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Structure and organization of a northern New England salt marsh plant community

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Summary

1 Northern New England marshes are characterized by mid-elevation areas of sparse vegetation, but high species diversity, which are not found in the well-studied marshes further south. These forb pannes occur in habitats that are more waterlogged and anoxic than adjacent clonal turf-dominated areas.

2 When the clonal turfs were transplanted into forb pannes, they showed reduced growth with and without neighbours present, suggesting that they are physically limited from invading the forb pannes. Conversely, when forb panne species were transplanted into surrounding turf areas, they flourished when neighbours were removed, but were suppressed when neighbours were present, suggesting that interspecific plant competition restricts the forbs to panne habitats.

3 Recovery of disturbance-generated bare patches was extremely slow, taking twice as long as in southern New England marshes. Secondary succession in northern New England marshes was driven by competitive interactions rather than by facilitative processes typical in southern New England marshes.

4 Differences in the structure and dynamics between northern and southern New England marsh systems may be due to differences in climate and human impacts. Waterlogged pannes are probably more common in northern marshes because they are generally larger and less ditched and drained. Reduced solar radiation and summer heating in northern New England reduces the potential for high soil salinities seen in southern marshes. This lack of the need for amelioration by neighbours probably explains the absence of facilitation.

Key-words: facilitation, redox, salt marsh, *Spartina*, succession, zonation

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Introduction

Coastal salt marshes are a major native habitat along the entire east coast of North America (Chapman 1974) and have long been important model systems for studying community and ecosystem level processes. Salt marshes are relatively simple systems, comprised of only a few dominant species, typically found in distinctive zonation patterns across a compact gradient of tidal flooding and salinity (Adam 1990). The distinct elevational gradients in edaphic factors and relatively simple plant assemblages make salt marshes attractive for experimental studies of community structure (Pennings & Bertness 2001). The plant zonation is thought generally to be caused by physical stress (waterlogged, anoxic soils) at low elevations and plant competition at high elevations. Competitively subordinate plants are excluded by their competitive superiors except at lower elevations where the anoxic soil conditions cannot be tolerated by the competitive dominants (Bertness & Pennings 2000). This picture of salt marsh plant communities, however, is overly simplistic because of positive feedbacks between marsh plants and potentially limiting physical stresses. At low elevations, initial colonization of reduced soils by *Spartina alterniflora* Loisel. increases soil oxygen in waterlogged anoxic soils and allows the success of other marsh plants, whereas at higher marsh elevations plant establishment is necessary to prevent the development of potentially limiting hypersaline soil conditions (Bertness 1991a; Bertness *et al.* 1992; Bertness & Hacker 1994). Similarly, at wave-exposed locations, initial plant colonization buffers further plant establishment from wave disturbance (Bruno 2000). Thus, whereas plant competition is largely responsible for the strong spatial segregation of plants across marsh landscapes, positive feedbacks and habitat modification are often necessary

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for the actual presence of marsh vegetation at a particular location.

A major weakness of our current understanding of the organization of salt marsh plant communities is that most of the work has come from just a handful of study sites. This is not surprising, given the labour-intensive nature of the experiments involved. As a consequence, we do not know how general our current conceptual model of marsh plant community organization is or know how far we can extrapolate our understanding of salt marshes to novel marsh systems.

In contrast to the well studied salt marshes of Southern New England (Massachusetts, Rhode Island and Connecticut) (Miller & Egler 1950; Niering & Warren 1980; Bertness & Ellison 1987; Bertness 1991a,b; Bertness 1992; Bertness & Hacker 1994), the salt marsh plant communities of northern New England (New Hampshire and Maine) have received relatively little attention (Theodose & Roths 1999; Bertness & Ewanchuk 2002; Ewanchuk & Bertness 2003). The plant communities of northern New England marshes differ conspicuously from their southern New England counterparts. First, northern marshes experience a cooler climate and more severe winter conditions, such that winter icing and ice damage is so severe that it limits low marsh vegetation. Although ice disturbance can destroy low marsh vegetation in southern New England, these areas generally recover quickly to dense monoculture of *S. alterniflora*. This establishment and recovery is prevented in the north by the frequency of icing events. Severe ice scour can also affect the high marsh in northern marshes, ripping holes in the vegetation matrix and leaving gaps without plants or the underlying peat (Mathieson *et al.* 1982; Hardwick-Witman 1985; Ewanchuk & Bertness 2003). Even less severe ice damage can simply kill high marsh vegetation by scouring or by depositing sediment and smothering vegetation. Cooler summer temperatures in northern marshes also lead to less evaporation of sediment pore water and therefore lower soil salinities (Bertness & Ewanchuk 2002). As a consequence, it has been suggested that the positive effects of neighbours, via amelioration of salt stress, are less common and less intense in northern salt marshes (Bertness & Ewanchuk 2002).

A second major difference between southern and northern New England salt marshes is the common occurrence in the north of mid-elevation areas of sparse vegetation cover. These so-called forb pannes have been hypothesized to represent areas of poor soil drainage and anoxia that limit plant success (Miller & Egler 1950; Theodose & Roths 1999).

We examine the basic structure and dynamics of a northern New England salt marsh plant community. Specifically, we experimentally examine (i) the factors responsible for generating their distinct zonation, and (ii) the mechanisms of secondary succession. Together these results will establish an initial framework with which to understand the structure and organization of these marshes.

Methods

STUDY SITE

All research was conducted at the Wells National Estuarine Research Reserve, Wells, Maine, USA, on the Little River marsh (43°20.410′ N, 70°32.340′ W), whose area (250 hectares) is typical of many coastal marshes in northern New England. The overall plant community pattern differs from the better studied marshes in southern New England (Miller & Egler 1950; Niering & Warren 1980; Bertness 1991a,b). In both areas, low marsh elevations, defined as habitats flooded daily by tides, are dominated by *S. alterniflora*, the seaward border of the high marsh by the marsh hay *Spartina patens* (Aiton) Muhl. and the terrestrial border of the high marsh by the black rush *Juncus gerardi* Loisel. However, middle and high marsh elevations in northern New England are dominated by a patchy mosaic of forb pannes and bare space. These forb pannes include a number of annual and perennial forb species (*Agalinis maritima* Raf., *Atriplex patula* var. *hastata* L., *Glaux maritima* L., *Limonium nashii* (Walter) Britton., *Plantago maritima* L., *Salicornia europaea* L., *Suaeda linearis* (Ell.) Moq., *Triglochin maritimum* L.), many of which occur in low abundance in southern New England marshes. In the south these forbs are generally restricted to disturbance-generated bare patches (Shumway & Bertness 1992), but in the north these forbs flourish in panne areas, which appear to be permanent features of the marsh surface.

QUANTIFICATION OF VEGETATION PATTERNS

The percentage cover of each species was determined using a 0.5 × 0.5 m quadrat subdivided into 100 (5 × 5 cm) sampling cells, which were censused for the presence and absence of each marsh plant. Quadrats were placed at 1-m intervals along 10 parallel, 50-metre transects across the marsh. Tidal elevation of each quadrat was determined using a surveyor's level and then corrected to National Oceanographic and Atmospheric Administration tidal predictions.

The forb panne community was studied more closely by placing a transect (15 m long) from the centre of each of 10 pannes towards the edge and into the adjacent zone. Along each transect we sampled the percentage cover of each species as well as the percentage bare space in 15 quadrats (0.25 × 0.25 m at 1-m intervals).

