COMPETITION AND SALT-MARSH PLANT ZONATION: STRESS TOLERATORS MAY BE DOMINANT COMPETITORS

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Abstract. Although a great deal of research has focused on the effects of nutrient supply on plant competition, few studies have explored how these processes interact with non-resource factors to determine community-level patterns. This study examined how resource competition interacts with physical stress to structure salt-marsh plant communities across a natural gradient in tidal stress. First, nutrient additions at naturally occurring species borders at zonal and patch boundaries in two Rhode Island (USA) marshes revealed that competitive outcomes were typically reversed when nutrients were abundant. These results, which are consistent with earlier findings in a third southern New England marsh, suggest that a nutrient-dependent competitive hierarchy is a general characteristic of salt marshes in this region. To test whether these shifts in competitive outcomes occur only at naturally occurring species borders or can lead to more significant shifts in zonation patterns, lower marsh species were transplanted into the matrix of each zonal species at higher tidal elevations, and the outcomes of plant competition in fertilized plots and unfertilized plots were compared. Results of this experiment indicate that nutrient effects on the competitive relations of marsh plants were independent of where the interactions took place along the tidal gradient. The stress-tolerant species were consistently the best competitors in fertilized treatments, showing that an increase in nutrient availability can lead to drastic shifts in the distributions of plants across marshes. Finally, a third experiment examined the interaction between nutrient supply and the above-ground and belowground components of plant competition using a reciprocal transplant design coupled with nutrient-addition and neighbor-removal treatments. Results suggest that competition is primarily belowground under ambient marsh conditions but is aboveground at high nutrient levels. Thus the mechanism underlying the nutrient-dependent competitive hierarchy may be driven by a trade-off between belowground and aboveground competitive abilities, although the potential interaction between above- and belowground effects was not examined. Together, the results of these experiments suggest that nutrient supplies may significantly affect the competitive dynamics between salt-marsh perennials and their resultant zonation across an environmental gradient in tidal stress. The result that stress tolerators can be dominant competitors is not predicted by any current model of plant competition and must be considered in future empirical and theoretical studies.

Key words: aboveground competition; belowground competition; competitive mechanisms; environmental gradients; marsh plants, stress, competition, and zonation; New England (USA) salt marshes; nutrient-dependent competitive hierarchy; plant competition; salt-marsh plant communities; Spartina, Juncus, and Distichlis; stress tolerance; trade-offs.

INTRODUCTION

Ecologists have long recognized the value of studying community patterns along environmental gradients to learn how abiotic and biotic factors affect the distributions of species. Many plant ecologists have taken an experimental approach to identify how resource availability interacts with interspecific competition (Austin and Austin 1980, Goldberg and Miller 1990, Wilson and Tilman 1991*a,* Belcher et al. 1995, Twolan-Strutt and Keddy 1996, Levine et al. 1998), herbivory (Furbish and Albano 1994, Bonser and Reader 1995,

John and Turkington 1995, Gough and Grace 1998), and/or disturbance (Wilson and Shay 1990, Wilson and Tilman 1991*b,* Turkington et al. 1993) to determine spatial patterns along productivity gradients. Others have explored gradients in non-resource, abiotic conditions and shown that species distributions can result from adaptation to specific niches along environmental clines (Strain and Billings 1974, Whittaker 1978, Greig-Smith 1982, Keddy 1984, Wilson and Keddy 1985, 1986*a, b,* Campbell and Grime 1992). But while the effects of resource availability and non-resource stress on species distributions have received a great deal of attention, the potential interaction of these two processes has been relatively ignored. In particular, the importance of resource competition along gradients in non-resource stress has remained largely unstudied (Grace 1990, 1991, Grace and Wetzel 1981).

The nature of competition under different levels of

resource availability has received considerable attention from plant community ecologists (Goldberg and Barton 1992). Grime's competitor/stress tolerator/ruderal theory (hereafter CSR theory) of plant life histories classifies plant strategies as competitive, stress-tolerant, or ruderal (Grime 1977, 1979). It predicts that the intensity of competition, or the degree to which the presence of neighbors reduces a population (Grace 1991), increases with productivity due to a trade-off between stress tolerance and competitive ability (Grime 1977, 1979, Huston 1979). This model further predicts that productive habitats are dominated by good competitors that can grow rapidly and have high capture rates for all resources, while the slow growth rates and low resource requirements of stress tolerators allow them to persist in stressful, unproductive habitats. In contrast, resource-based theories of competition predict that competition intensity remains constant across a resource gradient, but that the limiting resources change with productivity (Newman 1973, 1983, Tilman 1982, 1988, 1990). More specifically, Tilman's resource-ratio hypothesis predicts that competition is belowground for nutrients when nutrients are limiting, but shifts to aboveground competition for light as productivity increases (Tilman 1982, 1988, 1990, 1997, Wilson and Tilman 1991a, 1993). Competitive success is predicted to vary with productivity due to a trade-off between belowground and aboveground competitive abilities. Thus the competitive ability of a species is determined by its relative biomass allocation to roots, stems, and leaves, and the ratio of resources available at any given point along a productivity gradient (Tilman 1982, 1988, 1990).

The CSR and resource-ratio hypotheses do not distinguish between resource and non-resource stress when predicting the nature of plant interactions along environmental gradients (Grace 1990, 1991). Because the CSR theory claims that adaptation to any suboptimal environment diverts energy from resource exploitation and competitive ability, it predicts that gradients in physical stress and resource availability will show similar patterns of segregation of stress tolerators and good competitors (Grace and Wetzel 1981, Grace 1990, 1991). Tilman argues that non-resource stress affects competitive interactions simply by affecting the ability of a species to compete for a limiting resource (Tilman 1997). However, other ecologists have proposed that physiological responses to physical stress may interact with resource competition to have unique effects on community structure (Grace and Wetzel 1981, Brewer and Grace 1990, Bertness 1991a, b, Dunson and Travis 1991). Despite the drastically different predictions of each hypothesis, there has been relatively little empirical work testing the effects of non-resource stress on plant competitive interactions.

Salt-marsh plant communities are ideal systems for addressing questions about the interactions of physical stress, resource competition, and plant community structure. Tidal flooding establishes a strong non-resource stress gradient across the marsh landscape, with soil anoxia and waterlogging decreasing from the seaward edge to the terrestrial border (Mendelssohn et al. 1980, Howes et al. 1981, Mendelssohn et al. 1981). Moreover, the marsh plant community is dominated by only a few clonal perennial species that are typically distributed into distinct zones (Nixon 1982). Ecologists have historically emphasized the role of physical factors in determining the community structure of salt-marsh plants (Nixon 1982), but recent work has demonstrated that competitive processes are also important (Snow and Vince 1984, Bertness and Ellison 1987, Bertness 1991a, b, Pennings and Callaway 1992, Levine et al. 1998). Finally, salt marshes are nitrogen poor (Valiela and Teal 1974, Valiela et al. 1985) yet highly productive (Bertness 1992) and thus are potentially sensitive to changes in nutrient availability.

