Ecological Applications, 10(4), 2000, pp. 1110–1118

CLONAL INTEGRATION AND THE EXPANSION OF *PHRAGMITES AUSTRALIS*

LINDSAY AMSBERRY, MICHAEL A. BAKER, PATRICK J. EWANCHUK, AND MARK D. BERTNESS[1]

Department of Ecology and Evolutionary Biology, Brown University, Providence, Rhode Island 02912 USA

Abstract. The recent expansion of the reed *Phragmites australis* in western Atlantic salt marshes has become a conservation concern. Historically, *Phragmites* was restricted to the terrestrial border of marshes, but now it aggressively invades lower elevations. To explore factors influencing this expansion, we examined (1) the effects of physical factors and competitive interactions on the performance of *Phragmites* and (2) the role of clonal integration on the ability of *Phragmites* to invade low marsh habitats.

We transplanted *Phragmites* into vegetation along an elevation gradient, with and without neighboring plants. *Phragmites* died when transplanted to the lowest marsh zone but survived and expanded in higher marsh zones. This suggests that the low oxygen availability characteristic of waterlogged soils limits *Phragmites* growth in the low marsh. Neighboring vegetation reduced *Phragmites* growth in all zones, and severing *Phragmites* rhizomes invading the low marsh reduced the survivorship and photosynthetic rate of ramets.

These results suggest that *Phragmites* may invade low marsh habitats by initially establishing itself in the high marsh and then expanding into lower, less favorable habitats using clonal integration. This has important implications for understanding the changing dynamics of New England salt marsh plant communities and developing management strategies for the control of *Phragmites*.

Key words: clonal integration; New England salt marshes; Phragmites australis; *physiological stress; salt marsh ecology.*

INTRODUCTION

Understanding the biotic and abiotic forces that maintain species borders has long been one of the central goals of ecology. In New England, the clonal plants that dominate salt marshes have striking and characteristic patterns of zonation that follow tidal elevation and physical gradients (Niering and Warren 1980, Bertness and Ellison 1987, Bertness 1992, 1999). Physical gradients in salinity (Adam 1995) and oxygen (Howes et al. 1981, 1986) have long been thought to be responsible for the plant zonation patterns observed in marshes. Recently, however, plant species borders in salt marshes have also been shown to also be influenced by interspecific competition (Bertness 1991*a, b*, Levine et al. 1998). In a number of studies the lower elevational limits of marsh plants have been shown to be set by abiotic stresses associated with waterlogged soils, whereas the high elevational limits have been shown to be set by interspecific competition (Bertness 1991*a, b*, Levine et al. 1998). Over the last few decades, however, the plant zonation patterns that have historically characterized New England salt marshes have begun to be disrupted by the invasion of the common reed *Phragmites australis* (Cav.) Trin. ex Steud (formerly *Phragmites communis*). Invasive species often change the species distributions and diversity of native species (Mack 1986), and the expansion of *Phragmites* in New England marshes is dramatically changing these habitats (Buck 1995).

The common reed, *Phragmites australis* (hereafter referred to by its generic name), has been a natural component of brackish New England wetlands for at least 3000 years (Niering and Warren 1977). Historically, *Phragmites* was confined to high marsh habitats with low soil salinities and high soil oxygen levels. In the last twenty years, however, *Phragmites* has been invading low marsh habitats characterized by higher soil salinities and anoxic soils (Marks et al. 1994). This expansion of a large clonally propagating reed into the low marsh has reduced the distribution and abundance of native angiosperms (Phillips 1987, Marks et al. 1994, Buck 1995), and may eliminate vital habitat for fish, birds, and various invertebrates (Buck 1995, Baker 1996). The large impact that *Phragmites* has on marsh habitats is due to its influence as an ecosystem engineer (sensu Jones et al. 1994) or habitat-modifying organism. While only anecdotally documented (Dreyer and Niering 1995, Buck 1995), invasion of low marsh habitats by the robust aboveground and belowground growth of *Phragmites* appears to enhance sedimentation by slowing water flow (Orth 1977, Gambi et al. 1990, Irlandi and Peterson 1991), minimize low marsh sediment erosion, and wick water from marsh sediments by transpiration and passive evaporation, lowering the water table (Amsberry 1997).

The cause of the current expansion of *Phragmites* in

Manuscript received 19 January 1999; revised 26 July 1999; accepted 16 August 1999.

[1] Corresponding author: E-mail: Mark_Bertness@brown.edu.

western Atlantic marshes has been widely thought to be anthropogenic modification of marsh habitats (Mook and van der Toorn 1982, Roman et al. 1984, Phillips 1987, Marks et al. 1994). Human changes such as tidal restrictions which lower marsh soil salinities, runoff from lawns and farms which can increase marsh nutrient supply, and ditch-digging for mosquito control which can lower the water table and lead to less anoxic soils all can create a more favorable environment for *Phragmites* (Weisner and Graneli 1989, Marks et al. 1994). Suggestions for the control of *Phragmites* expansion based on these causes have included flooding or increasing the salinity of marshes being invaded by *Phragmites*, to make physical conditions too severe for it to persist (van der Toorn and Mook 1982, Thompson and Shay 1985, Marks et al. 1994). Studies, however, have not examined the mechanism by which *Phragmites* is able to spread into lower intertidal zones.