QUANTIFICATION OF PHYSICAL PARAMETERS ACROSS THE MARSH HABITAT

Substrate salinity and redox potential were quantified in June, July and August of each year in the *S. patens*, panne and *J. gerardi* zones. Pore water salinity was measured by extracting a small (2 × 2 × 2 cm) core of peat and squeezing out the core water through cotton gauze. Salinity of the pore water was quantified using a hand-held

NaCl refractometer. Soil redox potential was measured by removing a small (1 cm diameter × 2–3 cm deep) core from the marsh and inserting a redox electrode into the hole (portable pH/ISE meter, model 230 A, fitted with platinum redox electrode, model 96-78-00, filled with 4 mol/L KCL saturated with Ag/AgCl reference solution; Orion Research Inc., Beverly, MA, USA).

Soil moisture content was quantified by collecting 10 soil cores (10 × 10 × 10 cm) from each zone in July of 1999 and 2000. Cores were placed in Ziploc® bags, brought back to the laboratory, weighed and then dried at 60 °C for 2 weeks. Cores were then re-weighed to determine gravimetric water (% by weight).

Water table depth was quantified by measuring the depth to the water level in eight wells haphazardly located in each zone approximately 3 hours after high tide. Measurements were taken daily for a month to assess water table variation over a full lunar tidal cycle. Depth to the water table was used to assess marsh zone drainage patterns, and as an indication of the waterlogging experienced by plants in each of the zones.

PLANT ZONATION TRANSPLANTS

To examine the hypothesis that the zonation of plants in northern New England marshes is a result of a combination of abiotic stress and interspecific plant competition we set up a large reciprocal transplant experiment in March–April of 1998. Transplants were done with and without neighbours (i.e. with and without competition), using the three main zones or community types, *J. gerardi*, *S. patens* and *T. maritimum* (the dominant in the panne community). We transplanted large (20 × 20 × 25 cm deep) blocks of substrate containing live rhizomes, which were removed from monospecific stands of each of the dominant species and placed directly into one of the other marsh zones or back into their native zone ($n = 16$ per species per zone). Transplants were placed randomly in each zone, spaced by at least 2 m, and then randomly assigned to one of the competition treatments. The 'without competition' treatment was created by clipping back the surrounding above-ground vegetation within a 15-cm radius and trenching around the perimeter by cutting with a knife to a depth of 20 cm to sever all rhizome connections between the plots and the surrounding vegetation. Clipping was maintained for several weeks until the vegetation ceased to grow back and the clipped area was then covered with shade cloth to reduce evaporation from the soil surface and prevent an artificial increase in soil salinity (Bertness *et al.* 1992). This maintained the natural edaphic environment while removing the competitive effects of the neighbouring vegetation. The remaining (with competition) blocks were left with unmanipulated background vegetation. Each transplant was monitored annually in September (1998–2001) for change in species biomass by clipping above-ground biomass from a 10 × 10 cm area in one corner of each transplant. Samples were brought back to the laboratory, dried, sorted by species, and weighed. For simplicity, only biomass data from the last year of the transplants are presented. All data were analysed by a three-way fixed-effect ANOVA using Species, Zone and Competition as main effects. Biomass data were $\log(x + 1)$ transformed to increase homogeneity of variances and data set normality (Underwood 1997).

PANNE COMMUNITY TRANSPLANTS

To test the hypothesis that the whole forb panne plant community is restricted to areas of increased waterlogging and low redox potentials due to competition with the clonal turfs, 48 blocks (30 × 30 × 30 cm), representing the whole panne community, were transplanted into each of the three zones in spring of 1998. Large blocks of peat, including roots and rhizomes, were used to minimize any disturbance effects. Sixteen blocks were transplanted into each of the *S. patens* zone, the *J. gerardi* zone, and back into the panne habitat, and blocks were then randomly assigned to with or without competition treatments as before. At the end of the next three growing seasons in September, species percentage cover, richness and biomass data were collected. Percentage cover was estimated using the point intercept method (50 points). The first species hit under each of the intercept points was used to calculate the transplant percentage cover. Other species located under the same intercept point were then used in the calculations of species richness. Biomass samples were harvested and processed as described above, but only data from the final year are presented. All data were analysed by repeated-measures ANOVA using Zone and Competition as fixed main effects, and Zone × Competition as the interaction term. All biomass data were $\log(x + 1)$ transformed and all percentage cover data were arcsine square-root transformed to increase homogeneity of variances and normality (Underwood 1997). Data were analysed with JMP statistical software package, version 3.1 (SAS 1995).

MECHANISM OF SECONDARY SUCCESSION

To examine the hypothesis that mechanisms of secondary succession differ, we quantified species interactions during bare patch recovery in northern New England to compare with previous work in marshes (Bertness 1991a; Bertness & Shumway 1993). We located 32 (0.75 × 0.75 m) plots along each of the dominant species borders at the Little River marsh (*S. alterniflora*/*S. patens*, *S. patens*/*Juncus*, *S. patens*/forb panne, and *Juncus*/forb panne). Each plot was trenched around the perimeter to a depth of 20 cm to sever all rhizome connections to the surrounding vegetation. We then applied a systemic herbicide (Roundup®, Monsanto, St. Louis, USA), to each of the plots and then removed all remaining above-ground vegetation to make experimental bare patches. Trenching ensured that the herbicide was not translocated out of the patch area. These artificial bare patches have

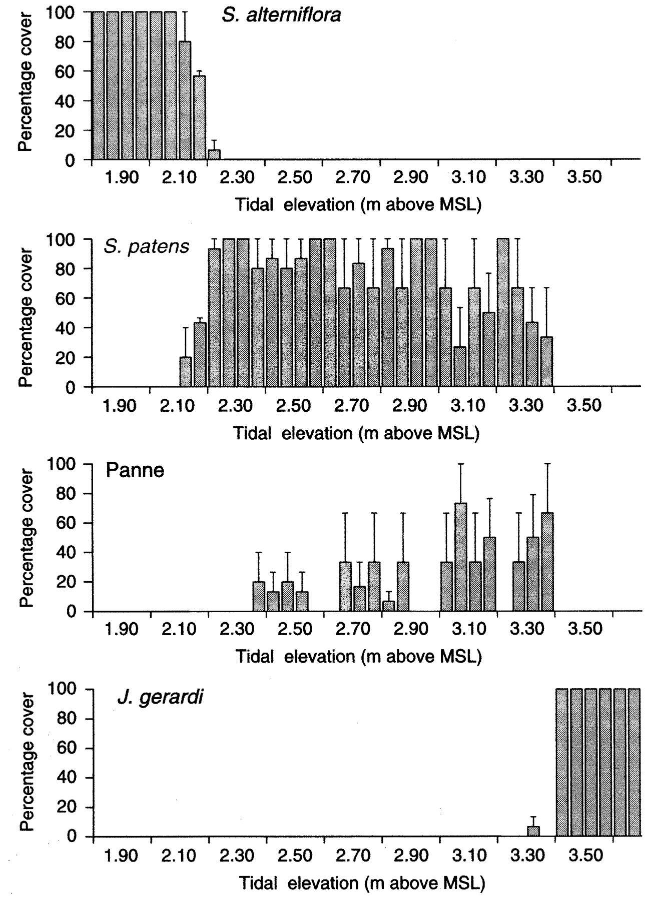

Fig. 1 Summary of transect survey of marsh vegetation at Little River marsh. Data are percentage cover estimates from 25-m^2 quadrats. Tidal elevation is given in metres above mean sea level (MSL). Percentage cover data are means of 10 transects ± SE.