In southern New England marshes, the low marsh is dominated by *Spartina alterniflora* Loisel. (smooth cordgrass), a large perennial grass with extensive rhizomes. The upper edge of *S. alterniflora* is bordered by *S. patens* (Aiton) Muhl. (saltmeadow cordgrass), a perennial turf grass, which is replaced at higher elevations by *Juncus gerardi* Loisel (black needle rush), another perennial with a dense turf morphology (Fig. 1; Nixon 1982, Bertness 1991a, b, Hacker and Bertness 1999, Pennings and Bertness 2001). While the low marsh experiences daily flooding by tides, the *S. patens* and *J. gerardi* zones are only inundated during high-tide cycles. These differences in the frequency and duration of tidal inundation establish a spatial gradient in soil anoxia and salinity across the marsh, with lower soil redox potential and higher salinity levels (in vegetation) in the lower marsh than at higher elevations (Bertness and Ellison 1987). Although productivity on the community level is relatively constant across the marsh landscape (Bertness and Ellison 1987, Bertness 1991b), transplant experiments have shown that the lower marsh zones are relatively more stressful for all perennials than are the conditions at higher elevations; in fact, the lower distribution of each species is determined by physiological tolerance to the physical stress of tidal inundation. Specifically, *S. patens* and *J. gerardi* transplants showed stunted growth or mortality when transplanted to lower tidal elevations (Bertness and Ellison 1987, Bertness 1991a, b). In contrast, *S. patens* and *S. alterniflora* each exhibited increased growth when transplanted to higher tidal elevations if neighbors were removed but were competitively excluded when neighbors were present, indicating that competition limits the upper distribution of each species in the salt-marsh intertidal (Bertness and Ellison 1987, Bertness 1991a, b). Thus although *S. patens* and *S. alterniflora* show greater vigor and productivity under the physical conditions of the high marsh, they are competitively excluded to the more stressful middle and lower marsh, respectively, where they exist at rel-

Increasing physical stress
(waterlogging and soil anoxia)

Lower borders set by physical stress

Upper borders set by competition

Distichlis spicata
(restricted to saline bare patches)

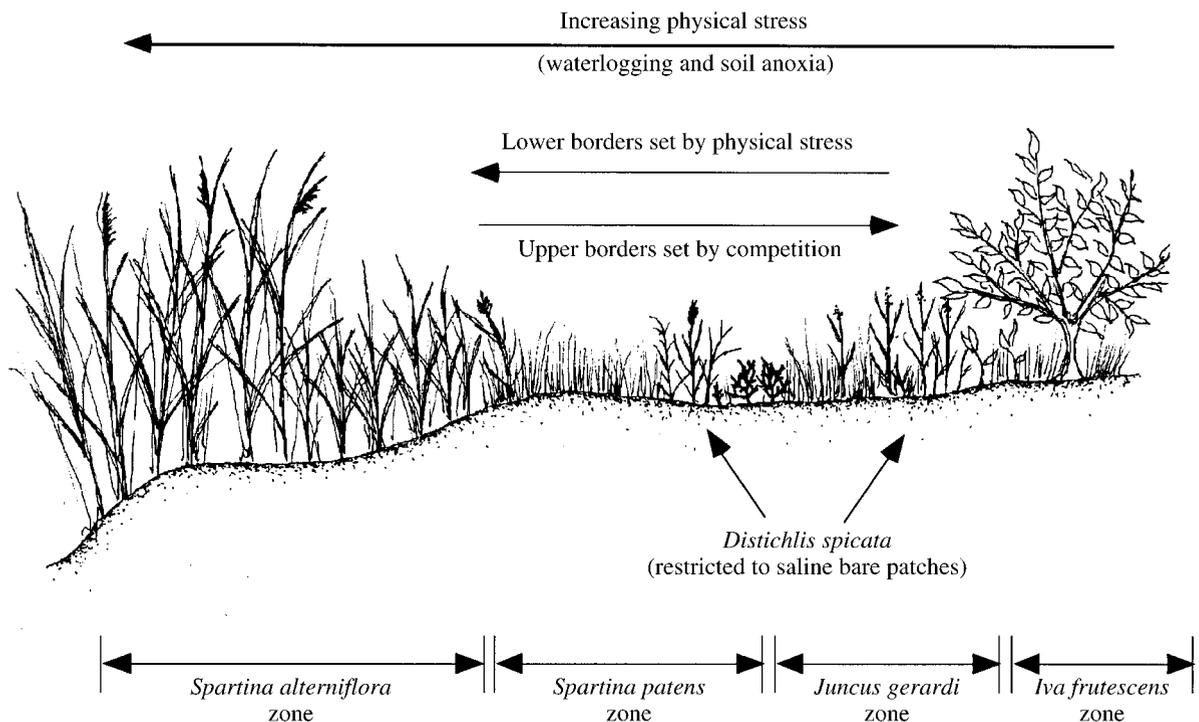| *Spartina alterniflora* zone | *Spartina patens* zone | *Juncus gerardi* zone | *Iva frutescens* zone |

FIG. 1. Zonation of the dominant perennials in a New England (USA) salt marsh.

atively lower productivity levels. Similarly, *Distichlis spicata* (L.) Greene (seashore salt grass), a perennial grass with long adventitious rhizomes, is competitively restricted to disturbance-generated, highly saline bare patches in the *J. gerardi* and *S. patens* zones. The dominants cannot tolerate the stressful conditions of these patches until salinity has been reduced by previously colonizing vegetation shading the substrate, while *D. spicata* is competitively excluded to these patches by the dominant high-marsh species (Bertness and Ellison 1987, Bertness 1992).

A recent study in one southern New England marsh showed that nutrient additions changed the outcome of competition at species borders and completely reversed the competitive hierarchy among the marsh perennials (Levine et al. 1998). This reversal was hypothesized to result from a shift from belowground to aboveground competition coupled with trade-offs in belowground and aboveground competitive abilities, as predicted by Tilman's resource-ratio model of plant competition along a productivity gradient (Tilman 1982, 1988, 1990). The decoupling of aboveground and belowground resources is a debated issue, and until now this hypothesis was untested in the salt-marsh perennial plant community. Furthermore, the generality of competitive reversals in response to nutrient additions both within and among southern New England salt marshes has not been examined. In this paper we present the results of a series of experiments that examine the generality of the effects of nutrients on naturally occurring

species borders, test the extent to which species distributions can shift in response to nutrient additions, and suggest the mechanistic basis for the effects of nutrient availability on the competitive relationships between marsh plants. Specifically, we ask three questions:

1) Is a nutrient-dependent competitive hierarchy at species borders a general characteristic of southern New England marshes? We predicted that because marshes are typically nitrogen poor, competition for N at species borders occurs in replicate southern New England marshes, and that adding fertilizer to these borders would consistently reverse competitive outcomes between zonal dominants. To test this hypothesis, we performed nutrient additions at zonal boundaries in two southern New England marshes to compare the results to those previously found in a third marsh by Levine et al. (1998).

2) Does the non-resource stress gradient across the marsh affect the outcome of resource competition between plants under different levels of nutrient availability? That is, to what extent can nutrient supplies shift zonal boundaries across the gradient in tidal stress? We tested the hypothesis that nutrient additions can result in large zonal shifts of the dominant perennials beyond naturally occurring species borders by performing a transplant experiment with nutrient addition treatments.

3) Are the effects of nutrient addition on the competitive hierarchy among marsh plants due to a shift

from belowground competition for nutrients to aboveground competition for light, coupled with trade-offs between aboveground and belowground competitive abilities? Greenhouse observations suggest that the species with the highest root:shoot ratio in each naturally occurring species mixture is dominant under ambient N conditions, while those shown to dominate in fertilized plots (Levine et al. 1998) have relatively more biomass allocated to aboveground structures. These observations suggest that a trade-off between aboveground and belowground biomass allocation may underlie a reversal in the outcome of competition between salt-marsh perennials. We predicted that competition among salt-marsh perennials is primarily belowground for nutrients at ambient N levels and aboveground for light in nutrient-enriched plots. This hypothesis was tested with a reciprocal transplant experiment that incorporated nutrient-addition and neighbor-removal treatments.

METHODS

Nutrient addition experiment at zonal boundaries

We tested the generality of the effects of nutrients on salt-marsh plant zonation by conducting a nutrient-addition experiment at naturally occurring species borders in two Rhode Island (USA) marshes: Nag Cove West and Nag Cove East. Both marshes are located at the Narragansett Bay National Estuarine Research Reserve on Prudence Island, Rhode Island, and have species zonation patterns typical of southern New England marshes (Bertness and Ellison 1987, Bertness 1992). The results of these experiments were compared to those of a similar experiment previously performed in a third Rhode Island salt marsh (Levine et al. 1998).