It is this mechanism that is the focus of the present study. We hypothesize that clonal integration may play a crucial role in the success of *Phragmites* invading historically unfavorable habitats. We base this hypothesis on our observations that *Phragmites* always recruits to New England salt marshes on their terrestrial borders and then, once established, clonally moves to lower, more physically stressful habitats by vegetative expansion. We have never seen the reverse colonization sequence, initial colonization of *Phragmites* into low marsh habitats in New England salt marshes by seeds or rhizome fragments, with the subsequent vegetative spread to higher elevations. These observations suggest that clonal integration or the physiological support of *Phragmites* ramets invading low marsh habitats may be necessary for *Phragmites* to invade low marsh habitats. We suggest that the clonal morphology of *Phragmites* may give it the ability to colonize habitats it is unable to invade directly with seeds or rhizome fragments.

Physiological integration among connected ramets within a clone has been described in many clonal organisms (Pitelka and Ashmun 1985, Abrahamson et al. 1991, Alpert 1991, Caraco and Kelly 1991). In a number of species, clonal integration allows clonal organisms to invade physically harsh habitats where they are unable to establish from seed (Hartnett and Bazazz 1983, Evans and Whitney 1992, Pennings and Callaway 1999). Physiological integration has previously been suggested to be important in the colonization ability of *Phragmites* (Hara et al. 1993, Baker 1996), but the role of clonal integration in the invasion by *Phragmites* of low marsh habitats has not been experimentally examined.

Our study addresses two simple questions about the expansion of *Phragmites*: (1) What is the effect of physical stresses and interspecific competition on the survivorship and expansion of *Phragmites* across New England marsh tidal gradients? and (2) Does physiological integration of *Phragmites* allow it to invade physically stressful habitats that it may be unable to invade otherwise?

METHODS

Study species

Phragmites is a clonal reed that grows from perennial underground rhizomes 0.2–0.5 m belowground. Studies by Haslam (1969*a, b, c,* 1970, 1972) describe the basic phenology of *Phragmites. Phragmites* sends up new ramets every year, although dead ramets remain standing for 1–2 years (Haslam 1969*b*). A ramet is defined as a modular unit of the clone, i.e., a vertical shoot and associated root that comprise a potentially self-sufficient unit. *Phragmites* has a phalanx clonal growth morphology (sensu Lovett-Doust 1981) where clonal expansion occurs as a dense front of roots, rhizomes and aboveground tillers. In expanding clones of *Phragmites*, belowground rhizomes spread horizontally ~1.0–1.5 m every year. Aboveground ramets are generally 1.5–5.0 m in height, and final height is highly correlated with emerging bud width (Haslam 1969*a*). In New England, buds generally appear in May, with growth occurring throughout the summer, and flowering occurring mostly in September. *Phragmites* grows optimally in fresh and brackish water with salinities of under 20 parts per thousand (Roman et al. 1984, Hellings and Gallagher 1992).

Study sites

Our experiments were conducted at the Adolf Rotundo Wildlife Sanctuary on the Palmer River, Rehoboth, Massachusetts, and at Rumstick Cove, Barrington, Rhode Island. The Palmer River site is a brackish marsh typically exposed to ambient water salinities less than 15 parts per thousand (ppt). The Rumstick Cove site borders Narragansett Bay and is subject to water with a higher salinity (20–30 ppt). Marshes at both sites have plant zonation typical of southern New England salt marshes (see Bertness 1992). At both sites a dense monoculture of the cordgrass *Spartina alterniflora* dominates low marsh habitats that are flooded daily by tides. The seaward border of the high marsh, the marsh area not daily flooded by tides, is dominated by dense clonal stands of the marsh hay, *Spartina patens*, while the terrestrial border of the high marsh is dominated by a dense cover of the black rush, *Juncus gerardi.* The Palmer River site also has vegetation characteristic of less saline marshes. In particular, stands of cattails, *Typha latifolia*, one of the clonal plants that dominate freshwater wetlands in North America, are common at lower elevations at the Palmer River. Cattail stands are not found at Rumstick Cove, presumably because of higher soil salinities. At both sites, large (>100 m^2) clones of *Phragmites* are common on the terrestrial border of the marsh, and many of them are currently expanding into the low marsh.

Transplant experiment

To test the effects of tidal elevation and interspecific competition between *Phragmites* and the dominant marsh species on *Phragmites* performance, transplants of *Phragmites* were moved into four marsh vegetation zones. From the seaward edge to the terrestrial border of the marsh, transplants were moved into the *Spartina alterniflora*, *Typha latifolia*, *Spartina patens*, and *Juncus gerardi* zones, respectively. Our transplant experiments were initiated at the Palmer River site in June 1995. As transplant material we used clusters of 2–5 shoots, 30–50 cm tall, expanding from the edge of a single large, mature clone of *Phragmites* in the *Juncus* zone. All transplants were taken from the same intact clone to minimize genetic differences among transplants, since there are potential genotypic differences between clones, even under similar conditions (Daniels 1991). Each transplant unit consisted of a turf plug ~30 cm in diameter and 30–40 cm deep, containing intact ramets and rhizomes.

