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THE ROLE OF WATERLOGGING IN MAINTAINING FORB PANNES IN NORTHERN NEW ENGLAND SALT MARSHES

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Abstract. Areas of high plant diversity, known as forb pannes, characterize many northern New England salt marshes. These pannes are physically harsh habitats where stress-tolerant forbs escape the competitively dominant clonal turfs. In this paper, we experimentally examine the hypothesis that soil waterlogging maintains forb pannes.

Experimentally draining pannes led to the replacement of typical panne vegetation by *Spartina patens*. After four years, *S. patens* cover increased by greater than 300% in the drained plots, while in adjacent, unmanipulated controls, its cover remained unchanged. In a second experiment, forb panne elevation was manipulated to either increase or decrease soil drainage. After three years elevated plots were dominated by *S. patens*, whereas lowered plots were dominated by *Spartina alterniflora*, with reduced forb densities.

Our results demonstrate that forb panne communities are the consequence of poor drainage and waterlogged soils that limit the success of competitively dominant clonal turfs and permit the persistence of panne forbs. These results imply that the extensive ditching of New England salt marshes over the past three centuries to increase the value of marshes for livestock grazing, development, and mosquito control has likely eradicated most of these forb panne habitats.

Key words: anoxia; forb panne; New England; plant community; plant competition; salt marsh; *Spartina*; waterlogging; Wells National Estuarine Research Reserve; zonation.

INTRODUCTION

The distinct zonation of New England salt marshes plants is characterized by monospecific bands of clonal turfs that are determined by a combination of physical stresses and interspecific competition (Nixon 1982, Bertness 1992). This zonation pattern is disrupted in northern New England marshes by large patches of halophytic forbs, called forb pannes (Theodose and Roths 1999, Ewanchuk and Bertness 2004). Despite discussion of forb pannes in the literature (Miller and Egler 1950, Warren and Niering 1993, Theodose and Roths 1999), much of their ecology remains unstudied.

Most of our understanding of forb patches comes from southern New England marshes, where forb patches are ephemeral features of marshes (Bertness and Ellison 1987, Shumway and Bertness 1994). Unlike the persistent forb pannes of northern New England, the forbs in these patch are outcompeted by clonal turfs within a few growing seasons (Bertness and Ellison 1987). Recent experimental work in northern New England has begun to investigate the ecology of these unique panne habitats (Ewanchuk and Bertness 2004). Forbs escape competition from clonal turf species by being able to tolerate the harsh physical conditions of the pannes (Ewanchuk and Bertness 2004). Forb pannes

have higher soil salinities and lower soil redox potentials than the adjacent habitats dominated by clonal turfs (Theodose and Roths 1999, Ewanchuk and Bertness 2004). These differences in edaphic conditions may result from changes in soil moisture or waterlogging associated with the pannes, which may limit the ability of clonal turfs to invade and fully colonize these areas (Ewanchuk and Bertness 2004).

Waterlogging in salt marshes limits the supply of oxygen to plant roots, which inhibites aerobic root respiration, plant growth, and survivorship (Saglio et al. 1983). Mendelssohn et al. (1981) demonstrated that the availability of most belowground nutrients is inversely related to soil waterlogging, affecting plant growth and competition, and plant community dynamics (Bradley and Morris 1990, Mendelssohn and Morris 2000).

The formation of forb pannes has been hypothesized to occur through a number of mechanisms, such as deposition of wrack, grazing by waterfowl, ice scour, and poor drainage (Miller and Egler 1950, Roberts and Robertson 1986, Chmura et al. 1997). Each of these disturbances may lead to the harsh edaphic conditions found in the panes; however, to date these mechanisms have not been experimentally tested in situ.

In this paper we investigate the role of soil waterlogging in forb panne communities. Specifically, we experimentally test the hypothesis that waterlogging is responsible for the maintenance and persistence of forb pannes in northern New England salt marshes.

MATERIALS AND METHODS

Our experiments were conducted in the Little River marsh (L.R.) and Drakes Island marsh (D.I.), in the

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Wells National Estuarine Research Reserve in Wells, Maine, USA (43°20.410' N, 70°32.340' W). Both marshes exhibit vegetation zonation typical of other northern New England salt marshes (Ewanchuk and Bertness 2004).