At each site, twenty 70 × 70 cm quadrats were selected at each naturally occurring species boundary: *Spartina alterniflora–S. patens, S. patens–Juncus gerardi,* and *J. gerardi–Distichlis spicata.* We did not include *S. patens–D. spicata* mixed plots because these species did not coexist in appropriate mixtures in these marshes. Each plot was initially placed so that it contained ~50% of each species, and plots were spaced ~2 m apart. In addition, 20 monoculture plots of each species were randomly selected and marked within 2 m of the zonal border. Although we kept monoculture and mixed plots as close together spatially as possible, it is likely that they were still subject to slightly different physical environments, and any quantitative comparisons between them would be confounded by factors associated with tidal height. Thus statistical comparisons were made only within mixed and monoculture plots and not between plots of different initial species compositions. All plots were marked before the beginning of the growing season in April 1996. For each set of 20 plots, 10 plots were randomly selected for nutrient-addition treatment and the remaining plots were left as controls at ambient nutrient levels. In this

and the following experiments, every two weeks the nutrient-addition plots received applications of Scotts Turfbuilder (Scotts Company, Marysville, Ohio) pelletized fertilizer, containing 29% N (15.6% urea N, 12.4% water-soluble organic N, 1% ammoniacal and water-insoluble N), 3% P (P_2O_5 form), and 4% K, in the amount of 60 g NPK/m². Pore-water ammonium concentration varies across the marsh, ranging between ~5 and 20 mol/L (Bertness and Ellison 1987), and decreases over the growing season (Valiela and Teal 1974). Consequently, a high application rate was necessary to ensure that nutrients were not limiting in any fertilization plot at any point in the season. This application rate is similar to fertilizer treatments used in other salt-marsh nutrient-addition studies (Valiela et al. 1985, Levine et al. 1998). In no cases did vegetation receiving nutrient-addition treatments exhibit any burning or other signs of overfertilization.

At the end of each growing season, percent cover and aboveground biomass in all mixed and monoculture plots were measured. Percent cover was estimated by placing a 0.5 × 0.5 m quadrat with a 5-cm² grid over each plot and counting the number of squares containing each species. To quantify biomass, a 10 × 10 cm sample of aboveground tillers was clipped with scissors from the center of each plot. In the laboratory these samples were cleaned of dead plant material, sorted by species, dried to a constant mass in a drying oven at 30°C, and weighed. Height measurements were taken on five representative tillers from each species per sample and were averaged to calculate a single mean height value per plot.

Biomass data were $\log_{10}(x + 1)$ transformed, height data were $\log_{10}(x)$ transformed, and percent cover data were arcsine square-root transformed to increase homogeneity of variances and normality (Underwood 1997). Data were analyzed with JMP statistical software (SAS Institute 1995) using a split-plot ANOVA with site, fertilization, plot(site, fertilization), and species as the main effects, and site × fertilization, species × site, species × fertilization, and species × site × fertilization as the interaction terms. Site was treated as a random effect in the model.

Transplant experiment with nutrient treatment

To test if fertilization has the same effect on competitive interactions across the marsh that it does at species borders, we transplanted lower marsh species to zones at higher elevations and compared their interactions with the neighboring vegetation in fertilized and unfertilized plots. This experiment was conducted at Rumstick Cove, Barrington, Rhode Island, where previous experiments had shown border shifts in response to nutrient additions (Levine et al. 1998). In April 1996, forty 0.5 × 0.5 × ~0.35 m plots were randomly selected within the *S. alternflora* zone. Twenty of these plots were then transplanted into the *S. patens* zone, and the remaining twenty were trans-

planted into the *J. gerardi* zone. Additionally, 20 *S. patens* plots were transplanted into the *J. gerardi* zone. All transplants were placed into size-matched holes, and any remaining gaps along the edges were filled with soil from the original plot. These are well-proven transplant procedures with few artifacts and no differential transplant effects between the salt-marsh dominant species (Bertness and Ellison 1987, Bertness 1988). The transplant size was large in order to minimize any confounding effects associated with the clonal integration of the matrix species. Edges were marked by flagging the corners of each plot. *D. spicata* was not abundant enough at the site to be included in this experiment.

For each set of species transplants in each zone, half of the plots were randomly selected to receive nutrient additions and the remaining plots were left as controls at ambient nutrient levels. Nutrient-addition plots received 60 g NPK/m^2 on a biweekly basis from May through August of 1996 and 1997, and May through June of 1998. Fertilizer was applied uniformly to the transplant plot and the surrounding vegetation within roughly 20 cm of the target species.

As in all other experiments, competition was measured as the ability of a species to dominate a plot. In this experiment, we were interested in the ability of a species to spread across the transplant edge by the production of lateral tillers. Consequently, competition was measured as the ability of the transplant species to invade the matrix vegetation and resist invasion by the surrounding species under both high and low nutrient levels. We quantified invasion by counting the number of tillers of each species that had crossed the original transplant edge (this is equivalent to the percent cover estimates at naturally occurring species borders, as done in the experiment where species borders were fertilized). Counts were done in August of 1996 and 1997 and in June 1998. Because the effects of transplantation and acclimation may have influenced invasion processes early in the experiment, only final data (from June 1998) were used for statistical analyses.

Tiller counts of all four sides of each transplant were averaged to give a mean value for tiller movement per edge for each replicate, which were then square-root ($x + 1$) transformed to increase normality and homogeneity of variances (Underwood 1997). Within each treatment, a paired *t* test was used to test for differential movement across the transplant edge between species within each fertilization treatment. A one-way ANOVA within species was performed for each transplant-species/matrix-species combination to test for the effects of fertilization on the ability of each species to invade across the transplant edge.

Transplant experiment with nutrient and competition treatments

We tested the hypothesis that competition among salt-marsh perennials is primarily belowground under ambient nutrient levels and aboveground under nutrient-enriched conditions with a simple experiment that separated the belowground and aboveground components of competition under high and low nutrient conditions. Our experimental design consisted of a randomly assigned factorial arrangement of transplant species, competition treatment, and fertilization level, which allowed us to compare the relative contributions of above- and belowground processes to the total effects of competition under different levels of nutrient availability.

This experiment was conducted in the high marsh of Nag Cove East on Prudence Island, Rhode Island. Preliminary results from the fertilization of the species-borders experiment suggested that this marsh showed similar border shifts in response to nutrient additions and was therefore an appropriate site for testing the mechanistic basis of these shifts. Reciprocal transplants between each species pair (*J. gerardi* and *S. patens, J. gerardi* and *D. spicata,* and *S. patens* and *D. spicata*) were carried out in mid-April 1997. For each species combination, 48 cores (7 cm diameter × 30 cm deep) of each species were extracted and transplanted into the center of 0.5 × 0.5 m monoculture plots of the other species in the pair (hereafter called the "matrix-species plots"). Previous experiments have shown that these transplant techniques have similar effects across species (Bertness and Ellison 1987); however, we found that *J. gerardi* transplant plugs across all treatments showed symptoms of transplant shock and consequently we eliminated all species combinations involving *J. gerardi* plugs from further consideration. To avoid any confounding factors associated with tidal height, all matrix species plots of *S. patens* were transplanted into the upper marsh where *J. gerardi* and *D. spicata* naturally occur. We severed the edges, lifted, and replaced *J. gerardi* and *D. spicata* matrix species plots to simulate the effects of transplanting *S. patens.*

Following transplantation, each plug was randomly assigned to one of three competition treatments: no competition (NC), belowground competition only (BC), or full competition (FC) (Wilson and Tilman 1991*a*, 1993). In NC treatments, the tillers of the matrix species were clipped and the roots were severed within a 5-cm radius of the target species. This treatment was maintained for several weeks until the neighbors ceased growing back into the neighbor-removal area. The clipped area was kept relatively small in order to minimize the effects of root decomposition and changes in the microbial community while still effectively removing all competitive effects on the target species. Clipped tillers were left on the ground in the bare area to reduce evaporation from the soil surface and prevent soil salinity levels from rising. This procedure maintained the natural edaphic environment while removing the competitive effects of neighboring vegetation (N. C. Emery, *personal observations*). In BC plots, the tillers of the matrix species within roughly 5 cm of the

target plug were pinned back with staples made of 2-mm-diameter plastic wire. In FC plots, the matrix species was left unmanipulated.