Five blocks of four transplants each were placed in each zone, for a total of 20 transplants per zone. Two of each of the four transplants in each block were randomly assigned to neighbor-removal or control treatments. For neighbor-removal treatments, neighboring plants were clipped with shears to a radius equal to their height, to reduce shading and aboveground competition. Litter was left on the ground to prevent salt accumulation in the bare area produced by clipping (Shumway and Bertness 1992). Neighbor-removal treatments were maintained by reclipping every other week throughout the course of the experiment. For the full-competition controls, neighbors were left unmanipulated.

To control for the transplanting procedure itself, two additional types of plots were established and monitored. Twenty similar patches of 2–5 ramets on the edge of the *Phragmites* source clone were located. Half of these were used to control for the effect of cutting and moving transplants ("cut controls"). These transplants were severed from the clone edge as above, removed, and then replaced. The other half, "uncut controls," were marked and then left ummanipulated. As with the neighbor-manipulation transplants among zones, the cut controls and uncut controls were also laid out in five blocks of four plots including with- and without-neighbor treatments.

All transplants were maintained for two years and censused monthly for ramet densities during the growing season in 1995 and 1996. To quantify aboveground expansion, the horizontal distance between the initial shoots from 1995 and the furthest new shoot produced in 1996 was measured (hereafter called expansion).

Rhizome-severing experiment

To test the effect of clonal integration among ramets on the ability of *Phragmites* to invade low marsh habitats, we compared the performance of experimentally severed and unsevered rhizomes invading high and low marsh habitats. We reasoned that if clonal integration was critical for the invasion of more waterlogged, low marsh soils, severing clonal connections should have a greater adverse influence on ramets invading low marsh habitats than it would on those invading high marsh habitats. This experiment was done at both Rumstick Cove and Palmer River, in each case on a high marsh clone that was invading the low marsh.

In early June 1996, at both study sites, 20 *Phragmites* runners (rhizomes) invading low and 20 runners invading high marsh habitats were marked on the leading edges of the clone. Marked runners consisted of a discrete group of 2–4 young ramets clearly expanding from the mother clone on a single belowground rhizome. We excavated a number of these runners before selecting the runners we used, until we were convinced that we could differentiate invading ramets (young ramets expanding out from the established clone) from older, established ramets. Half of the runners in each zone were then randomly chosen to be severed with a knife, isolating invading ramets from their neighbors in the mother clone.

All marked ramets were censused once before severing and subsequently censused biweekly for survival of the originally marked ramets and total number of ramets produced/replicated until the end of August 1996. Photosynthetic rates (μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$) of one randomly chosen ramet/replicate were also measured four times over the course of the study with a portable infrared gas analyzer (Analytical Development Company Limited, model ADC-LCA-2, London, UK). Measurements were made between 1000 and 1400 on sunny, cloudless days. Since photosynthesis rates were virtually identical on all four of the days that we made these measurements, only data from one day will be presented. At the end of this experiment we excavated all experimental runners to insure that our severing had isolated invading ramets from their clonemates in dense vegetation.

To quantify edaphic conditions in the rhizome-severing experiment, soil salinity and redox potential were measured in the soil adjacent to each experimental ramet in both the habitat being invaded (either high or low marsh) and in the dense vegetation of the mother clone. These latter measurements were taken 50 cm into the dense vegetation of the mother clone. Soil salinity was quantified by removing a 2-cm^3 plug, squeezing pore water through cotton gauze, and measuring salinity with a refractometer (accuracy ± 1.0 mg/g). Soil redox potential was measured by removing a plug of soil (1 cm diameter × 5 cm deep) and inserting a redox electrode into the hole (Orian Research, Boston, Massachusetts).

Statistical analyses

For the transplant experiment, unmanipulated controls were initially compared to cut controls using AN-

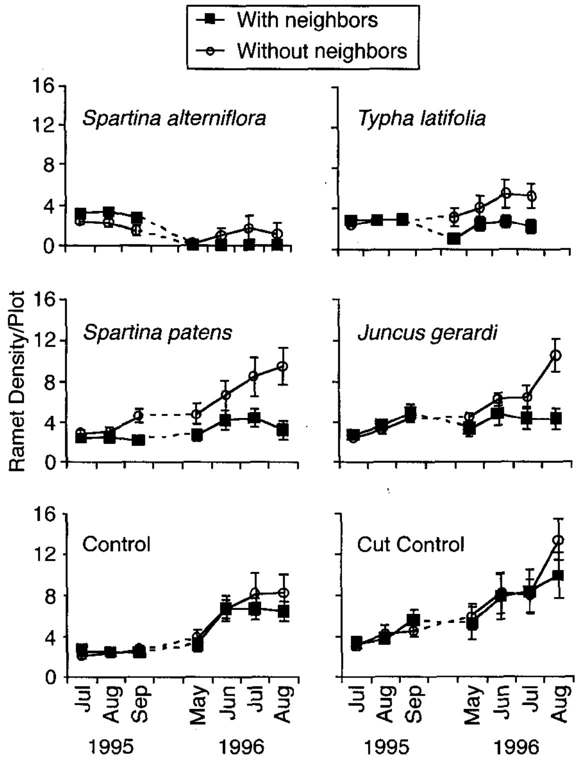

FIG. 1. Ramet densities in the *Phragmites* transplant experiment over both years and in all zones. Points represent means (± 1 SE) for 10 plots in each vegetation zone with and without neighbors.