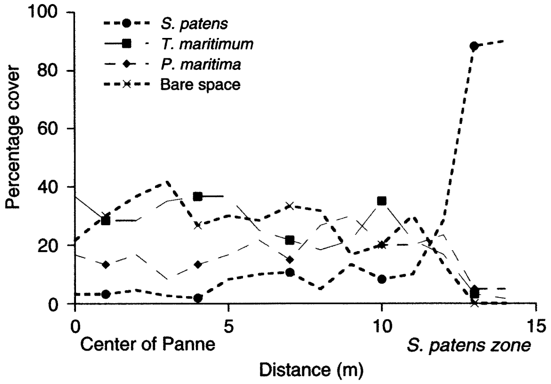

Fig. 2 Percentage cover of *T. maritimum* and *P. maritima* within the forb pannes. The percentage cover of *S. patens* is also shown.

been shown to have colonization patterns virtually identical to natural bare patches (Bertness 1991a; Bertness & Shumway 1993). Patches in each marsh zone were then randomly assigned to one of four different removal treatments: (i) border species A, (ii) border species B, (iii) all seedlings, and (iv) an unmanipulated control. The seedling removal was included to examine the affect of sexual reproduction on the re-colonization of the disturbances. The target removal species was weeded out of each plot weekly during the early growing season and then biweekly for the rest of the summer for 4 years (1998–2001). Colonization of each plot was monitored at the end of each summer (September) by quantifying the percentage cover of each species in each plot. Percentage cover data for each species was arcsine square-root transformed and used as response variable in a two factor ANOVA using Border and Removal as fixed main effects.

Substrate salinity of each bare patch was quantified in June, July and August of each year (1998–2001) using methods described above.

Results

MARSH ZONATION SURVEYS

Northern New England salt marshes are best described as mosaics of discrete patches of low density forb pannes and monospecific stands of *S. patens* and *J. gerardi* (Fig. 1). Although the forb pannes are found within both the *S. patens* and *J. gerardi* zones, the majority of them are found at tidal elevations normally dominated by *S. patens* (Fig. 1).

Quadrat sampling along transects through the forb pannes indicated that two species, *T. maritimum* and *P. maritima*, generally make up 50–60% of the vegetation in the panne community and there is a sharp border between the forb panne areas and the surrounding vegetation matrix (Fig. 2). There is overall lower vegetation

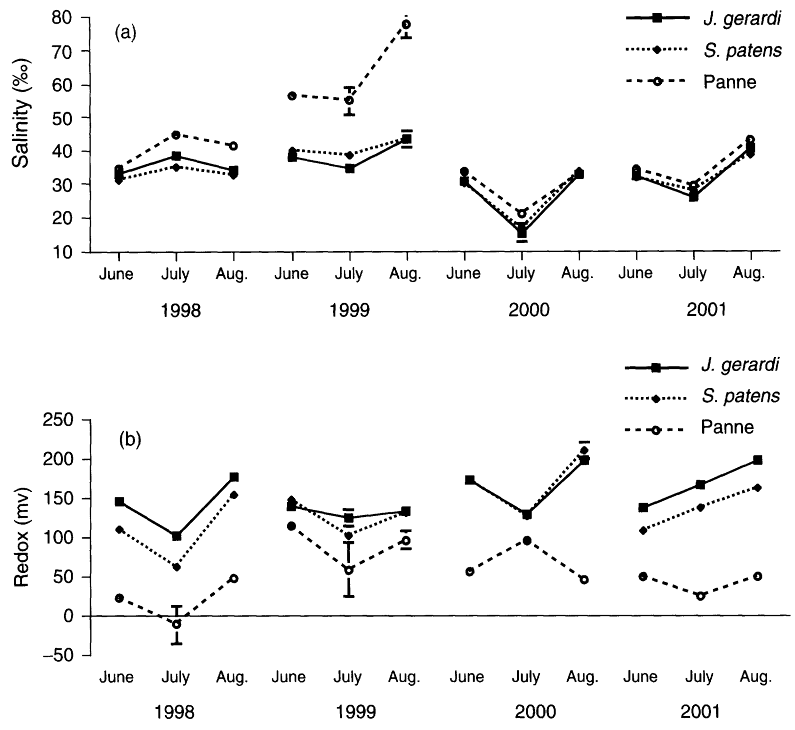

Fig. 3 Surface salinity (a) and redox potential (b) of soil in the three middle marsh zones.

Table 1 Summary of the repeated measures analysis of variance on substrate salinity and redox potential in each of the three zones (*J. gerardi*, *S. patens* and Panne) (Fig. 3)

	Salinity (‰)		Redox (mv)	
Year	d.f.	Wilk's Λ	d.f.	Wilk's Λ
1998				
Location	2,33	0.06***	2,33	0.16***
Time	2,32	0.06***	2,32	0.24***
Location × time	4,64	0.15***	4,64	0.88
1999				
Location	2,33	0.16***	2,33	0.55**
Time	2,32	0.15***	2,32	0.01**
Location × time	4,64	0.27***	4,64	0.72
2000				
Location	2,33	0.75**	2,33	0.06***
Time	2,32	0.09***	2,32	0.61***
Location × time	4,64	0.46***	4,64	0.33***
2001				
Location	2,33	0.26***	2,33	0.08***
Time	2,32	0.02***	2,32	0.30***
Location × time	4,64	0.59**	4,64	0.50***

$*P < 0.05$, $**P < 0.01$, $***P < 0.001$.

cover and a relatively large amount of bare space or unvegetated substrate in the pannes compared with their surroundings (Fig. 2).

PHYSICAL PARAMETERS ACROSS THE MARSH ZONES

Soil salinity generally increased in each of the zones over the summer months (Fig. 3, Table 1), and was generally higher in the forb pannes than either the *S. patens* or *J. gerardi* zones. The magnitude of the differences among months and among zones was not, however, consistent between years (Fig. 3). Soil redox potential was consistently lower in the forb pannes than in either of the other two zones, with the *J. gerardi* zone typically having the highest, although there was much variability between years (Fig. 3, Table 1).

Soil water content was significantly different among zones ($P < 0.001$). Water content was highest (*c.* 50%) in the forb pannes and lower in *J. gerardi* (Fig. 4).

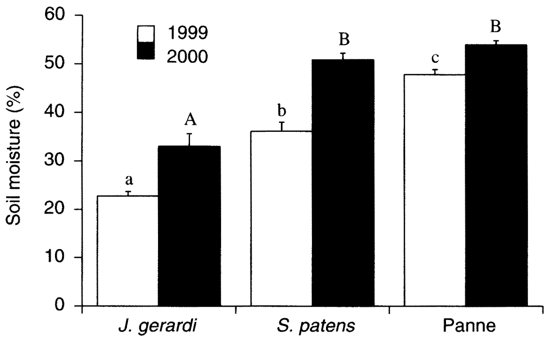

Fig. 4 The percentage soil moisture in each of the three middle marsh zones. Moisture data were collected in July of both 1999 and 2000. Letters identify statistical groupings from post hoc test; bars with different letters indicate statistically significant differences. Error bars are standard errors of the percentages.