After competition treatments were assigned, half of the plots were randomly selected for high nutrient treatment and the remaining plots were designated as controls to remain at ambient nutrient levels. The high nutrient plots received biweekly fertilizer treatments of 60 g NPK/m² of Scott's Turfbuilder spread uniformly over the plug and the matrix species within the plot between mid-May and the end of August in 1997 and 1998. Light availability was quantified once in July 1997 and again in July 1998. Instantaneous measurements were taken directly above the tillers of the target species and at the plug–plot interface at ground level on a cloudless day between 1000 and 1400 (LI-COR solar monitor, Model 1776). Percentage light transmittance was calculated as $100 \times$ (light above tillers − light at ground level)/light above tillers. Aboveground biomass was harvested at the end of the growing season in 1998 by clipping all tillers in the original plug of each target-species transplant. In the laboratory, samples were cleaned and sorted by species. We measured the heights of five representative tillers, dried each sample to a constant mass in a drying oven at 30°C, and then weighed each sample. The five height measurements were averaged to give one height value per sample.

Biomass data were $\log_{10}(x + 1)$ transformed, height data were $\log_{10}(x)$ transformed and percentage light transmittance data were arcsine square-root transformed to increase homogeneity of variances and normality (Underwood 1997). A two-way ANOVA within each transplant species × matrix species combination was performed to test for the effects of competition and fertilization treatments on target biomass and height and light transmittance. We then used contrasts (JMP Version 3.1 [SAS Institute 1995]) to test a priori hypotheses about the effects of fertilization on biomass, height, and light transmittance within each competition treatment and the effects of each competition treatment within fertilization treatment.

Importantly, our method of separating the aboveground and belowground effects of competition assumes that these components are additive. Although greenhouse experiments have suggested that aboveground and belowground processes are more often additive than nonadditive (Wilson 1988), one field study has shown significant interactions between aboveground and belowground effects (Cahill 1999). We did not design this experiment to test for interactions between above- and belowground processes. To do so, aboveground competition must be directly measured by removing belowground competition without manipulating aboveground structures, which can be accomplished in some systems by using root-exclusion tubes. Such a design is impractical for clonal plants, however, as root movement out of the initial plug is essential for

transplant establishment. To restrict this movement would inhibit growth and tiller production and would therefore affect aboveground processes. Thus while this design incorporates the most convenient method for identifying aboveground and belowground competitive effects in the salt-marsh perennial system, it does not allow us to evaluate interactions between these processes, and consequently its results must be interpreted with caution. It does, however, provide insight into the potential importance of aboveground and belowground competitive ability in determining species distributions and is a valuable step toward understanding the mechanisms underlying the nutrient-dependent competitive hierarchy of southern New England salt marsh plant communities.

RESULTS

Nutrient addition experiment at zonal boundaries

At both Nag Cove East and Nag Cove West (Rhode Island, USA), fertilization affected the relative abundance and distribution of each species in mixed plots for all species pairs. Initially, all plots contained ~50% of each species. Control plots either maintained this proportion or became slightly dominated by the species known to be competitively dominant under ambient conditions (Fig. 2; Bertness 1991a, b). In fertilized plots, the species that were competitively suppressed under ambient conditions increased in abundance and shifted to dominate their respective plots.

A significant species × fertilization interaction in percent cover for all species pairs indicated that fertilization affected species distributions at every border. The lack of any species × site × fertilization effects indicates that similar responses to competition and fertilization treatments were found at Nag Cove East and Nag Cove West (Table 1). At the J. gerardi–S. patens border in Nag Cove East, J. gerardi monopolized control plots, while J. gerardi and S. patens maintained roughly equal proportions at Nag Cove West. In both marshes, fertilization at least doubled the abundance of S. patens and severely reduced the relative proportions of J. gerardi (Fig. 2). Whole-plot site effects for this species reflect differences between these populations in their distributions independent of fertilization treatment. Similar results were found in both marshes at J. gerardi–D. spicata borders: J. gerardi monopolized control plots but was severely reduced in fertilized plots, and D. spicata increased from ~20% cover under ambient nutrient levels to ~80% cover in fertilized plots. Finally, S. patens dominated mixed plots at the S. patens–S. alterniflora border in control plots, while the fertilization treatment resulted in a large increase in S. alterniflora and decrease in S. patens.

Shifts in absolute biomass at each species border corresponded to the changes in percent cover (Tables 1 and 2). In all cases, fertilization increased the biomass of the competitive subordinate under ambient marsh
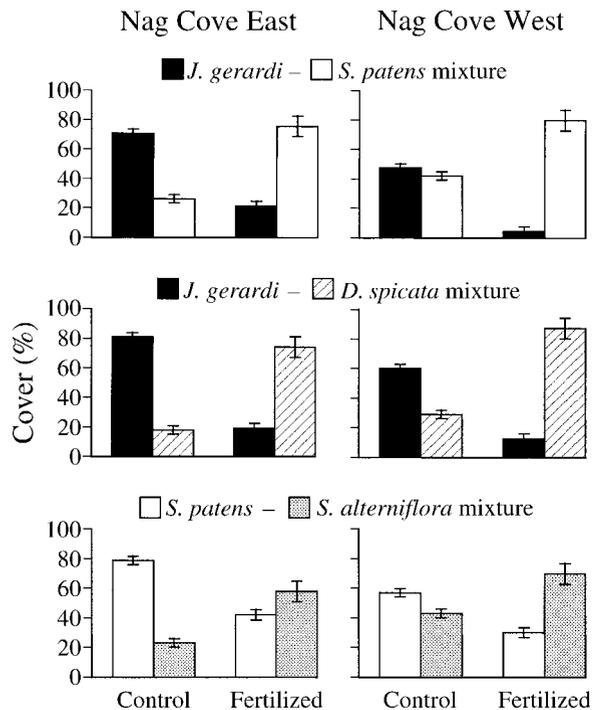
Nag Cove East   Nag Cove West

FIG. 2. The effect of fertilization on a species' ability to dominate a plot at naturally occurring species borders in two Rhode Island (USA) salt marshes. Data are percent cover (means ±1 SE) of each species (*Spartina, Juncus,* or *Distichlis*) in a mixture. Initial plot compositions were roughly 50% of each species in the pair. In every case, nutrient addition resulted in the competitive subordinate under ambient marsh conditions shifting to dominate the plot.

nutrient levels while reducing the biomass of the other species in the mixture (Table 2). Significant species × fertilization × site interactions for average biomass were due to differences in the magnitudes of these responses between marshes. A whole-plot site effect found for the *J. gerardi–S. patens* border reflects differences between populations at each site that are independent of fertilization effects.

Fertilization also had differential effects on the tiller heights of species in border plots, as indicated by a significant species × fertilization interaction for all species pairs (Table 1). In general, the competitive subordinate under ambient nutrient levels (Bertness 1991*a, b*) was taller than the competing species in fertilized plots, but was often either shorter or roughly equivalent in height in the control treatment (Table 2). *J. gerardi* and *S. patens* had roughly equivalent heights in control plots at both Nag Cove East and Nag Cove West, but in fertilized plots *S. patens* grew another 8 cm while *J. gerardi* showed a slight decrease in growth, particularly at Nag Cove West. A similar pattern occurred at the *J. gerardi–D. spicata* border at Nag Cove East, where *D. spicata* was shorter than *J. gerardi* in control plots but taller in fertilized plots. At Nag Cove West, *D. spicata* was taller than *J. gerardi* in both control

and fertilized plots. Finally, under the control treatment *S. patens* was taller than *S. alterniflora* at Nag Cove East and shorter at Nag Cove West; at both sites, *S. alterniflora* showed a large positive response to fertilization and on average was >20 cm taller than *S. patens* in nutrient-addition plots. The effects of fertilization on the relative heights of species in mixed plots were the same at both sites for the *J. gerardi–S. patens* and *J. gerardi–D. spicata* plots (Table 1). A significant species × fertilization × site interaction in *S. patens–S. alterniflora* mixture was due to differences in the *S. patens* response to fertilization at this border, which was significant at Nag Cove West but not at Nag Cove East (contrasts. Nag Cove West, *P* < 0.05; Nag Cove East, *P* > 0.05). Whole-plot site effects for *J. gerardi–S. patens* and *J. gerardi–D. spicata* combinations are due to differences between populations at each marsh that are independent of treatment (Table 2).