OVA to determine any effects of transplantation. Since all main effects and interactions for tiller densities and spread were statistically insignificant ($P > 0.05$), revealing that cutting and transplantation did not influence the plant variables we were measuring, results of the transplant experiment were subsequently analyzed without including controls, using a three-way ANOVA (zone × competition treatment × block) with nested effects. One block in the *S. alterniflora* zone was lost due to winter ice disturbance and thus was eliminated from the analysis. For the analyses and figures, plots with no shoots were scored as zero for spread.

For the rhizome-severing experiment, ramet survivorship and photosynthetic rate data were analyzed with a three-way (site × severing treatment × zone) ANOVA. Changes in shoot number data were analyzed with a three-way (site × severing treatment × zone) ANCOVA, with initial shoot number as a covariate. Four replicates were eliminated from these analyses, since we discovered after the experiment that the runners had been not completely severed. Salinities and redox potentials were analyzed by a two-way (site × zone) ANOVA. All data were transformed as necessary to meet the assumptions of ANOVA.

RESULTS

Transplant experiments

Shoot densities of the *Phragmites* transplants varied significantly with marsh zone and the presence or absence of neighbors, but the effect of neighbors on shoot densities did not vary with marsh zone (Fig. 1, Table 1). Transplant shoot densities were lowest in the low marsh habitats that are daily flooded by tides. After two growing seasons, no transplant shoots survived in the *Spartina alterniflora* zone when neighbors were present, and very few survived in the *Spartina alterniflora* zone even when neighbors were removed (Fig. 1). Transplant shoot densities also remained relatively low in low marsh *Typha* stands. In contrast to the poor performance of *Phragmites* transplanted to low marsh habitats, the shoot densities of *Phragmites* transplanted to high marsh habitats without neighbors increased markedly (Fig. 1). In both the *Spartina patens* and *Juncus gerardi* zones, shoot densities after two growing seasons were 2–5 times higher than those in the low marsh transplants, and removing high marsh neighbors increased transplant shoot densities by a factor of 2–4.

The horizontal expansion of *Phragmites* from the original transplants varied significantly with marsh zone, with a strong trend for neighbors to inhibit expansion (Fig. 2, Table 1). The effect of neighbors on the horizontal expansion of *Phragmites* shoots did not, however, vary with marsh zone (Fig. 2, Table 1). The least horizontal expansion was seen in the low marsh *Spartina alterniflora* zone, where expansion was less than 5 cm. In contrast, in high marsh habitats, horizontal expansion from the original transplant was >30 cm in both the *Spartina patens* and *Juncus gerardi* zones when neighbors where removed.

Rhizome-severing experiments

Severing *Phragmites* rhizomes that were vegetatively spreading from established stands lowered the sur-

TABLE 1. Three-way ANOVA with nested effects to test the effect of zone and competition treatment on transplant shoot density and shoot expansion.

	Shoot density			Expansion		
Source of variation	df	*F*	*P*	df	*F*	*P*
Zone	4, 15	5.16	0.01	4, 15	12.34	0.01
Competition	1, 15	13.86	0.01	1, 15	3.76	0.07
Zone × Competition	4, 15	1.19	0.35	4, 15	1.46	0.26
Competition × Block [Zone]	15, 40	0.62	0.84	15, 40	0.69	0.78
Block [Zone]	15, 40	1.37	0.21	15, 40	0.84	0.63

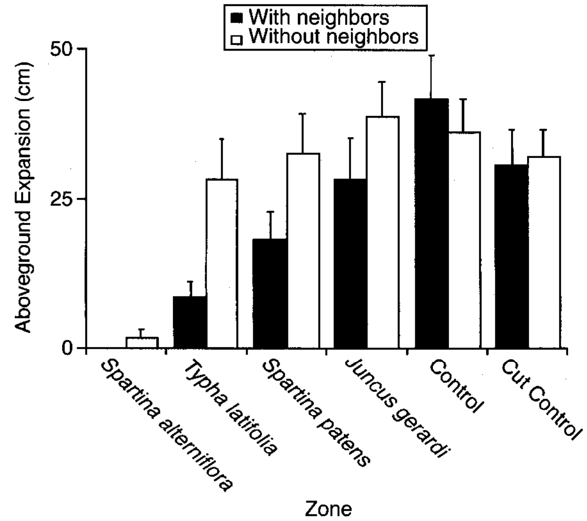

FIG. 2. Aboveground horizontal expansion (cm) in the transplant experiment. Measurements were made from the initial shoots transplanted in May 1995 to the farthest distance shoots had moved from the transplants in August 1996. Bars show means + 1 SE.

vivorship of physiologically isolated ramets, particularly those invading the low marsh (Fig. 3A, Table 2). Severing effects on ramet survivorship, however, were much stronger at Rumstick Cove than at Palmer River (Fig. 3A, Table 2). At Rumstick Cove, severing rhizomes invading the low marsh led to <45% survivorship of isolated ramets, whereas at Palmer River, severed-ramet survivorship in the low marsh was nearly 80%. At both sites severing rhizomes invading the high marsh had little effect on the survivorship of isolated ramets (Fig. 3A).

