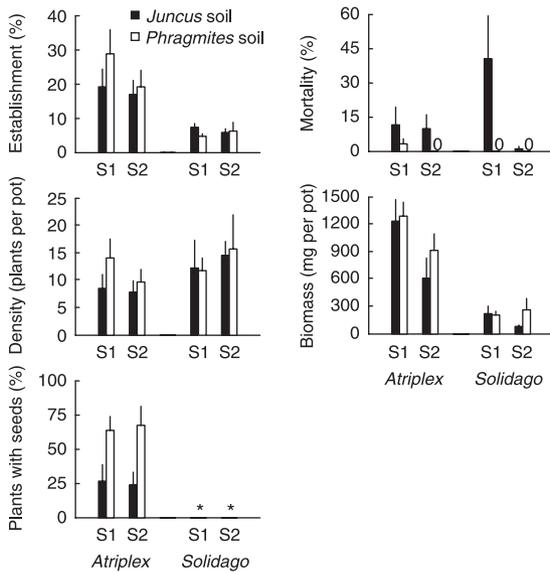
Table 1 Analyses of soil salinity, soil redox potential, percentage soil moisture and biomass of sediment accumulated in the presence or absence of shoots in the *Juncus* and *Phragmites* zones at each of two sites (see data in Fig. 2). Results are estimates of mean squares (MS) and probability levels (P) of analysis of variance. Data were not transformed

Source	d.f.	Salinity		Redox		Moisture		Sediment	
		MS	P	MS	P	MS	P	MS	P
Site: S	1	9.0	0.173	18 727	< 0.001	44.9	0.048	6 557	0.053
Zone: Z	1	67.6	0.410	4 520	0.817	1509.2	0.046	68 141	0.194
Shoot: Sh	1	4.2	0.275	2 481	0.056	39.8	0.386	1 024	0.376
S \times Z	1	38.0	0.007	51 883	< 0.001	8.0	0.392	6 767	0.049
S \times Sh	1	0.9	0.663	20	0.905	19.2	0.189	460	0.598
Z \times Sh	1	126.0	< 0.001*	491	0.702	32.4	0.304	2 124	0.035
S \times Z \times Sh	1	1.6	0.561	1 925	0.243	8.6	0.374	6	0.950
Residual	32	4.6		1 363		10.6		1 624	

*To increase the power of the test, the estimate of MS used in the denominator of the F -ratio is a pooled estimate from the MS of the S \times Z \times Sh interaction and the residual, and then the effect of Z \times Sh was tested with 1 and 33 d.f. (see Winer *et al.* 1991 for pooling procedures).

Table 2 Percentage frequency distribution of grain sizes of the soil in the *Juncus* and *Phragmites* zones at each of two sites

Particle type	Grain size (mm)	Site 1		Site 2	
		<i>Juncus</i>	<i>Phragmites</i>	<i>Juncus</i>	<i>Phragmites</i>
Macro-organic	> 2	21.4	5.3	15.7	3.7
Very coarse sand	1–2	7.8	3.3	2.7	0.7
Coarse sand	0.5–1	6.7	8.9	7.5	10.3
Medium sand	0.25–0.5	8.4	6.1	7.2	12.7
Fine sand	0.125–0.25	11.3	10.4	12.0	18.1
Very fine sand	0.063–0.125	11.4	12.2	9.6	10.6
Silt and clay	< 0.063	33.0	53.8	45.3	43.9

**Fig. 3** Mean (\pm SE) percentage establishment, percentage mortality, density, biomass, and percentage of plants with seeds (*Atriplex* only; '*' indicates not measured), for *Atriplex* and *Solidago* grown in the glasshouse in soil from either the *Juncus* or *Phragmites* zone at each site.

site 1, which had significantly greater mortality than seedlings in the other treatments (Fig. 3, Table 3, SNK results for interaction between site and zone). The density of plants at the end of the experiment did not vary significantly among soil types for either species (Fig. 3, Table 3). In contrast, the total biomass of plants per pot, which integrates both the density and individual biomass of plants, was significantly greater in *Phragmites* than in *Juncus* soil for *Solidago*, with a similar non-significant pattern for *Atriplex* (Fig. 3, Table 3). The percentage of *Atriplex* plants grown in *Phragmites* soil that produced seeds was more than double and significantly greater than that for plants grown in *Juncus* soil (Fig. 3, Table 3).