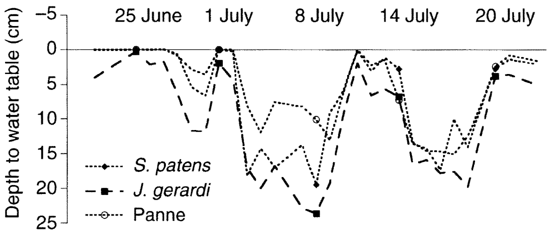

Fig. 5 Depth to water table in each of the middle marsh zones, measured over a full lunar tidal cycle.

WATER TABLE

Quantification of water table depth over a lunar tidal cycle indicated that during the spring tides there is very little difference between zones in the marsh (Fig. 5). In the drier periods of the month, during neap tides, however, the water table in the panne community areas is significantly higher (Fig. 5), a difference reflected in higher soil water content and lower redox potentials (Figs 3 and 4).

ZONATION TRANSPLANTS

Transplantation of the zonal dominants indicated that both abiotic and biotic factors control the overall zonation pattern of northern New England salt marshes. When *T. maritimum* was transplanted out of the panne habitat into the surrounding zones it grew just as well in the *S. patens* zone, than when it was transplanted back into the panne habitat (Fig. 6a, Table 2). In the *S. patens* zone, its biomass was more than double without than with competition competitors (Fig. 6a), suggesting that it is competitively excluded from this zone. When *T. maritimum* was transplanted to the *J. gerardi* zone it again showed reduced growth when competitors were present (Fig. 6a, Table 2). *Plantago maritima*, which was inadvertently transplanted along with the *T. maritimum*, also showed increased biomass when transplanted into the *J. gerardi* and *S. patens* zones without competition (Fig. 6a, Table 2). *Plantago maritima*, however, grew better without competitors in both the *J. gerardi* and *S. patens* zones than it did in the panne habitat where it normally is found.

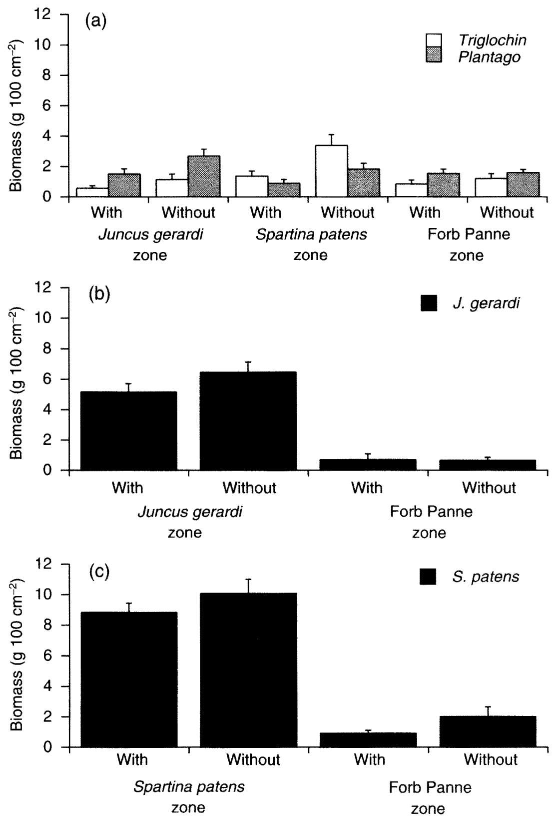

Fig. 6 The effect of transplant location and competition on the biomass of each of the dominant zone species: (a) panne (*T. maritimum* and *Plantago maritima*), (b) *J. gerardi* and (c) *S. patens*. Bars represent average above-ground biomass at the end of the experiment (means ± SE).

Table 2 Results of analysis of variance on the final year (2001) biomass data of plant zonation transplants (Fig. 6). For each species the data are the results of a two-way (Location × Competition) ANOVA on $\log(x + 1)$ transformed data. *Spartina patens* and *J. gerardi* were both transplanted into the panne zone (foreign) and back into their native zones. *T. maritimum* and *P. maritima* were both transplanted into *S. patens* and *J. gerardi* zones (foreign) as well as back into their native panne

Species	Location (native or foreign habitat)	Competition (with or without)	Interaction
Spartina patens	$P < 0.001$	$P < 0.041$	$P > 0.245$
Juncus gerardi	$P < 0.001$	$P > 0.325$	$P > 0.550$
Triglochin maritimum	$P < 0.001$	$P < 0.006$	$P > 0.311$
Plantago maritima	$P > 0.132$	$P < 0.012$	$P > 0.296$

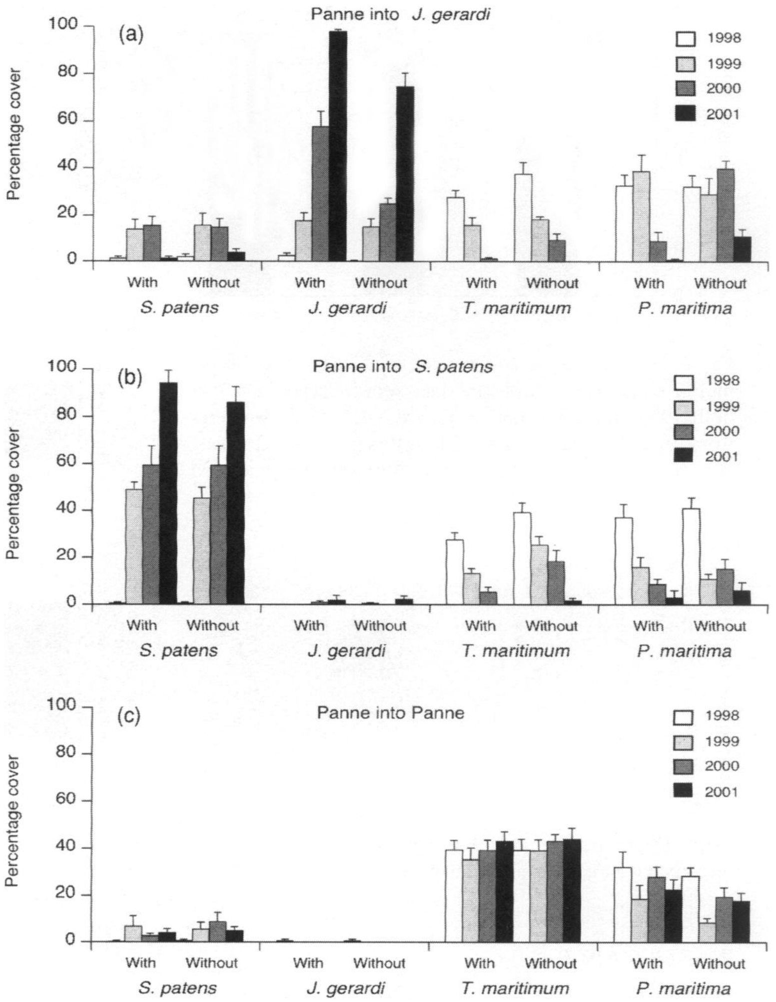

Fig. 7 The effect of transplant location, (a) *J. gerardi*, (b) *S. patens* and (c) Panne, and competition on percentage cover of the panne community. Percentage cover of the dominant species is shown in each transplant zone for all 4 years of the experiment (means ± SE).