Severing rhizomes also had strong effects on *Phragmites* shoot production that differed significantly between sites and zones (Fig. 3B, Table 2). At Palmer River, severing increased the shoot production of isolated ramets, particularly ramets invading the high marsh (Fig. 3B). Increased shoot production of severed ramets probably reflects allocation of resources into

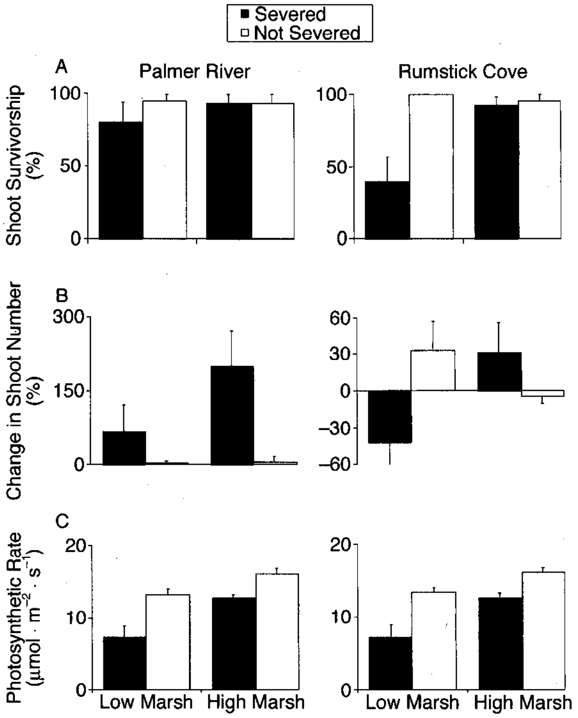

FIG. 3. (A) Survivorship of marked shoots in the rhizome-severing experiment. (B) Percentage change in total shoot number/rhizome replicate in the rhizome-severing experiment. (C) Photosynthetic rate of severed and unsevered ramets in the rhizome-severing experiment. All bars show means + 1 SE.

shoots rather than rhizomes, once rhizome connections had been lost. In contrast to Palmer River, at Rumstick Cove, severing increased the shoot production of rhizomes invading the high marsh, but not in the low marsh where total shoot numbers declined, reflecting a net loss of shoots due to shoot mortality.

Severing rhizomes also significantly affected the photosynthetic rate of severed ramets, particularly those invading the low marsh (Fig. 3C, Table 2). Severing lowered the photosynthetic rate of isolated ramets

TABLE 2. Two-way ANOVA for Palmer River and Rumstick Cove testing the effects of zone and severing on ramet survivorship, shoot number, and photosynthetic rate at the conclusion of the rhizome-severing experiment in August 1996.

Source of variation	Survivorship			Percentage change in shoot number			Photosynthetic rate		
	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*
Palmer River									
Zone	1, 20	0.49	0.52	1, 20	2.06	0.16	1, 20	19.46	0.01
Severing	1, 20	0.80	0.38	1, 20	7.57	0.01	1, 20	25.56	0.01
Zone × Severing	3, 40	0.80	0.38	3, 40	1.98	0.17	3, 40	2.18	0.15
Rumstick Cove									
Zone	1, 20	7.66	0.01	1, 20	0.63	0.43	1, 20	1.81	0.19
Severing	1, 20	13.7	0.01	1, 20	0.76	0.39	1, 20	19.44	0.01
Zone × Severing	3, 40	11.1	0.01	3, 40	6.44	0.02	3, 40	4.55	0.04

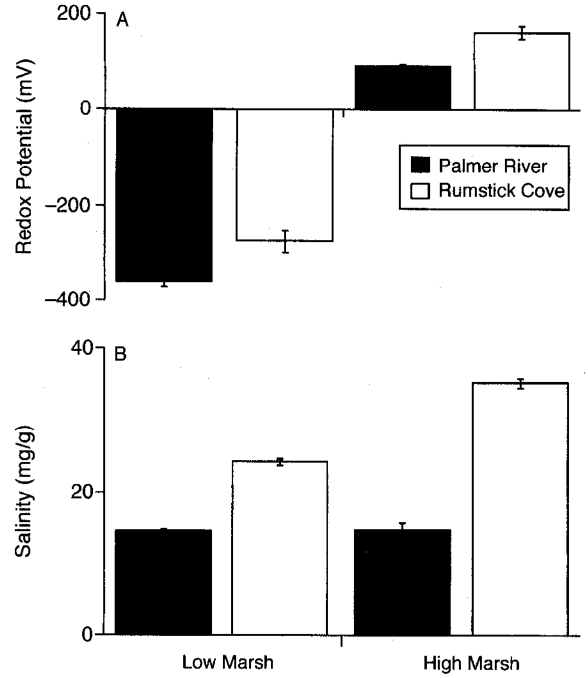

FIG. 4. (A) Soil salinity (mg/g) and (B) soil redox potential (mV) in low and high marsh habitats adjacent to severed and unsevered ramets in the rhizome severing experiment at the Palmer River and Rumstick Cove study sites. Bars show means ± 1 SE.

at both study sites and at both high and low marsh elevations, but the reduction in photosynthesis of isolated ramets was nearly twice as severe for ramets invading the low marsh as it was for ramets invading the high marsh (Fig. 3C).