The influence of shoots and litter

On average, establishment of seedlings was greater for *Atriplex* than for *Solidago*, at site 1 than at site 2, in the *Juncus* zone than in the *Phragmites* zone, and where shoots or litter had been removed than where they were present (Fig. 4). In the *Phragmites* zone, litter dramatically and significantly reduced the establishment of

Table 3 Analyses of percentage establishment, percentage mortality, density, biomass, and percentage of plants with seeds (*Atriplex* only), for *Atriplex* and *Solidago* grown in the glasshouse in soil from the *Juncus* or *Phragmites* zones at two sites (see data in Fig. 3). Results are estimates of mean squares (MS) and probability levels (*P*) of analysis of variance. Density and biomass were transformed to their natural logarithms and proportions to the arcsine of their square roots

Source (d.f.)	Site: S (d.f. = 1)		Zone: Z (d.f. = 1)		S \times Z (d.f. = 1)		Residual (d.f. = 16)
	MS	<i>P</i>	MS	<i>P</i>	MS	<i>P</i>	
<i>Atriplex</i>							
Establishment	0.027	0.301	0.025	0.353	0.009	0.535	0.023
Mortality	0.025	0.464	0.184	0.162	0.012	0.604	0.044
Density	0.347	0.432	0.625	0.280	0.138	0.618	0.534
Biomass	2.386	0.028	0.842	0.403	0.455	0.308	0.410
Percentage with seeds	0.013	0.749	1.452	0.035	0.004	0.854	0.125
<i>Solidago</i>							
Establishment	0.0001	0.906	0.0042	0.452	0.0031	0.428	0.0047
Mortality	0.422	0.029	0.587	0.448	0.422	0.029	0.074
Density	0.572	0.366	0.084	0.706	0.340	0.483	0.660
Biomass	0.520	0.578	2.923	0.016	0.002	0.973	1.615

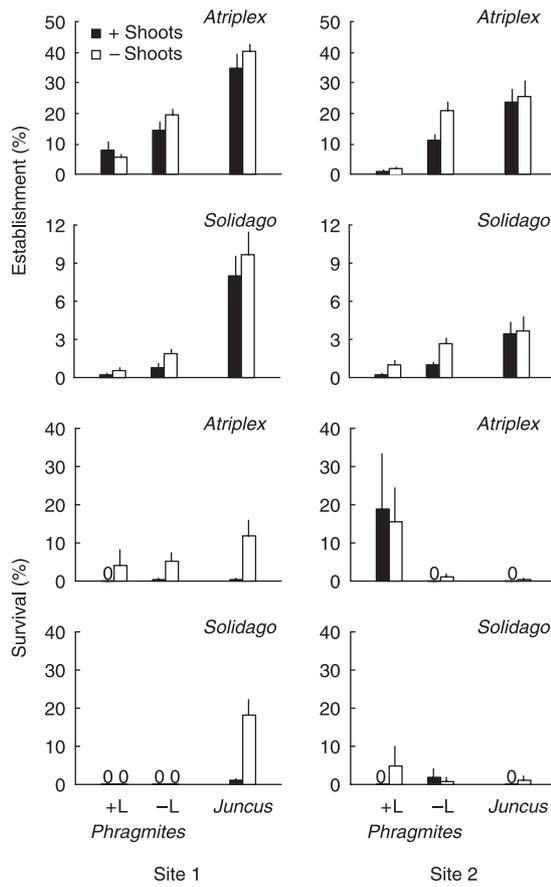


Fig. 4 Mean (\pm SE) percentage establishment and percentage survival of *Atriplex* and *Solidago* in the presence or absence of shoots and litter (L) in the *Phragmites* zone and the presence or absence of shoots in the *Juncus* zone at each of two sites.

Atriplex and *Solidago*, and this result was consistent in the presence or absence of shoots and at both sites (Fig. 4, Table 4, SNK results for interaction between shoots and litter). In contrast, at both sites the effect of

removing *Phragmites* shoots on the establishment of *Atriplex* and *Solidago* was dependent on the presence or absence of litter (Fig. 4, Table 4). In the presence of litter, there was no effect of removing *Phragmites* shoots on the establishment of forbs, whereas in the absence of litter, the removal of shoots significantly increased the establishment of both species (Fig. 4, Table 4, SNK results for interaction between shoots and litter). For both species, establishment in the *Juncus* zone was not significantly affected by removing shoots (Fig. 4, Table 5, SNK results for interaction between zone and shoots for *Atriplex*). For both *Atriplex* and *Solidago*, establishment at both sites was significantly greater in the *Juncus* zone than in areas without litter in the *Phragmites* zone (Fig. 4, Table 5, SNK results for interaction between zone and shoots for *Atriplex* and site and zone for *Solidago*).