In contrast to the panne species, both *J. gerardi* and *S. patens* grew much better in their native habitats than in the panne (Fig. 6b,c, Table 2). The reduced growth of both species in the panne with or without neighbours present showed that the physical conditions in the panne limited their success (Fig. 6b,c, Table 2). With *S. patens*, however, the inhibitory effect was reduced by removing neighbours, showing that the native panne species were competitively suppressing *S. patens* performance (Fig. 6c). Even without neighbours, however, *S. patens* performance in forb pannes was more than four times less than in its native zone.

PANNE COMMUNITY TRANSPLANTS

When large blocks of the panne community were transplanted into *J. gerardi* and *S. patens* zones, the zonal species dominated the transplants, almost displacing the dominant panne species, within 4 years (Fig. 7a,b, $P < 0.001$ ANOVA). Vegetative runners of *J. gerardi* and *S. patens* were able to invade the transplants, imposing some competition in the no competition treatments, and removing any competition effect (Fig. 7a,b). In contrast, the cover of *T. maritimum* and *P. maritima* remained relatively consistent when blocks were transplanted back into the panne (Fig. 7c, $P = 0.345$ ANOVA).

When the panne community was replaced in panne habitat, average species richness did not change over time, with or without competition (Fig. 8), but in the *S. patens* and *J. gerardi* zones, species richness declined over time with competition but did not change when competition was removed (Fig. 8).

When the panne community was transplanted into either the *J. gerardi* or *S. patens* zones there was an increase in above-ground production (Fig. 9a,b, Table 3). By the last year of the experiment the effect of the no competition blocks had been reduced by invasion of native species, particularly *S. patens* (Fig. 9b, Table 3).

When the blocks were transplanted back into the panne without neighbours a sharp increase in panne community biomass was seen and the competition effect persisted (Fig. 9c, Table 3). As the panne community is sparsely vegetated, with 30–40% bare space, light would not be expected to be limiting, suggesting that below-ground competition for nutrients is important here.

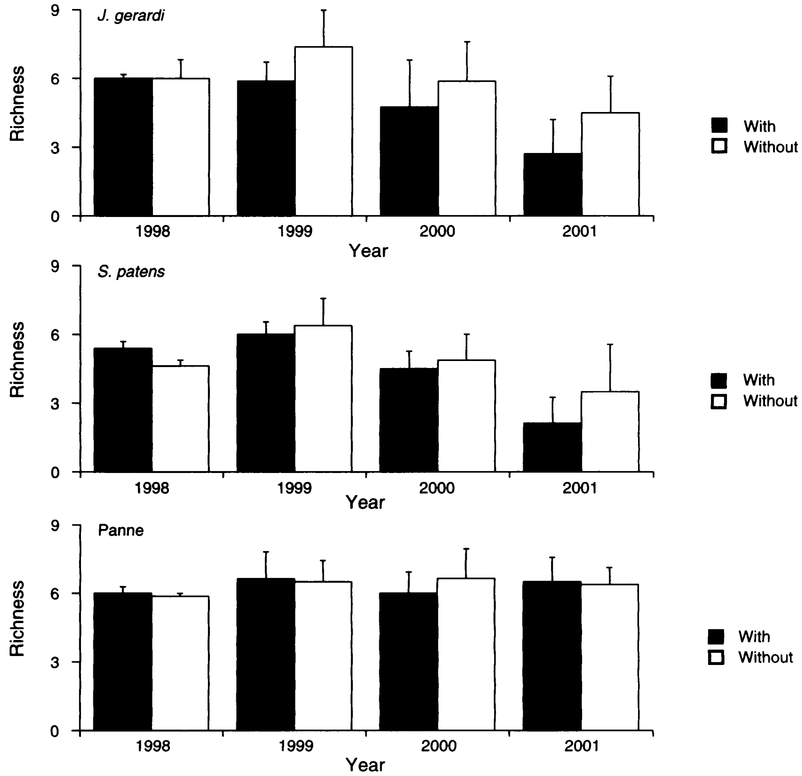

Fig. 8 Average species richness of the panne community transplants in each of the three transplant zones with and without competition. Species richness declines significantly in both the *J. gerardi* and *S. patens* zones with competition (MANOVA $P < 0.001$). Bars represent the means (± SE) of each transplant in each zone.

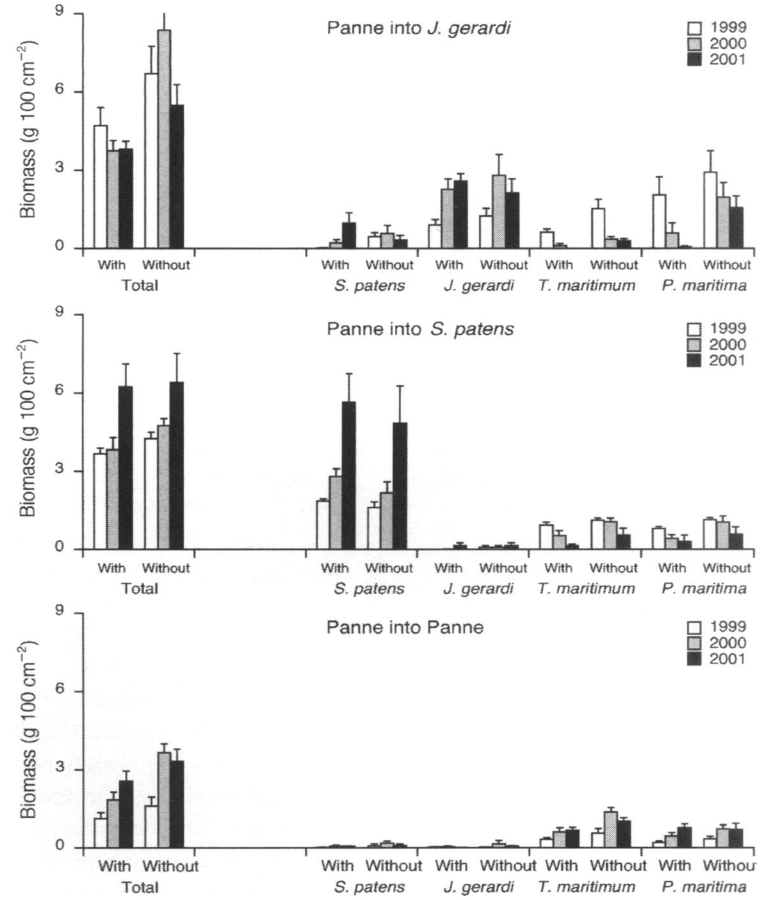

Fig. 9 The effect of transplant location and competition on the biomass of each of the panne community transplants, (a) *J. gerardi*, (b) *S. patens* and (c) Panne. Bars represent average above-ground biomass at the end of the experiment (means ± SE).