The effects of fertilization on each species in monoculture indicate that the results in mixed plots are due to competitive effects and not fertilization having differentially negative and positive effects on different species (Table 3). In monoculture, all species showed either a positive or neutral response to the nutrient-addition treatment. Fertilization significantly increased both the average biomass and tiller height for *S. patens, D. spicata,* and *S. alterniflora. J. gerardi* showed no significant response to fertilization in either biomass or tiller height. The small and statistically insignificant decrease in fertilized *J. gerardi* monocultures at the Nag West marsh (contrast testing a priori hypotheses, *P* > 0.05) likely reflects damage due to temporary wrack burial earlier in the season rather than a negative effect of fertilization (N. C. Emery, *personal observations*). These plots still showed a slight increase in average tiller height, further supporting that *J. gerardi* responded positively to nutrient addition in monoculture at Nag West as it did at Nag East. Because fertilizer alone has either a positive or neutral effect on all species, any decreases in species abundance in fertilized mixed plots can be attributed to the effects of competition.

Transplant experiment with nutrient treatment

In general, nutrient addition had similar effects on interspecific plant competition at higher tidal elevations (i.e., at reduced levels of non-resource stress) as was found at naturally occurring species borders. At all elevations, interspecific differences in responses to fertilization reversed the direction and magnitude of invasion and as a result changed the pattern of vegetative spread (Fig. 3). In general, transplants of lower marsh species in unfertilized plots were invaded by the matrix species, while fertilized transplants spread into the surrounding matrix vegetation and were relatively resistant to invasion. In the *S. patens* zone, *S. alterniflora* transplants had become heavily invaded by *S. patens* and showed little spread into the *S. patens* matrix veg-

TABLE 1. Statistical results from split-plot ANOVA testing the effects of site (S), fertilization treatment (F), plot (P), and species (Sp) on percent cover, biomass, and tiller height in 1998. The species used were *Spartina*, *Juncus*, and *Distichlis* in two Rhode Island salt marshes.

Species mixture	Effect	df	Percent cover		Biomass		Tiller height	
			MS	F	MS	F	MS	F
J. gerardi–S. patens	Whole plot							
	S	1	0.08	12.56**	0.06	4.31*	0.04	8.69*
	F	1	0.03	4.42*	0.08	5.81*	<0.01	0.81
	S × F	1	0.02	3.81	0.01	0.78	<0.01	0.54
	P(S, F)	24	0.01	0.12	0.01	0.35	0.01	2.78*
	Split-plot							
	Sp	1	0.89	17.23**	0.14	3.69	0.03	17.75**
	Sp × S	1	0.51	9.84**	0.87	22.34**	0.03	12.07**
	Sp × F	1	3.84	74.32**	4.42	113.07**	0.03	18.17**
	Sp × S × F	1	0.01	0.67	0.30	7.61*	<0.01	0.8
J. gerardi–D. spicata	Whole plot							
	S	1	<0.00	0.03	<0.01	0.05	0.06	23.35**
	F	1	<0.01	0.10	0.22	8.93*	0.06	22.90**
	S × F	1	0.02	1.09	<0.01	0.15	<0.01	0.74
	P(S, F)	22	0.02	0.69	0.02	1.03	<0.01	1.27
	Split-plot							
	Sp	1	0.13	4.15	0.10	4.01	0.01	2.45
	Sp × S	1	0.24	7.64*	0.52	21.48**	<0.01	0.01
	Sp × F	1	4.33	136.25**	0.96	39.95**	0.02	9.66**
	Sp × S × F	1	0.01	0.35	0.11	4.54*	<0.01	<0.01
S. patens–S. alterniflora	Whole plot							
	S	1	<0.01	4.79*	0.04	0.96	0.02	1.97
	F	1	<0.01	<0.01	0.56	15.03**	0.71	79.72**
	S × F	1	<0.01	6.97*	0.06	1.70	0.02	2.16
	P(S, F)	31	<0.01	<0.01	0.04	0.45	0.01	1.42
	Split-plot							
	Sp	1	0.04	0.40	0.44	5.39*	0.16	24.83**
	Sp × S	1	0.67	6.05*	0.46	5.62*	0.06	9.06**
	Sp × F	1	2.21	20.00**	4.46	54.68**	0.06	10.29**
	Sp × S × F	1	0.09	0.78	0.43	5.29*	0.03	4.92*

* $P < 0.05$, ** $P < 0.01$.

TABLE 2. Results of fertilization treatment at species borders of the major marsh perennials at Nag Cove East and Nag Cove West (two salt marshes in Rhode Island, USA). Data are means ± 1 SE.

Species border	Site	Treatment	Species	Biomass (g/100 cm²)	Avg. tiller height (cm)
J. gerardi–S. patens	Nag Cove East	control	*J. gerardi*	6.20 ± 0.70	44.08 ± 1.52
			S. patens	0.95 ± 0.17	41.47 ± 2.48
		fertilized	*J. gerardi*	3.01 ± 0.92	42.94 ± 1.39
			S. patens	5.91 ± 1.17	49.06 ± 2.42
	Nag Cove West	control	*J. gerardi*	4.32 ± 0.74	36.65 ± 2.22
			S. patens	1.23 ± 0.17	39.96 ± 3.15
		fertilized	*J. gerardi*	0.10 ± 0.06	31.23 ± 0.78
			S. patens	12.32 ± 1.53	47.16 ± 3.01
J. gerardi–D. spicata	Nag Cove East	control	*J. gerardi*	8.08 ± 0.67	38.39 ± 1.13
			D. spicata	0.89 ± 0.29	32.64 ± 1.95
		fertilized	*J. gerardi*	4.13 ± 1.95	39.33 ± 0.96
			D. spicata	5.23 ± 0.93	41.95 ± 1.21
	Nag Cove West	control	*J. gerardi*	3.28 ± 0.64	43.72 ± 2.44
			D. spicata	2.47 ± 0.28	47.97 ± 1.55
		fertilized	*J. gerardi*	2.87 ± 0.86	49.03 ± 1.85
			D. spicata	7.36 ± 2.17	50.81 ± 1.31
S. patens–S. alterniflora	Nag Cove East	control	*S. patens*	10.37 ± 0.80	48.31 ± 1.10
			S. alterniflora	2.17 ± 0.67	44.51 ± 6.08
		fertilized	*S. patens*	3.98 ± 1.97	56.64 ± 2.85
			S. alterniflora	15.20 ± 2.76	78.59 ± 3.08
	Nag Cove West	control	*S. patens*	4.48 ± 0.67	33.18 ± 1.68
			S. alterniflora	4.23 ± 0.68	45.66 ± 2.90
		fertilized	*S. patens*	3.65 ± 0.73	54.64 ± 1.49
			S. alterniflora	18.69 ± 2.15	81.74 ± 2.82

TABLE 3.   Results of nutrient additions to monoculture plots of the major perennials in two Rhode Island (USA) salt marshes: Nag cove East and Nag Cove West. Data are means ± 1 SE.