The overall survival of forbs was low, with only 155 plants (1.29% of seeds) surviving in the *Juncus* zone and 25 (0.042% of seeds) in the *Phragmites* zone over both years (Fig. 4, Table 6). In the *Phragmites* zone at both sites, the presence of shoots significantly reduced the survival of *Atriplex* in the absence of litter, but there were no effects of shoots on *Atriplex* in the presence of litter (Fig. 4, Table 4, SNK results for interaction between shoots and litter). Similarly, in the absence of litter, removing shoots increased the survival of *Atriplex* in both the *Phragmites* and *Juncus* zones at both sites, but this effect was only significant at site 1 (Fig. 4, Table 5, SNK results for interaction between site and shoots). Given the small number of *Solidago* surviving in the *Phragmites* zone, it is not surprising that there were no statistical differences in survival among any of the treatments (Fig. 4, Table 4). Survival of *Solidago* in the *Juncus* zone at site 1 was significantly greater where shoots had been removed than where they were present but, as for *Atriplex*, this effect was not significant

Table 4 Analyses of percentage establishment and percentage survival of *Atriplex* and *Solidago* in the presence or absence of shoots and litter in each of five plots in the *Phragmites* zone at each of two sites. Results are estimates of mean squares (MS) and probability levels (*P*) of analysis of variance. Data were not transformed

Source	d.f.	Establishment (%)				Survival (%)			
		<i>Atriplex</i>		<i>Solidago</i>		<i>Atriplex</i>		<i>Solidago</i>	
		MS	<i>P</i>	MS	<i>P</i>	MS	<i>P</i>	MS	<i>P</i>
Site: S	1	174	0.143	2.24	0.186	338.3	0.322	75.9	0.153
Shoots: Sh	1	211	0.351	19.40	0.149	41.4	0.414	1.5	0.510
S \times Sh	1	80	0.311	1.10	0.347	23.9	0.789	1.5	0.833
Plot(S \times Sh): P(S \times Sh)	16	73	0.016	1.18	0.012	323.9	0.064	33.7	0.775
Litter: L	1	3075	0.109	23.98	0.072	468.5	0.533	22.7	0.519
P(S \times Sh) \times L	16	18	0.888	0.46	0.534	338.5	0.052	40.1	0.646
S \times L	1	92	0.038	0.31	0.420	577.6	0.210	25.6	0.436
Sh \times L	1	312	0.004*	3.12	0.040	0.8	< 0.001	0.0	0.445
S \times Sh \times L	1	5	0.606	0.01	0.871	0.0	1.000	0.0	1.000
Residual		32		0.49		174.7		48.4	
d.f. in residual		40		40		34		31	

*To increase the power of the test, the estimate of MS used in the denominator of the *F*-ratio is a pooled estimate from the MS of S \times Sh \times L, P(S \times Sh) \times L, and the residual, and then the effect of Sh \times L was tested with 1 and 47 d.f. (see Winer *et al.* 1991 for pooling procedures).

Table 5 Analyses of percentage establishment and percentage survival of *Atriplex* and *Solidago* in the presence or absence of shoots (and in the absence of litter in the *Phragmites* zone) in the *Juncus* and *Phragmites* zones at each of two sites. Results are estimates of mean squares (MS) and probability levels (*P*) of analysis of variance. Data were not transformed

Source	d.f.	Establishment (%)				Survival (%)			
		<i>Atriplex</i>		<i>Solidago</i>		<i>Atriplex</i>		<i>Solidago</i>	
		MS	<i>P</i>	MS	<i>P</i>	MS	<i>P</i>	MS	<i>P</i>
Site: S	1	616	0.010	59.8	0.018	2.6	0.863	163	0.022
Zone: Z	1	3497	0.176	243.5	0.329	16.4	0.849	222	0.493
Shoots: Sh	1	931	0.069	22.6	0.057	13.0	0.889	234	0.405
S × Z	1	281	0.074	78.7	0.008	278.6	0.083	213	0.010
S × Sh	1	11	0.717	0.2	0.892	419.8	0.036	128	0.041
Z × Sh	1	348	0.048*	3.3	0.452	219.7	0.142	181	0.493
S × Z × Sh	1	90	0.303	2.5	0.619	11.3	0.721	173	0.019
Residual		82		9.7		86.9		28	
d.f. in residual		32		32		31		31	

*To increase the power of the test, the estimate of MS used in the denominator of the *F*-ratio is a pooled estimate from the MS of the S × Z × Sh interaction and the residual, and then the effect of Z × Sh was tested with 1 and 33 d.f. (see Winer *et al.* 1991 for pooling procedures).