At both sites, the low marsh habitat was characterized by highly anoxic (low redox potential) soils, while the high marsh was characterized by oxidized (high redox potential) soils (Fig. 4, ANOVA: zone, $P < 0.001$; site, $P < 0.001$; zone × site, $P < 0.001$). Soil salinities, however, were much higher at Rumstick Cove than at Palmer River (Fig. 4, ANOVA: zone, $P < 0.001$; site, $P < 0.001$; zone × site, $P < 0.001$). Thus, while ramets invading low marsh habitats at both sites encounter anoxic soils, at Rumstick Cove ramets invading low marsh habitats encounter anoxic soils that are much more saline.

DISCUSSION

Our results show that the harsh edaphic conditions typically found at low marsh elevations can potentially limit the performance and colonization of *Phragmites*, but that *Phragmites* can invade harsh low marsh habitats with the aid of clonal integration where ramets colonizing physiologically harsh habitats are supported by ramets in more physically benign habitats. Our results also show that competition with the dense clonal vegetation that typically dominates New England salt marshes limits the clonal spread of *Phragmites*. These results enhance our mechanistic understanding of the current expansion of *Phragmites* in New England marshes and provide insight that may be valuable in designing *Phragmites* control strategies.

Transplant experiments

Our transplant experiments demonstrate that, like the halophytic plants that are found in marsh habitats (Snow and Vince 1984, Bertness and Ellison 1987, Bertness 1991*a*, *b*, Bertness et al. 1992*a*), the success of *Phragmites* in marshes is limited at low elevations by physical stress. In New England where the plant zonation of salt marshes has been intensively studied, all of the numerically dominant zone-forming plants have lower intertidal borders that are set by their inability to deal with harsh lower intertidal physical conditions, whereas high intertidal borders are maintained by competition from competitively superior plants at higher elevations (Bertness 1999). The physical factor usually thought to limit plant success at low marsh elevations is low soil oxygen levels (Howes et al. 1981, 1986), but our results suggest that soil salinity may interact with waterlogging to limit plants from colonizing the low marsh. Low marsh soils are often saturated with water, and in waterlogged soils, oxygen depletion by microorganisms and root respiration, and the low diffusion of oxygen commonly leads to anoxic soil conditions. Our transplant experiment also showed that interspecific competition from neighboring plants can inhibit the growth and expansion of *Phragmites* (Figs. 1 and 2).

Rhizome-severing experiment

The failure of the *Phragmites* transplants to establish in the *Spartina alterniflora* zone suggests that the success of *Phragmites* in the low marsh can be limited by harsh physical conditions found there, and implies that recruitment of *Phragmites* to the low marsh by seeds or clonal fragments may be limited. If this is the case, how is *Phragmites* currently invading low marsh habitats in New England? One potential explanation for the successful colonization of physically harsh low marsh habitats by *Phragmites* is vegetative colonization aided by clonal integration. The rhizome-severing experiment examined this possibility.

Results of the rhizome-severing experiment support the hypothesis that clonal expansion of *Phragmites* into low marsh habitats is aided by clonal integration, but also suggest that the dependency of rhizomes invading low marsh habitats on clonemates in the high marsh varies among marshes. At Rumstick Cove, where low marsh soils are both anoxic and highly saline (Fig. 4), severing rhizomes lowered the survivorship, growth, and photosynthetic rate of ramets invading the low marsh (Fig. 3). Moreover, at Rumstick Cove severing rhizomes differentially affected ramets invading low and high marsh habitats. Rhizome severing had much more pronounced effects on ramets invading the low marsh than on ramets invading the high marsh, suggesting that clonal integration is important in supporting ramets invading physically harsh habitats, but not in physically benign habitats. At Palmer River the results of severing were much less pronounced. Severing rhizomes did not influence ramet survivorship at the Palmer River site, and the effects of severing on shoot production and photosynthesis were not as marked as at Rumstick Cove. These site differences in the response of rhizomes to severing may reflect differences in physical stresses between the sites. Clonal integration may be more critical for the invasion of *Phragmites* into the low marsh at Rumstick Cove than at the Palmer River because higher soil salinities at Rumstick Cove make invading the low marsh more difficult. However, without examining site difference in the relative importance of clonal integration, our data are insufficient to make about the ability of *Phragmites* to colonize low marsh habitats.

Implications for marsh conservation

The invasion of *Phragmites* into low marsh habitats on the east coast of North America, where it has traditionally been absent, is a current conservation concern. *Phragmites* has been a member of New England marsh communities for thousands of years, but its expansion from high to low marsh habitats has largely occurred over the past three decades (Niering and Warren 1980). This range expansion is of concern because it is thought to be due to anthropogenic causes, is resulting in a loss of marsh plant diversity, and is potentially reducing the value of marshes as nursery grounds for estuarine populations (Phillips 1987, Marks et al. 1994, Buck 1995, Baker 1996). While our results do not explain what is driving the current expansion of the range of *Phragmites*, they elucidate potential physical constraints on the spread of *Phragmites* and suggest that clonal integration and disturbance are important in the ability of *Phragmites* to expand into low marsh habitats.