| Species	Site	Treatment	Biomass (g/100 cm^2)	Avg. tiller height (cm)
J. gerardi	Nag Cove East	control	9.26 ± 1.03	42.24 ± 1.85
		fertilized	9.55 ± 0.54	44.57 ± 2.10
	Nag Cove West	control	9.25 ± 0.69	46.35 ± 1.84
		fertilized	7.77 ± 0.52	50.19 ± 2.34
S. patens	Nag Cove East	control	12.56 ± 0.73	47.03 ± 2.18
		fertilized	15.05 ± 1.52	56.12 ± 2.56
	Nag Cove West	control	7.50 ± 0.63	36.62 ± 2.29
		fertilized	15.18 ± 2.29	50.94 ± 3.17
D. spicata	Nag Cove East	control	5.83 ± 0.83	37.51 ± 1.94
		fertilized	11.50 ± 0.91	53.46 ± 2.59
	Nag Cove West	control	3.80 ± 0.39	32.63 ± 1.94
		fertilized	13.12 ± 3.24	55.57 ± 3.75
S. alterniflora	Nag Cove East	control	9.97 ± 0.65	66.09 ± 2.58
		fertilized	18.49 ± 1.28	82.22 ± 3.32
	Nag Cove West	control	8.62 ± 0.61	58.61 ± 2.97
		fertilized	19.36 ± 1.48	87.67 ± 2.80
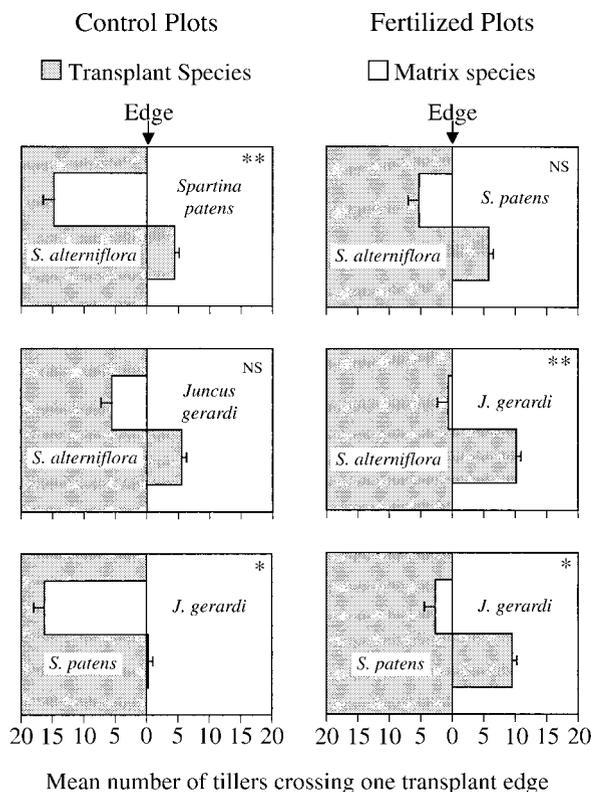
FIG. 3.   Effects of fertilization on resource competition at different levels of non-resource stress (i.e., at different tidal elevations). Each panel represents a transplant plot and illustrates the degree to which the transplant species invaded the surrounding (matrix) vegetation and the extent to which it was invaded by the matrix species. Bars represent tiller number crossing a transplant edge (mean ± 1 SE). Asterisks represent a statistically significant difference between transplant and matrix tiller movement within each fertilization treatment (Student's *t* test: * $P < 0.05$; ** $P < 0.01$; NS, not significant ($P > 0.05$).

etation. However, in the fertilized plots the vegetative spread of *S. alterniflora* was equivalent to that of *S. patens*. *Spartina alterniflora* and *J. gerardi* showed similar spread across transplant borders in the control treatment, but in fertilized plots *S. alterniflora* had significantly greater spread across the edge. Finally, under ambient nutrient levels *J. gerardi* was more invasive than *S. patens,* but in fertilized plots *S. patens* showed greater movement across the transplant border.

Nutrient addition reversed the direction of invasion across the transplant edge by differentially affecting the competitive abilities of the competing species. In all cases, nutrient addition significantly reduced the degree to which the matrix species invaded the transplants, indicating an increase in the ability of the transplant to resist invasion (Table 4). Additionally, the invasive abilities of *S. alterniflora* and *S. patens* transplants were significantly enhanced by nutrient addition in the *J. gerardi* zone; this was also the trend for *S. alterniflora* in *S. patens* but it was not significant.

Transplant experiment with nutrient and competition treatments

Both fertilization treatment and competition treatment (NC = no competition, BC = belowground competition only, and FC = full competition) influenced the amount of light available to the target species, growth of the target species, and ultimately the degree to which each target-species transplant was affected by its neighbors (Tables 5 and 6). Light transmittance was significantly reduced in FC plots but was consistently >80% in both BC and NC plots (Table 5), indicating that our BC treatment effectively removed aboveground neighbor effects. Also, light transmittance was generally lower in fertilized FC plots than in the controls, although this effect was never statistically significant. Fertilization had a positive effect on biomass

TABLE 4. The effects of fertilization on tiller movement across transplant edges at different marsh elevations.

Transplant spp. (target)	Matrix spp. (zone)	Treatment	Matrix species movement into transplant			
			No. tillers (mean ± 1 SE)	df	MS	F
S. patens	J. gerardi	control	16.25 ± 7.22	1	21.53	9.00*
		fertilized	2.73 ± 1.96			
S. alterniflora	J. gerardi	control	5.56 ± 0.69	1	8.27	36.91**
		fertilized	0.64 ± 0.64			
S. alterniflora	S. patens	control	14.8 ± 1.70	1	10.31	23.96**
		fertilized	5.28 ± 0.98			

Note: A one-factor ANOVA tested for differences in the amount of tiller movement of each species between fertilized and unfertilized treatments within each species–matrix combination.

* $P < 0.05$; ** $P < 0.01$; level of significant difference in tiller movement between fertilized and control plots for a species.

and tiller height for all target species regardless of competition treatment, confirming that nutrients are a limiting resource in these marshes (Table 5). Both competition and fertilization treatments had highly significant effects on the total biomass of the target species in every species pair (Table 6). The competition × fertilization interaction, which tests if fertilization has differential effects on aboveground and belowground competition, was significant for *D. spicata* in *J. gerardi, S. patens,* and *S. patens* in *J. gerardi,* but was not significant for *D. spicata* in *S. patens.*

The interactions between fertilization and competition treatment were due to differences in the relative contributions of aboveground and belowground processes to the total effect of competition on plant biomass in fertilized and control plots (Fig. 4). The overall effect of competition can be understood as simply the difference in plant biomass between FC and NC treatments. Assuming that the aboveground and belowground components of competition were additive, the effect of belowground competition is the difference in biomass between plants in BC and NC treatments, and aboveground competitive effect accounts for biomass differences between plants in BC and FC treatments. For all species pairs in both control and fertilized plots there was a significant difference in plant biomass between NC and FC treatments, indicating that competition occurred at both ambient and high nutrient levels. In the control treatment, BC and FC treatments had similar biomass production for *S. patens* transplants in *D. spicata, D. spicata* transplants in *J. gerardi,* and *D. spicata* transplants in *S. patens,* indicating that belowground processes account for the majority of the effects of competition under ambient nutrient levels for these species combinations. In fertilized plots, however, biomass production was relatively similar among plants from NC and BC treatments while the average biomass in the FC treatment was consistently lower. This pattern was statistically verified for *S. patens* in *D. spictata* and *D. spicata* in *J. gerardi.* Thus in these plots, plants experiencing only belowground competition did just as well as those that had no neighbors when nutrients were abundant. These patterns were not found for *S. patens*

transplants in the *J. gerardi* zone, in which case all competition treatments were significantly different from one another within fertilization level. This suggests that for this species pair, aboveground and belowground processes each have important effects on total competition under both ambient and elevated nutrient levels. Similarly, significant differences between all competition treatments in fertilized *D. spicata* plugs in *S. patens* suggests that aboveground and belowground competition contribute to the total competitive effect at high nutrient levels.

DISCUSSION

Our results suggest that nutrient additions in southern New England (USA) marshes reversed the outcome of competitive interactions between the common marsh perennials, and that these competitive reversals could lead to substantial shifts in the zonation of plants across tidal gradients with increasing levels of nutrient availability. These shifts most likely occurred because nutrient supply determines whether competitive dominance was dictated by aboveground competition for light or belowground competition for nutrients coupled with inherent trade-offs between aboveground and belowground competitive abilities in marsh perennials. These results have implications for both plant competition theory and salt-marsh conservation.