Table 6 Total number of *Atriplex* and *Solidago* (and total number with seeds) surviving until the end of the growing season in the presence (+L) or absence (–L) of litter and presence (+Sh) or absence (–Sh) of shoots in the *Juncus* and *Phragmites* zones at each of two sites. Mean (± SD) dry biomass (mg) per plant, total dry biomass for all plants (mg), mean (± SD) number of seeds per plant for plants producing seeds, and total number of seeds produced by all plants for *Atriplex* and *Solidago* surviving until the end of the growing season in both years at both sites

Forb and zone	Treatment		Plants				Biomass (mg)			Seeds		
	Litter	Shoots	Site 1	Site 2	Total	Total with seeds	Mean	SD	Total	Mean	SD	Total
<i>Atriplex</i>												
<i>Phragmites</i>	+L	+Sh	0	2	2	2	2071	850	4 142	178	57	356
	+L	–Sh	5	4	9	2	364	284	3 277	6	5	11
	–L	+Sh	1	0	1	1	460		460	42		42
	–L	–Sh	8	2	10	5	6838	15 625	68 383	892	1020	4461
<i>Juncus</i>		+Sh	1	0	1	0	24		24			
		–Sh	44	2	46	16	28	20	1 271	7	5	112
<i>Solidago</i>												
<i>Phragmites</i>	+L	+Sh	0	0	0							
	+L	–Sh	0	1	1		1		1			
	–L	+Sh	0	1	1		40		40			
	–L	–Sh	0	1	1		79		79			
<i>Juncus</i>		+Sh	4	0	4		3	2	11			
		–Sh	98	6	104		18	17	1 856			

at site 2 where few plants survived (Fig. 4, Table 5, SNK results for interaction between site, zone and shoots).

There was substantial variation in the size and reproductive output of individual plants (Table 6). Similar to the glasshouse study, however, *Atriplex* were significantly larger and produced significantly more seeds in the *Phragmites* zone than in the *Juncus* zone (Table 6, independent *t*-test using plants producing seeds for all treatments in the *Phragmites* zone and, to balance the design, for 10 randomly selected plants from the *Juncus* zone: biomass, $t = 4.8$, $P < 0.001$, $n = 10$; seeds, $t = 3.0$, $P = 0.008$, $n = 10$; all data were ln-transformed). The largest plants for either species occurred where both litter and shoots had been removed in the *Phragmites* zone. For *Atriplex*, the largest individual had 5980 leaves, a dry biomass of 50.4 g, and produced 2541 seeds.

Discussion

Abundances of the two study forbs and marsh turf generally decreased as the abundance of shoots and litter of *Phragmites* increased within the marsh, suggesting that *Phragmites* is displacing forbs and marsh vegetation. Investigations demonstrated that *Phragmites* limits the abundance of *Atriplex* and *Solidago* through competitive interactions that affect fundamental demographic processes at multiple life-history stages of the forbs. The supply of seeds and establishment of seedlings were dramatically reduced within stands of *Phragmites* compared with areas of the high marsh dominated by *Juncus*, but the post-recruitment environment within stands of *Phragmites* imposes the most severe constraints on these forbs. The influence of litter and shoots of *Phragmites*, rather than changes to the soil associated with

the invasion of *Phragmites*, appear to be the dominant means by which *Phragmites* competitively excludes forbs from this coastal brackish marsh. Both species of forbs followed the same patterns of abundance and responded in the same way to manipulations, suggesting that the results here may be generally applicable to the suite of forbs in coastal marshes threatened by this invader.