Table 3 Summary of analysis of variance on the final biomass data (2001) of the panne community transplants (Fig. 9). For total biomass and biomass of each of the main species, the data are the result of a two-way (Zone × Competition) ANOVA on $\log(x + 1)$ transformed data

Biomass	Zone (*S. patens*, *J. gerardi*, or Panne)	Competition (with or without)	Interaction
Total	$P < 0.001$	$P > 0.107$	$P > 0.524$
S. patens	$P < 0.001$	$P > 0.205$	$P > 0.521$
J. gerardi	$P < 0.001$	$P > 0.459$	$P > 0.354$
T. maritimum	$P < 0.001$	$P < 0.002$	$P > 0.941$
P. maritima	$P > 0.211$	$P < 0.014$	$P < 0.016$

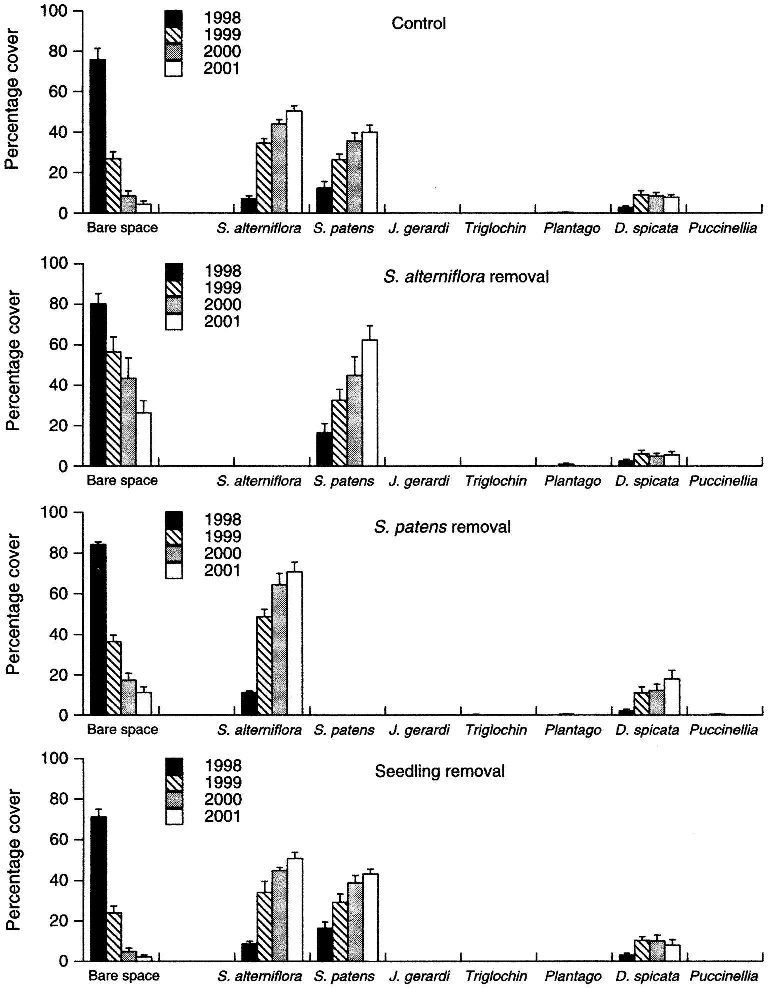

Fig. 10 Recovery of bare patches along the *S. alterniflora*/*S. patens* border. For each of the removal treatments, change in percentage bare space and of the dominant species is shown for the 4 years of the experiment (1998–2001). Bars represent means (± SE) of the eight replicates.

SECONDARY SUCCESSION OF DISTURBANCE-GENERATED BARE SPACE

In comparison with southern New England, bare patch recovery in northern New England salt marshes was slow and characterized by competitive interactions, with no evidence of facilitation, and in some zones also by seedling recruitment.

Substrate soil salinities revealed both seasonal and location variation similar to that found in the marsh zones (Fig. 3), and was never affected by removal treatment (repeated measures ANOVA $P > 0.05$).

On the *S. alterniflora*/*S. patens* border, removing invading *S. patens* tillers increased the invasion of *S. alterniflora* and *Distichlis spicata* L. tillers, and removing colonizing *S. alterniflora* increased *S. patens* colonization, showing that both species suppress invaders during colonization (Fig. 10). Removing seedlings had

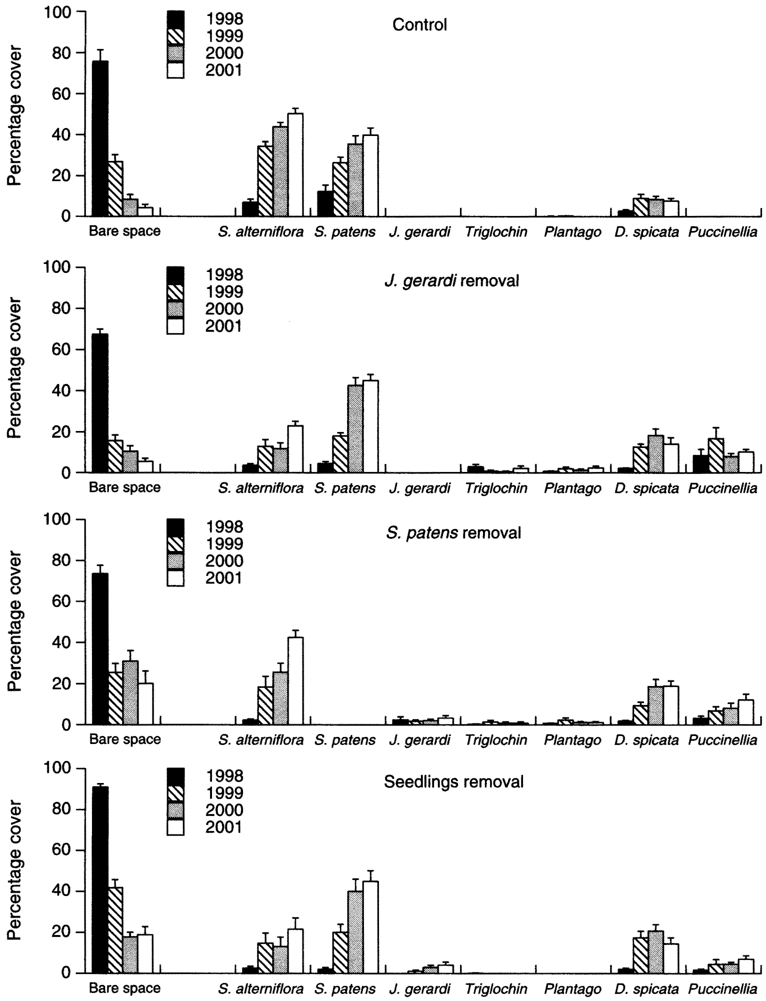

Fig. 11 Recovery of bare patches along the *J. gerardi*/*S. patens* border. For each of the removal treatments, change in percentage bare space and of the dominant species is shown for the 4 years of the experiment (1998–2001). Bars represent means (± SE) of the eight replicates.

no significant effect, indicating that succession of the *S. alterniflora*/*S. patens* border is entirely dictated by vegetative colonization (Fig. 10).

On the *J. gerardi*/*S. patens* border 95% of the control patches were covered by vegetation, but there was very little evidence for interspecific interactions after 4 years (Fig. 11). Removing invading *S. patens* did not influence *J. gerardi* invasion success, but did nearly double the invasion of *S. alterniflora* into the bare patches, while removing *J. gerardi* had no effects (Fig. 11). Despite being bordered by a dense stand of *J. gerardi*, after 4 years none of the treatments had more than 10% *J. gerardi* cover. Removing seedlings revealed that seedling recruitment played an important role in the patch colonization by *Puccinellia maritima* (Huds.) Parl. (hereafter *Puc. maritima*) (Fig. 11).