The ultimate cause of the expansion of *Phragmites* is likely due to a variety of human-induced changes in coastal habitats acting synergistically, rather than a single proximate cause. Lower soil salinities have been suggested as a common cause for the spread of *Phragmites* into salt marsh habitats (Roman et al. 1984). Restricting tidal exchange in salt marshes due to road construction, and shoreline development that removes terrestrial vegetation surrounding marshes, increasing freshwater runoff, can both reduce soil salinities (Niering and Warren 1977, Dreyer and Niering 1995). Draining and ditching marshes can also increase *Phragmites* invasion by lowering the water table and limiting the development of low marsh anoxic soil conditions (Bertness et al. 1992*b*). Moreover, increased physical disturbances in marshes can also initiate and accelerate *Phragmites* expansion. Disturbances by foot traffic and increased amounts of floating debris (wrack) in estuarine waters can both lead to unvegetated bare space in high marsh habitats that can enhance the establishment of *Phragmites* seedlings, and accelerate the vegetative spread of *Phragmites* stands by reducing competition with neighboring vegetation (T. Minchinton and J. Simpson, *unpublished data*).

The eutrophication of estuarine habitats (Valiela et al. 1992, Vitousek et al. 1997) may also be playing an important role in the current expansion of *Phragmites* in New England marshes (T. Minchinton, *unpublished data*). The traditional zonation of marsh plants in New England has been shown to have been driven by competition for nutrients, and when nutrients are no longer limiting, competition for light may become the leading determinant of marsh plant zonation patterns (Levine et al. 1998). Since *Phragmites* is one of the tallest common marsh plants, it may be a dominant competitor for light, and its expansion could at least partially be due to increased levels of nitrogen in New England estuaries. The recent spread of *Phragmites* has also been suggested to be due to a genetic shift in North American *Phragmites* that allows it to live at lower elevations (K. Saltonstall, *personal communication*).

While our work does not shed light on which of the above potential driving forces is contributing the most to the current spread of *Phragmites*, it does explain mechanistically some of the characteristics of *Phragmites* invasions, and suggests how the spread can best be controlled. Our results show that *Phragmites* growth and survivorship can be strongly suppressed at low elevations and by dense neighboring vegetation, but that *Phragmites* can vegetatively expand to lower elevations with clonal integration supporting the ramets colonizing physically harsh low marsh elevations. Thus, invasion of low marsh habitats by *Phragmites* may best be envisioned as large clones moving across shoreline landscapes, utilizing clonal integration to invade harsh habitats unsuitable for sexual recruitment. Similar scenarios have been suggested when other clonal low marsh plants have been introduced to novel shorelines.

Our results suggest that the best strategy for preventing the expansion of *Phragmites* into low marsh habitats is to minimize disturbance to marsh vegetation, naturally slowing the spread of *Phragmites*, and to control clonal development in the high marsh before low marsh habitats are colonized and modified. In southern New England, *Phragmites* often establishes by seed in the high marsh in disturbed habitats where vegetation cover has been reduced, and lives innocuously at low densities for years before rapidly accelerating its growth and spreading into low marsh habitats (M. D. Bertness, *personal observations*). Controlling high marsh *Phragmites* establishment by limiting disturbances that enhance seedling colonization, and removing *Phragmites* that colonize the high marsh before they reach a large size is often a realistic objective, and will limit colonization of low marsh habitats due to the dependency of *Phragmites* on clonal integration to invade to low marsh habitats. This management strategy can limit the ecosystem engineering by *Phragmites* that leads to the loss of low marsh habitats and the estuarine populations they may support (Marks et al. 1994).

ACKNOWLEDGMENTS

We thank Nancy Emery, John Bruno, Tatyana Rand, and Todd Minchinton for discussion, advice, and field assistance, and Tatyana Rand, two anonymous reviewers, and Laura Huenneke for comments on the manuscript. Our work was supported by an Undergraduate Teaching and Research Assistantship from Brown University to Lindsay Amsberry, a Research Experience for Undergraduate grant from the Ecology Program of the National Science Foundation and Rhode Island Sea Grant.

LITERATURE CITED

Abrahamson, W. G., K. Anderson, and K. D. McCrea. 1991. Clonal integration: nutrient sharing between sister ramets of *Solidago altissima* (Compositae). American Journal of Botany **78**:1508–1514.

Adam, P. 1995. Salt marsh ecology. Cambridge University Press, Cambridge, UK.

Alpert, P. 1991. Nitrogen sharing among ramets increases clonal growth in *Fragaria chiloensis*. Ecology **72**:69–80.

Amsberry, L. 1997. Factors regulating the invasion of *Phragmites australis* into southern New England salt marshes. Thesis. Brown University, Providence, Rhode Island, USA.

Baker, M. A. 1996. Clonal integration and the invasion of *Phragmites australis* into New England Salt Marsh Communities. Thesis. Brown University, Providence, Rhode Island, USA.

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

Bertness, M. D. 1991*b*. Zonation of *Spartina patens* and *Spartina alterniflora* in a New England salt marsh. Ecology **72**: 138–148.

Bertness, M. D. 1992. The ecology of a New England salt marsh. American Scientist **80**:260–268.

Bertness, M. D. 1999. The ecology of Atlantic shorelines. Sinauer Associates, Sunderland, Massachusetts, USA.