Nutrient-addition experiment at zonal boundaries: species border responses to fertilization

The effect of fertilization on the competitive interactions between marsh perennials in the Nag East and Nag West marshes (Rhode Island, USA) were similar to those found by Levine et al. (1998). At all sites, fertilization of species borders resulted in the competitive subordinate under ambient nutrient levels (Bertness 1991*a, b*) dominating the plot in both percent cover and biomass, as well as reaching a taller average height than the other species in the mixture (Tables 2 and 3, Fig. 2).

Previous transplant experiments have shown that the lower marsh species can persist at higher elevations only if the neighboring vegetation is removed, and sim-

TABLE 4. Extended.

| Transplant species movement into matrix | | | |
No. tillers (mean $\pm$ 1 SE)	df	MS	F
0.29 $\pm$ 0.19 9.48 $\pm$ 1.47	1	16.03	54.93**
5.55 $\pm$ 1.29 10.14 $\pm$ 1.34	1	3.17	6.45*
4.38 $\pm$ 0.74 5.78 $\pm$ 1.36	1	0.38	0.82

ilarly that *Distichlis spicata* is competitively excluded to saline bare patches in the *Juncus gerardi* and *Spartina patens* zones (Bertness and Ellison 1987, Bertness 1991*a, b*). Thus at zonal boundaries under ambient marsh conditions *J. gerardi* is the dominant competitor, followed by *S. patens* and then *S. alterniflora* and *D. spicata*. Our results show that fertilization of these borders completely reverses this hierarchy. The experiments here demonstrate that the effects of nutrient additions at species borders are robust across three replicate marshes and can likely be generalized to similar southern New England salt marshes.

Transplant experiment with nutrient treatment: the effects of tidal elevation on nutrient competition

The nutrient-addition experiments at naturally occurring species borders do not tell us the extent to which species distributions can shift in response to nutrient addition; however, the results of the transplant experiment across zonal boundaries indicate that nutrient availability has similar effects on the competitive interactions between marsh plants across the entire marsh landscape as was found at species borders. That is, the nutrient-dependent competitive hierarchies found at species borders were also detected in transplant mixtures at higher elevations (Table 4, Fig. 3). Nutrient addition reversed the direction of invasion across the transplant edges, increasing the competitive ability of the lower marsh species and reversing the outcome of competition between the transplant and the surrounding vegetation. Because fertilization reversed the competitive hierarchy of marsh plants even away from zonal boundaries, our results suggest that nutrient addition can cause substantial shifts in plant zonation across the marsh landscape. Increased nutrient availability at the landscape-level scale could lead to substantial increases in *S. alterniflora* and *D. spicata* and the gradual exclusion of *S. patens* and *J. gerardi* (Levine et al. 1998).

The results of this transplant experiment suggest that the role of the non-resource stress gradient in structuring the salt-marsh plant community changes with nutrient availability. Under ambient nutrient conditions, areas of high non-resource stress—such as the anoxic, waterlogged low-marsh habitat or the highly saline bare patches—serve as a refuge from competi-

TABLE 5. Results from a two-factor ANOVA testing the effects of fertilization and competition treatment on tiller height and light transmittance for *Spartina*, *Juncus*, and *Distichlis*.

Target	Matrix	Competition‡	Fertilization	Tiller height (cm)		Light transmittance (%)	
				Mean	1 SE	Mean	1 SE
S. patens	*J. gerardi*	NC	control	[A,B]37.59**	1.92	[a]87.82	3.15
			fertilized	[a]55.09	2.82	[A]88.94	2.76
		BC	control	[A]41.73	8.41	[a]89.29	3.87
			fertilized	[a]48.63	1.80	[A]88.25	2.44
		FC	control	[B]37.10	2.52	[b]21.31	5.46
			fertilized	[a]40.69	4.89	[B]14.97	5.32
S. patens	*D. spicata*	NC	control	[A]36.07**	1.34	[A]88.12	3.54
			fertilized	[a]54.26	3.16	[a]83.65	3.88
		BC	control	[B]30.94**	1.23	[A]85.91	3.36
			fertilized	[b]45.70	1.53	[a]90.76	2.31
		FC	control	[C]40.08**	1.06	[B]14.78	3.87
			fertilized	[a]54.48	2.06	[b]7.08	2.37
D. spicata	*J. gerardi*	NC	control	[A]33.58	1.84	[A]91.76	2.56
			fertilized	[a]35.95	0.99	[a]94.24	1.38
		BC	control	[B]24.26**	2.09	[A]91.31	2.05
			fertilized	[a]33.68	1.09	[a]89.66	4.69
		FC	control	[A]35.88	4.03	[A]14.30	5.02
			fertilized	[a]35.47	2.00	[b]15.87	6.19
D. spicata	*S. patens*	NC	control	[A,B]31.50	0.92	[A]85.81	5.40
			fertilized	[a]37.55	0.68	[a]76.05	6.07
		BC	control	[B]25.91*	0.98	[A]84.87	10.26
			fertilized	[a]32.02	1.21	[a]81.11	5.18
		FC	control	[A]32.60	0.81	[B]19.36	6.99
			fertilized	[a]34.84	1.60	[b]16.26	6.17

Notes: Within each species pair, data with different superscript letters are significantly different ($P < 0.05$) between competition treatments. Capital letters refer to control plots and lowercase letters refer to fertilized plots.

* $P < 0.05$; ** $P < 0.01$; significant differences between control and fertilized plots within competition treatment.

‡ NC = no competition, BC = belowground competition only, FC = full competition.

TABLE 6. Results from a two-factor ANOVA testing the effects of competition treatment, C (full competition, belowground competition, and no competition), and fertilization treatments, F, on plant biomass, (*Spartina, Juncus,* and *Distichlis*).

Target	Matrix	Effect	ANOVA		
			df	MS	F
S. patens	*J. gerardi*	C	2	6.04	60.27**
		F	1	1.90	39.19**
		C × F	2	0.71	7.36**
S. patens	*D. spicata*	C	2	0.70	13.68**
		F	1	1.42	55.32**
		C × F	2	0.26	5.05*
D. spicata	*J. gerardi*	C	2	0.89	15.23**
		F	1	1.71	58.75**
		C × F	2	0.20	3.49*
D. spicata	*S. patens*	C	2	0.94	14.46**
		F	1	1.88	27.09**
		C × F	2	0.86	1.32

Note: Tests were performed within each species pair combination (total df = 5 per test).
  * $P < 0.05$; ** $P < 0.01$.

tion for the subordinates. However, when nutrients are abundant, the stress tolerators become competitively dominant and can shift their distributions toward the less stressful areas of the marsh. Under these nutrient-rich conditions the non-resource stress gradient does not counter the competitive hierarchy to allow the co-existence of the competitive subordinates with the dominants; rather, those species that can tolerate the stressful conditions are also able to dominate the more benign areas of the marsh.

Transplant experiment with nutrient and competition treatments: mechanisms of competition

The consistent reversal in the outcome of competition between zonal dominants when nutrients are added suggests that a simple mechanism may be driving the interactions between marsh plants. A trade-off between aboveground and belowground competitive abilities would explain the nutrient-dependent competitive hierarchy if fertilization shifts the interaction from belowground to aboveground competition. We found that in control plots, the average plant biomass in BC (belowground competition only) treatments was similar to that in FC (full-competition) treatments in control plots, but in fertilized plots the BC treatment had similar effects on plant biomass as the NC (no-competition) treatment (Table 5, Fig. 4). Although significant differences were found between all competition treatments in fertilized *D. spicata* plugs in *S. patens* plots, the relative differences between competition treatments still support this interpretation. This pattern indicates that belowground processes account for the competitive effects at low nutrient levels and aboveground processes contribute more to the effects of competition at high nutrient availability. This was least evident for *S. patens* transplants with *J. gerardi* neighbors, where we found statistically significant differences in biomass

between all competition treatments in both control and fertilized plots. This suggests that both belowground competition and aboveground competition occur between *J. gerardi* and *S. patens* at high and low nutrient levels. Importantly, our interpretations of these results assume that above- and belowground competitive effects are additive and therefore sum to the effects of total competition. More elaborate experiments are necessary in order to identify if interactions between above- and belowground competition exist in these perennials and how such interactions affect the outcome of competition under different nutrient conditions.