Unmanipulated control bare patches on the *J. gerardi*/panne border had less than 10% unvegetated bare space after 4 years, but showed relatively weak interspecific interactions (Fig. 12). Removing *T. maritimum* increased *S. patens* and *S. alterniflora* slightly, showing that the panne dominant competitively suppresses invasion (Fig. 12). *Juncus gerardi* invasion was again weak; control plots had less than 10% cover of *J. gerardi* after 4 years and *J. gerardi* removal did not significantly influence the invasion of any other plant (Fig. 12). Seedling recruitment was important for invasion by *Puc. maritima*, *P. maritima* and *T. maritimum*, and colonization by *D. spicata* and *S. alterniflora*, suggesting that they were normally suppressed by seedlings (Fig. 12).

Control bare patches of the *S. patens*/panne border were 90% revegetated after 4 years, but again without strong interspecific interactions (Fig. 13). In plots where *S. patens* was removed both *S. alterniflora* and *P. maritima* had greater invasion success, revealing that they were competitively suppressed in the controls (Fig. 13). Removal of the panne dominant *T. maritimum* slightly, but significantly, increased the invasion success of *S. alterniflora*, but did not influence the abundance of any other species (Fig. 13). Seedling removal from the *S. patens*/panne border bare patches showed that *Puc. maritima* and *P. maritima* relied on seedlings for much of their bare patch invasion and that seedling recruitment into these bare patches suppresses the invasion success of *S. alterniflora* (Fig. 13).

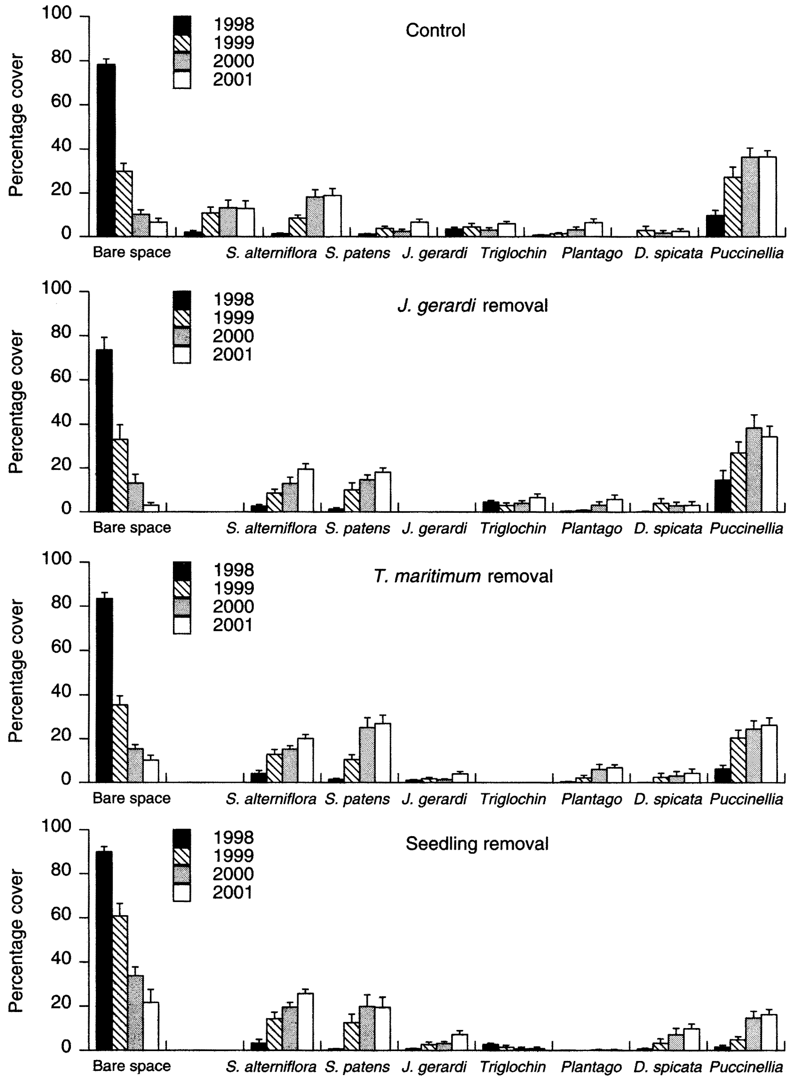

Fig. 12 Recovery of bare patches along the *J. gerardi* / Panne border. For each of the removal treatments, change in percentage bare space and of the dominant species is shown for the 4 years of the experiment (1998–2001). Bars represent means (± SE) of the eight replicates.

Discussion

Our results reveal that plant zonation in northern New England marshes is the product of both interspecific competition and physiological tolerances. Transplant studies indicate that competitively dominant plants displace competitively subordinate plants to physiologically stressful habitats. In addition, recovery experiments indicate that secondary succession of disturbance-generated bare space is a slow process dominated by competitive interactions. Comparing these results with earlier work on southern New England salt marsh plant communities elucidates potential differences linked to differences in climate and level of human impact.

MECHANISMS OF PLANT ZONATION IN NORTHERN NEW ENGLAND SALT MARSHES

The zonation patterns of northern and southern New England salt marsh plant communities are quite different, but our results show that the processes generating zonation are similar in both systems. In southern New England, salt marsh plant zonation is characterized by conspicuous bands of monospecific stands of clonal turfs paralleling the shoreline, whereas, further north zonation is apparent, but not nearly as conspicuous. The lack of a pronounced low marsh in northern New England is due to chronic and severe ice damage limiting the colonization ability of cordgrass (Hardwick-Witman 1985, 1986). Cordgrass is commonly seen invading lower elevations with extensive vegetative runners, but typically is scoured back by the frequent winter icing events.

The second major difference between northern and southern New England salt marsh plant zonation is the presence of low species cover, high species diversity forb pannes that occur at intermediate elevations in northern New England marshes. These communities occur in habitats that are waterlogged and have anoxic sediments (Figs 3, 4 and 5, also see Theodose & Roths 1999), and presumably are absent from southern New