DISPERSAL LIMITATION

The patterns of dispersal and seed supply paralleled those of the adult forbs, with a dramatic reduction in the number of seeds within stands of *Phragmites* only metres away from source populations of *Atriplex* and *Solidago*. The decline in the density of trapped seeds from the *Juncus* to the *Phragmites* zone might reflect the increasing distance to source populations of forbs or an enhanced physical barrier to dispersal as *Phragmites* shoots became more dense from the edge to the back of the stands. Extremely localized dispersal of seeds is a more likely explanation because another study examining the dispersal of the same species of forbs in a salt marsh unobstructed by *Phragmites* also found that the majority of seeds dispersed very short distances (Rand 2000). Moreover, we observed at one site that seeds from nearby *Solidago* only metres away on the other side of the tidal creek could penetrate the densest part of the stand. Regardless of the exact explanation, these patterns indicate that, as *Phragmites* stands increase in area and exclude source populations of adult forbs, dispersal and seed supply of forbs into these stands will become increasingly limited. The maintenance of local populations of forbs through a seed bank is unlikely. We observed the potential for a limited seed bank as forbs emerged in the year following seed addition, but after 2 years seeds were exhausted (see also Rand 2000). Moreover, apart from where we added seeds, seedlings were not found within stands of *Phragmites*. Dispersal or seed limitation is thus an important process precluding the recruitment of forbs within stands of *Phragmites*.

ESTABLISHMENT LIMITATION

Supplying seeds dramatically increased the density of seedlings of *Atriplex* and *Solidago* within stands of *Phragmites*, substantiating the hypothesis that dispersal can limit forb abundance. Forbs seeded in *Phragmites* and *Juncus* soil under benign conditions of freshwater and abundant sunlight in the glasshouse established with similar success, demonstrating that the soil *per se* (i.e. finer sediments, reduced macro-organic component) within stands of *Phragmites* does not directly limit recruitment of *Atriplex* or *Solidago*. In contrast to the glasshouse results, when we removed the above-ground biotic influences of litter and shoots in the field, *Atriplex* and *Solidago* established more successfully in the *Juncus* than in the *Phragmites* zone. This suggests that the physico-chemical conditions of the soil associated with tidal influences

within stands of *Phragmites* limit the establishment of forbs compared with *Juncus*-dominated areas of the marsh not invaded by *Phragmites*. Rand (2000) found that these same species of forbs establish more successfully at higher than at lower tidal elevations of the marsh, where there is greater soil oxygen availability (see also Windham & Lathrop 1999). Redox potentials and establishment success of both species were greater in the *Juncus* zone at site 1 than in the *Phragmites* zone at site 1 and the *Juncus* zone at site 2, which is consistent with the results of Rand (2000). In contrast, the *Juncus* zone at site 2 was at a lower tidal elevation and had lower redox potentials than the other zones, but seedlings of both forbs still established more successfully in this zone than in both the *Phragmites* zones. Oxygen availability alone therefore cannot account for all the differences in establishment success of forbs between the *Juncus* and *Phragmites* zones, but it is probably one of several important edaphic conditions. Sedimentation rate was substantially greater in the *Phragmites* than in the *Juncus* zone, which is also a possible explanation for the reduced establishment of forbs within stands of *Phragmites*.

Within stands of *Phragmites*, shoots and, particularly, litter dramatically reduced the establishment of both forb species, with their combination having the greatest negative effect. Litter reduced the transmittance of light, but only to the same degree as the presence of shoots in the absence of litter, indicating that its influence on establishment is not only through shading. The negative impact of litter on the establishment of plants is multifaceted (see Facelli & Pickett 1991; Minchinton 2002a), but it is likely that litter suspended by the tides simply rips out or smothers fragile, recently established seedlings.

Floating plant litter, or wrack, is common in these coastal marshes (primarily the grass *S. alterniflora*, but also *Phragmites*), and forbs commonly find refuge in bare patches that are generated where wrack stranded in the open marsh smothers native marsh turf, but is subsequently removed by the tides (Bertness & Ellison 1987; Ellison 1987; Brewer *et al.* 1997; Minchinton 2002a). The residency time of litter within stands of *Phragmites* appears to be much longer than that which typically produces bare patches in the open marsh, and few plants establish in the marsh where wrack remains in place (e.g. Minchinton 2002a). Within stands, the shoots of *Phragmites*, which die annually but may remain upright for several years, trap the litter and, consequently, much of it remains there until it decomposes. Therefore, although seasonal wrack deposition in the open marsh may have a positive effect on forbs by providing habitat refuges in bare patches, the continual presence of litter within stands of *Phragmites* has a negative impact on the colonization of forbs similar to the chronic stranding of wrack in the open marsh (Minchinton 2002a). The supply and retention of a continual cover of litter on the substratum is likely to be a primary mechanism by which *Phragmites* excludes forbs.