Bertness, M. D., T. Chatkupt, and K. Wikler. 1992*b*. Flood tolerances and the distribution of *Iva frutescens* across New England salt marshes. Oecologia **91**:171–178.

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., L. Gough, and S. Shumway. 1992*a*. Salt tolerances and the distribution of fugitive salt marsh plants. Ecology **73**:1842–1851.

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.

Caraco, T., and C. K. Kelly. 1991. On the adaptive value of physiological integration in clonal plants. Ecology **72**:81–93.

Daniels, R. E. 1991. Variation in performance of *Phragmites australis* in experimental culture. Aquatic Botany **42**:41–48.

Dreyer, G. D., and W. A. Niering 1995. Tidal marshes of Long Island Sound. Connecticut College Arboretum Bulletin **34**.

Evans, J. P., and S. Whitney. 1992. Clonal integration across a salt gradient by a nonhalophyte, *Hydrocotyle bonariensis* (Apiaceae). American Journal of Botany **79**:1344–1347.

Gambi, M. C., A. R. Nowell, and P. A. Jumars. 1990. Flume observations on flow dynamics in *Zostera marina* (eelgrass) beds. Marine Ecology Progress Series **61**:159–169.

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

Hartnett, D. C., and F. A. Bazazz. 1983. Physiological integration among intraclonal ramets in *Solidago canadensis*. Ecology **64**:779–788.

Haslam, S. M. 1969*a*. The development of shoots in *Phragmites communis* Trin. Annals of Botany **33**:695–709.

Haslam, S. M. 1969*b*. Stem types in *Phragmites communis* Trin. Annals of Botany **33**:127–131.

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

Haslam, S. M. 1970. The development of the annual population in *Phragmites communis* Trin. Annals of Botany **34**: 571–591.

Haslam, S. M. 1972. *Phragmites communis* Trin. Biological Flora of the British Isles, Number 128. 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.

Howes, B. L., J. W. H. Dacey, and D. D. Goehringer. 1986. Factors controlling the growth form of *Spartina alterniflora*: feedbacks between above-ground production, sediment oxidation, nitrogen and salinity. Journal of Ecology **74**: 881–898.

Howes, B. L., R. W. Howarth, J. M. Teal, and I. Valiela. 1981. Oxidation–reduction potentials in a salt marsh: Spatial patterns and interactions with primary production. Limnology and Oceanography **26**:350–360.

Irlandi, E. A., and C. H. Peterson. 1991. Modification of animal habitat by large plants: mechanisms by which seagrasses influence clam growth. Oecologia **87**:307–318.

Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. Oikos **69**:373–386.

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.

Lovett-Doust, L. 1981. Population dynamics and local specialization in a clonal perennial (*Ranunculus repens*). I. The dynamics of ramets in contrasting habitats. Journal of Ecology **69**:743–755.

Mack, R. N. 1986. Alien plant invasion into the intermountain west: a case history. Pages 191–213 in H. A. Mooney and J. A. Drake, editors. Ecology of biological invasions of North America and Hawaii, Springer-Verlag, New York, New York, USA.

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

Mook, J. H., and J. van der Toorn. 1982. The influence of environmental factors and management of stands of *Phragmites australis*. II. Effects on yield and its relationships with shoot density. Journal of Applied Ecology **19**:501–517.

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

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

Orth, R. J. 1977. The importance of sediment stability in seagrass communities. Pages 281–300 *in* Ecology of marine benthos. B. C. Coull, editor. University of South Carolina Press, Columbia, South Carolina, USA.

Pennings, S. C., and R. M. Callaway. 1999. A communitywide test of the role of clonal integration in competition and stress tolerance. Ecology, *in press*.

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

Pitelka, L. F., and J. W. Ashmun. 1985. Physiology and integration of ramets in clonal plants. Pages 399–435 *in* J. B. C. Jackson, L. W. Buss, and R. E. Cook, editors. Population biology and evolution in clonal organisms. Yale University Press, New Haven, Connecticut, USA.

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.

Shumway, S. W., and M. D. Bertness. 1992. Salt stress limitation of seedling recruitment in a salt marsh plant community. Oecologia **92**:490–497.

Snow, A., and S. Vince. 1984. Plant zonation in an Alaskan salt marsh. II. An experimental study of the role of edaphic conditions. Journal of Ecology **72**:669–684.

Thompson, D. J., and J. M. Shay. 1985. The effects of fire on *Phragmites australis* in the Delta Marsh, Manitoba. Canadian Journal of Botany **63**:1864–1869.

Valiela, I., P. Peckol, C. D'Avanzo, C. H. Sham, and K. Lajtha. 1992. Couplings of watersheds and coastal waters: sources and consequences of nutrient enrichment in Waquoit Bay, Massachusetts. Estuaries **15**:443–457.

van der Toorn, J., and J. H. Mook. 1982. The influence of environmental factors and management on stands of *Phragmites australis*. I. Effects of burning, frost, and insect damage on shoot density and shoot size. Journal of Applied Ecology **19**:477–499.

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

Weisner, S. E. B., and W. Graneli. 1989. Influence of substrate conditions on the growth of *Phragmites australis* after a reduction in oxygen transport to below-ground parts. Aquatic Botany **35**:71–80.