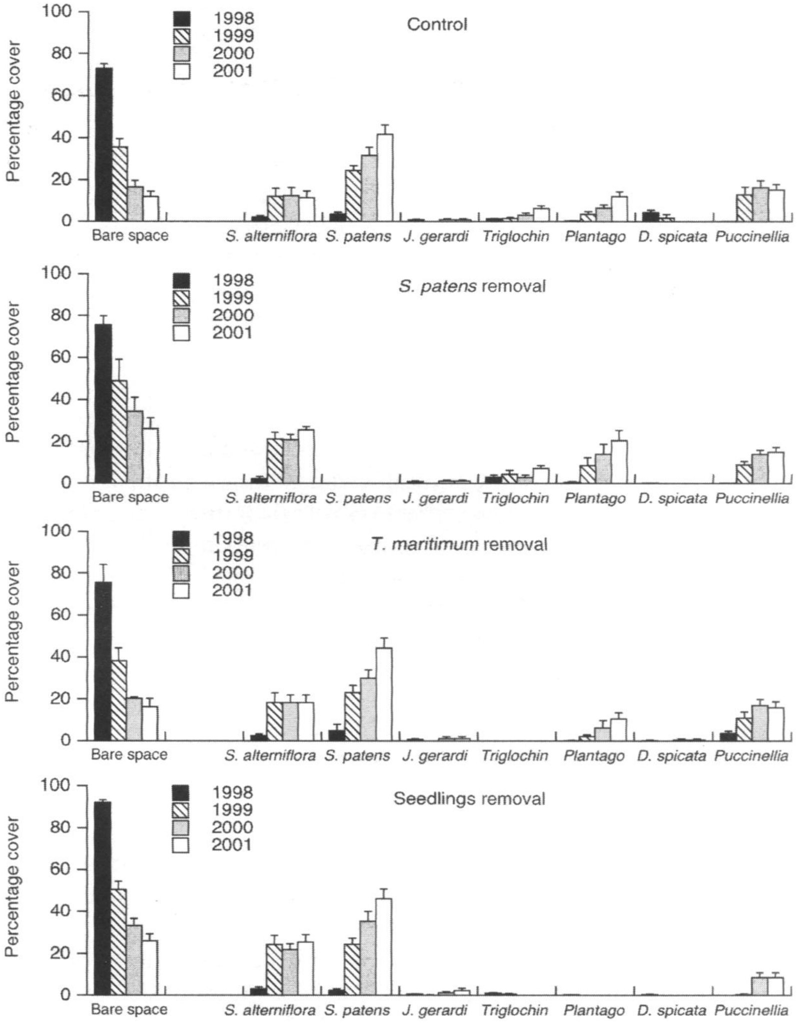

Fig. 13 Recovery of bare patches along the *S. patens*/Panne border. For each of the removal treatments, change in percentage bare space and of the dominant species is shown for the 4 years of the experiment (1998–2001). Bars represent means (± SE) of the eight replicates.

England marshes because waterlogging has been reduced by heavy draining and ditching for agriculture and insect control since colonial times (Niering & Warren 1980; Ewanchuk 2003). Northern New England marshes have not been as extensively manipulated and their larger areas (smaller surface area to perimeter ratios) may decrease drainage. Most of the remaining marshes in southern New England that have survived coastline development are smaller marshes that are well drained and less likely to have waterlogged pannes. The northern coastal marshes of Maine, like the ones we have studied at the Wells National Estuarine Research Reserve, are also extremely dynamic systems that are subject to relatively frequent storm and overwash deposits (Pethick 1992). Overwash events, by depositing a layer of fine sediment or clay on the marsh surface, may contribute to these marshes having poor drainage and drainage patterns that are not spatially as predictable as marshes that have developed without external disturbance (Pethick 1992).

Our transplant studies demonstrate that the plant zonation across northern New England salt marshes is largely the product of *S. patens* and *J. gerardi* being physically excluded from waterlogged panne habitats, while the forbs that numerically dominate pannes are competitively excluded from the more physically benign clonal turf zones. Thus both *S. patens* and *J. gerardi* performance was dramatically reduced when they were transplanted to the panne habitat with or without neighbours present (Figs 7 and 9), whereas panne species typically did as well or better in *S. patens* or *J. gerardi* zones than they did in the panne habitat when neighbours were removed, but did poorly when neighbours were present (Figs 7 and 9).

MAINTENANCE AND PERSISTENCE OF THE PANNE COMMUNITY

A number of species are able to tolerate the physical conditions of the pannes and contribute significantly to the overall species richness of the salt marsh. Many of these forb species are also able to survive within the vegetative matrix of both *S. patens* and *J. gerardi*, although at much lower abundance. Our panne community transplants demonstrate that they are generally restricted to the harsh conditions of the pannes by competition with the clonal turfs. The reduction in survivorship within the clonal turfs appears to be the result of direct competition for light (Figs 6, 7 and 9).

Waterlogging and the associated changes to the edaphic conditions of the marsh substrate within the panne areas may play a role in the maintenance and persistence of the forb panne community. Forb panne soils seem to retain more water than the adjacent areas (Fig. 3), and thus may dramatically reduce the amount of oxygen available for the plant roots. Many of the forbs are only able to persist in *S. patens* and *J. gerardi* zones when direct competition is removed, and even then the clonal turfs are able to exclude the forbs within a few growing seasons. The physical conditions associated with waterlogging thus appear to provide the forbs with areas where they are free from competition although this hypothesis has not been explicitly tested (Ewanchuk 2003). The mechanisms of generation of waterlogged areas discussed above may, however, explain the patchy distribution of pannes.

DISTURBANCE AND MECHANISMS OF SECONDARY SUCCESSION

Our results are strikingly different from those of similar experiments in southern New England salt marshes (Bertness & Ellison 1987; Bertness 1991a; Bertness & Shumway 1993). In these Rhode Island studies, experimental and naturally occurring disturbance-generated bare patches recovered rapidly, with patch closure typically occurring after only 2 or 3 years. Seedling recruitment played a very small role in patch recovery, with vegetative colonization by clonal runners largely responsible for patch closure. Moreover, at middle marsh elevations, patch closure was strongly driven by facilitative processes where initial colonizers facilitated the ultimate invasion of the competitive dominants. These effects all result from bare patches in southern New England marshes becoming hypersaline due to the evaporation of soil porewater in the absence of vegetation. This increased salinity limits seed germination and is lethal to the seedlings of most of the dominant New England marsh plants, so that recovery requires salt-tolerant plants, many of which rely on physiological integration of ramets to first colonize these areas. These first colonizers then lead to facilitative succession as they shade the substrate, lowering the salinity and thus paving the way for the invasion of less salt-tolerant plants.

Northern New England bare patch closure took more than twice as long than in Rhode Island: after 4 years most of the bare patches still had unvegetated bare space. Other differences were that seedling recruitment played an important role in closure and no evidence of facilitated secondary succession was seen in the northern studies.

The slow rate of recovery of disturbance-generated bare space in northern New England marshes may be due to the cooler climate and the fact that these marshes are subject to less anthropogenic nitrogen additions. The cooler climate, compared with south of Cape Cod, has been well documented and results in a shorter growing season, with plants in northern New England emerging in mid-May, rather than mid-April The marshes in southern New England are also almost all exposed to high levels of anthropogenic nitrogen input (Bertness *et al.* 2002), as they are usually abutted by developed shorelines that can no longer buffer marshes from nitrogen inputs, and shoreline development of farms, housing developments, golf courses and parks adds artificial nitrogen to shoreline systems (Howes *et al.* 1996). Such influences are less common in Maine, and the pore water ammonium concentrations at the study site are half those found in Narragansett Bay salt marshes (P. J. Ewanchuk, unpublished data).

Differences between northern and southern New England marshes in the importance of seedlings in bare patch recolonization and mechanisms of secondary succession are likely to be closely linked to climatic differences. In an earlier paper (Bertness & Ewanchuk 2002), we showed that the 3–5 °C difference in summer soil surface temperatures between southern Maine and Narragansett Bay translates into marked differences in the soil salinity of unvegetated marsh substrate. Whereas middle elevation marsh surface salinities in Rhode Island often exceed 100 ppt, similar habitats in Maine rarely have substrate salinities over 60 ppt. These differences in soil salinity conditions influence the nature and strength of interspecific plant interactions, positive in Rhode Island, negative in Maine (Bertness & Ewanchuk 2002). In Rhode Island salt marshes, high soil salinities in bare patches have been shown to limit seedling germination and success, requiring salt-tolerant species to first colonize and ameliorate the build-up of salt and facilitate colonization and recovery (Bertness & Shumway 1993). With a cooler climate the need for facilitated reduction of salinity will not be as critical in northern New England marshes.

This study illustrates how understanding mechanistically the structure and dynamics of natural communities is vital if we are going to be able to accurately predict how future human impacts and global climate change will affect natural communities.

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