In the absence of litter, the presence of shoots within stands of *Phragmites* had a negative influence on the

establishment of forbs. This effect of shoots on establishment was not as evident where shoots had been removed in the *Juncus* zone, even though there was a similar reduction in the availability of light (see also Rand 2000). Therefore, environmental conditions during establishment, such as sedimentation and the presence of litter and shoots, place another constraint on the recruitment of forbs after the arrival of seeds within *Phragmites* stands.

SURVIVAL LIMITATION

Although the dispersal of seeds and establishment of seedlings limited the abundance of forbs growing within stands of *Phragmites*, further severe constraints on survival occurred once seedlings had become established, and few seedlings survived to the end of the growing season. In the absence of litter, mortality of established forbs between zones and sites was linked to soil oxygen availability, with the waterlogged *Juncus* zone at site 2 showing the greatest mortality of seedlings and the lowest redox potentials. Similarly, Rand (2000) found increasing mortality of these forbs with decreasing tidal elevation and redox levels. The *Phragmites* and *Juncus* zones at site 1 were at similar tidal elevations, yet the *Phragmites* zone had lower redox potentials, indicating that *Phragmites* may reduce the survival of forbs through limitations on soil oxygen availability. More studies measuring soil redox potentials in different marsh vegetation types at equivalent tidal levels are needed, however, to validate this conclusion, which is based on a single comparison between two zones.

Although litter impeded the establishment of seedlings in stands of *Phragmites*, once forbs became established they appeared to survive equally well in areas with or without litter. Because so few individuals survived, however, these results should be viewed tentatively. One clear effect on survival was that seedlings of both species survived better where shoots of *Phragmites* (in the absence of litter) or marsh turf had been removed (see also Rand 2000). Similar to the establishment of seedlings, shoots of *Phragmites* and *Juncus* probably reduce survivorship by shading the forbs. Interestingly, *Atriplex* within stands of *Phragmites* was able to survive and reproduce in areas with litter and shoots, highlighting the importance of microhabitats as temporary refuges within stands of *Phragmites*.

Despite fewer forbs surviving within stands of *Phragmites* compared with the *Juncus* zone, individuals of both species grew substantially larger and, for *Atriplex*, more than twice as many individuals became reproductive, and these produced on average two orders of magnitude more seeds. For both species, individuals grew largest and produced the most seeds in the absence of litter and competing shoots. These results are identical to those in the glasshouse, providing further evidence that *Phragmites* soil might be better for the growth of forbs than *Juncus* soil. Either *Phragmites* soil contains

more nutrient resources or the lower biomass of roots and rhizomes reduces below-ground competition for limiting resources in the immediate environment.

INVASION OF *PHRAGMITES* AND THE EXCLUSION OF COASTAL MARSH PLANTS

The field experiments of Minchinton & Bertness (2003) have documented that *Phragmites* can out-compete the dominant grasses and rushes comprising the marsh turf in only a couple of years (see also Burdick & Konisky 2003). This study has demonstrated that *Phragmites* is also a superior competitor to two species of forbs and that the continued invasion of *Phragmites* is likely to result in the exclusion of local populations from coastal brackish and salt marshes of southern New England, USA, with the possibility of local extinctions of vulnerable species. As for invasive plant species in terrestrial communities (Levine *et al.* 2003; Vilà & Weiner 2004), exclusion of coastal marsh forbs by *Phragmites* appears to occur through competitive processes, particularly the impacts of shoots and their eventual breakdown into litter. The performance of invasive plants in terrestrial habitats is typically increased under disturbed conditions, enhancing their competitive advantage over natives (Daehler 2003). With increased production of *Phragmites* under elevated nutrient loads (see Minchinton & Bertness 2003) and the continued urbanization of estuaries, *Phragmites* is expected to become a stronger competitor, displacing resident marsh plants at an accelerated rate.

Although it may be simple to assume that large and dominant invasive species, such as *Phragmites*, competitively exclude smaller plants by overgrowing them, results here demonstrate that this is only one mechanism. Production and retention of *Phragmites* litter and, perhaps, increased sedimentation may limit the abundance of forbs even in the absence of shoots. Importantly, *Phragmites* is a particularly successful invader because it engineers the marsh habitat, modifying both the abiotic and biotic environments in diverse ways and reducing forb populations by limiting demographic processes across multiple stages of their life history. Understanding the key mechanisms by which invasive species exclude natives and determining the life-history stage most sensitive to invasion will allow managers to target their conservation and restoration efforts in the control of invasive species.

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