Greenhouse observations and the results of this study support that interspecific differences in aboveground and belowground biomass allocation determine each species' competitive ability at different resource levels. *Juncus gerardi,* the dominant competitor under ambient nutrient conditions, has relatively more biomass allocated to belowground, nutrient-gathering structures than to aboveground photosynthetic tillers (J. S. Brewer, T. Rand, J. M. Levine, and M. D. Bertness, *unpublished data*), which is expected for a species that is a good belowground competitor and poor aboveground competitor (Tilman 1982, 1988, 1990, Berendse and
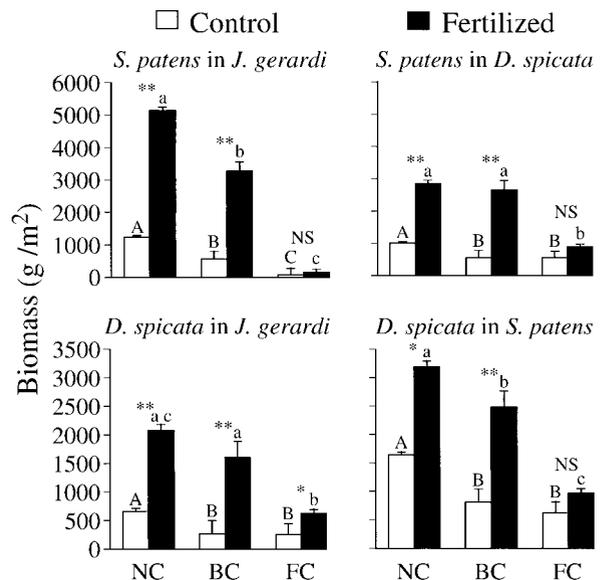

FIG. 4. The effects of fertilization on plant biomass (*Spartina, Juncus,* and *Distichlis*) in each of three competition treatments: no competition, NC; belowground competition only, BC; and full competition, FC. Bars represent average biomass (means and 1 SE) scaled to 1-m² plots. Asterisks indicate a statistically significant difference between fertilized and control plots within competition treatment (one-way ANOVA: *$P < 0.05$; **$P > 0.01$; NS, not significant [$P < 0.05$]). Letters identify statistical groupings from a one-way ANOVA between competition treatments within each fertilization treatment; bars with different letters indicate statistically significant differences between competition treatments, and capital letters refer to control plots while lowercase letters refer to fertilized plots.

Elberse 1990). Also, those species that dominated under fertilized conditions were taller and thus more likely to be better competitors for light (Tables 1 and 2; Levine et al. 1998). The relative importance of both above- and belowground processes under high and low nutrient levels for *S. patens* transplants in *J. gerardi* is expected because these two are the most morphologically similar of any species pair in this experiment. However, subtle differences in belowground and aboveground competitive abilities still drive the dynamics of the interaction: at ambient nutrient levels *J. gerardi* dominates due to its slightly greater allocation to belowground structures, but fertilization tips the competitive balance in favor of *S. patens* due to its slightly taller tillers in highly productive plots.

Salt marshes and competition theory

The predominant theories of competition do not account for the potentially unique effects of non-resource stress when predicting the nature and importance of competition along environmental gradients (Grace 1990, 1991). Our results show that this distinction is necessary in order to understand the processes that structure salt-marsh plant communities, where we have found that a non-resource stress gradient established by tidal flooding interacts with resource competition to determine the zonal distributions of the common marsh perennials.

Under ambient marsh conditions, the physically stressful areas of the marsh provide a refuge from competition for the competitive subordinates (Bertness 1991*a, b*). Initially, this appears to fit the predictions of the CSR (competitor/stress tolerator/ruderal) theory of competition, which hypothesizes that some species are good competitors while others are stress tolerators, regardless if that stress is due to resource limitation or physical factors (Grime 1977, 1979, Huston 1979). However, our results indicate that at high productivity (i.e., when nutrients are abundant), the stress tolerators are also the competitive dominants. Thus adaptation to low nutrients and tidal stress are decoupled in salt-marsh perennials, and consequently these species cannot be classified strictly as either ''stress tolerators'' or ''good competitors.'' Our results also are not predicted by the resource-ratio theory of competition, which predicts that non-resource stress influences species distributions simply by affecting the ability of each species to compete for a limiting resource. While this theory claims that interspecific competition occurs across a gradient in non-resource stress, experiments in the salt marsh have shown that competition does not occur at increased levels of tidal stress, i.e., when species are transplanted below their natural tidal-height distribution (Bertness and Ellison 1987). Rather than competitive ability, it was each species' ability to tolerate tidal stress that determined its seaward distribution. However, we did find that competition occurs across a gradient in nutrient availability, as competitive effects were seen in both our fertilized and unfertilized transplants in the high marsh. Furthermore, a trade-off between aboveground and belowground competitive abilities determined a species' success at different ratios of resources in our experiments. Thus while the effects of nutrients on marsh-plant competition alone agreed with the predictions of the resource-based theory of competition (Newman 1973, 1983, Tilman 1982, 1988, 1990), the non-resource gradient had unique effects on plant community structure not accounted for by this hypothesis. That is, the reduction of non-resource stress alone did not change the outcome of competition simply by affecting productivity levels (Table 4, Fig. 3); rather, the natural gradient in non-resource stress prevented the competitive exclusion of the competitively inferior species at specific ratios of resources.

In the salt-marsh plant community, a trade-off between belowground competitive ability and the ability to tolerate the physical stressors of the marsh (soil anoxia and high salinity levels in the low marsh, and high salinity levels in the bare patches) appears to drive plant zonation patterns across the salt-marsh landscape. Importantly, the non-resource stress gradient in the marsh does not correspond to a productivity gradient on the community level (Bertness and Ellison 1987, Bertness 1991*a*). Because stress tolerators can also be good competitors, as demonstrated here, it cannot be assumed a priori that a non-resource stress gradient corresponds to the inverse of a productivity gradient at the community level. Instead, a non-resource stress gradient is reflected in the potential productivity of each species and can only be identified through transplant experiments. Consequently, the potential for non-resource stress to interact with competitive ability to determine community structure cannot be inferred from experiments along productivity gradients, and may require explicit attention in other communities that are distributed along gradients in non-resource stress.

Implications for conservation

The results of this study have bearing on our understanding of anthropogenic effects on salt marshes. Recent human activities, such as the manufacturing of artificial fertilizer, the massive production of legume crops, and the burning of fossil fuels, have at least doubled the amount of fixed nitrogen available on our planet (Vitousek et al. 1997). Coastal waters have experienced heavy eutrophication over the past century (Ryther and Dunstan 1971, Neilson and Cronin 1981, Howarth 1988, Vitousek et al. 1997, Carpenter et al. 1998, Holligan and Reiners 1992), and salt marshes are particularly vulnerable to rising nutrient levels because they are naturally N-limited (Valiela and Teal 1974, Valiela et al. 1985). Our results demonstrate that the striking zonation of New England marsh perennials, which has been used as a classic example of plant community organization (Johnson and York 1915, Clements 1916, Miller and Egler 1950), is partially driven

by competition for nutrients, most likely nitrogen (Valiela and Teal 1974, Valiela et al. 1985). Moreover, our results predict that eutrophication of marsh communities will lead to the competitive exclusion of those species that dominate the upper marsh under the naturally low-N conditions (Levine et al. 1998). Such a shift in the plant species composition and distribution would likely affect other trophic levels and result in a dramatic change in the salt-marsh community (Hacker and Gaines 1997). However, only by continuing to develop a more detailed mechanistic understanding of how biotic and abiotic factors interact to structure salt-marsh communities will we be able to predict the effects of anthropogenic impact and develop effective strategies for marsh conservation.

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