To test the hypothesis that waterlogging maintains the forb panne areas, two large panne areas (3.0 × 3.0 m) were marked in each marsh in March 1998. Trenches were dug around the perimeter and through the middle of each area by removing large sections of intact peat (0.3 × 0.3 × 0.3 m in length, width, and height). Landscape drainage pipe (13.4 cm [6 inch] diameter) was then laid in each trench, and peat block removed during trenching were trimmed to accommodate the pipe and replaced, leaving the marsh surface relatively undisturbed. Water entering the drainage pipe would then flow through the pipe and drain into an adjacent tidal channel. Areas adjacent to each drained area served as our unmanipulated controls. No disturbance controls were included in this experiment, since our previous work, involving the movement of large blocks of vegetation, showed no effects of disturbance (Emery et al. 2001). In addition, we wanted to minimize the impact of our experiments at the reserve. Areas were then divided into four 1 × 1 m plots and monitored for changes in species percent cover at the end of the growing season (August) by point intercept method ($n = 100$ points). At each intercept, the first species touched was recorded and used to estimate the percent cover. To estimate the change in the whole plant community, all understory species encountered at each intercept were also recorded. To determine the percentage of abundance of each species the number of times each species was encountered per plot was divided by the total number of encounters per plot (for all species combined). Biomass was determined by clipping all the aboveground vegetation in a 10 × 10 cm quadrat, haphazardly placed in each plot in August. Samples were then sorted by species, dried at 60°C, and then weighed. Biomass data were $\log(x + 1)$ -transformed and all percent cover data were arcsine square-root transformed to increase homogeneity of variances and data set normality (Underwood 1997). Data from the final year of the experiment were analyzed with a two-way nested ANOVA considering site and drainage treatment our main effects, with plots nested within site and drainage treatment using JMP, version 3.1 (SAS 1995).

In addition, in March 1999 we manipulated forb pannes by elevating plots to increase soil drainage or lowering plots to decrease soil drainage. Twenty-four 0.5 × 0.5 m plots were randomly located in a large 50 × 40 m panne and randomly assigned to one of three treatments. Each plot (0.5 × 0.5 × 0.3 m in length, width, and height) was removed from the marsh keeping plant roots and rhizomes intact, and then adjusted by either removing 10 cm of peat from the bottom (lowering treatment) or by adding the removed peat to

other holes before blocks were replaced (raised treatment). To stabilize the raised blocks, the aboveground portion of the plot was wrapped in plastic window-screening material. The plastic screening held the aboveground portion of the block together, but did not restrict the belowground expansion of the clonal plants into the block.

Change in species percent cover and biomass was monitored for the following three years, using methods described above. Biomass data were $\log(x + 1)$ -transformed and all percent cover data were arcsine square-root transformed to increase homogeneity of variances and data set normality (Underwood 1997) and analyzed via ANOVA considering lifting treatments as the main effect, using JMP, version 3.1 (SAS 1995).

Edaphic conditions

To examine the effectiveness of our drainage treatments water table depth was measured in two wells located in each drainage area daily for 40 days, approximately three hours after high tide. Substrate salinity and redox potential were quantified during the neap tide series in June, July, and August of each year by extracting a small peat core (2 × 2 × 2 cm) and squeezing out the pore water through cotton gauze and then quantified using a hand-held NaCl refractometer (model SR1, Aquatic Ecosystems, Apopka, Florida, USA). Soil redox potential was measured by inserting a redox probe 2 cm into the soil (portable pH/ISE meter, model 230A, fitted with a platinum electrode, Orion Research, Incorporated, Beverly, Massachusetts, USA). Data were analyzed for each year using repeated-measures ANOVA with site and treatment (drained or not drained) as main factors, and month of sample as the repeated measure.

RESULTS

Our drainage manipulation consistently lowered the water table by greater than 6 cm in the experimental plots relative to the control plots throughout the experiment (L.R. mean difference = 6.36 cm, D.I. mean difference = 10.90 cm). However, our experimental draining did not significantly influence soil salinity at either site (Wilks' lambda = 0.921, $F_{1,28} = 2.38$, $P = 0.133$). Significant variation in salinity was found within and among years, due to yearly climate variation. Soil redox values were consistently higher in the experimentally drained plots throughout the experiment (drained = 139–215 mV, not drained = 17–142 mV). Increased redox values and higher soil oxygen are consistent with changes in soil drainage. While the soil redox values varied within and between years, the relative increase in redox of 30–70% in the drained plots remained (Wilks' lambda = 0.793, $F_{2,29} = 3.78$, $P = 0.03$).

Increasing soil drainage produced a consistent and dramatic effect on the panne plant community structure. Over four years, *Spartina patens* cover signifi-

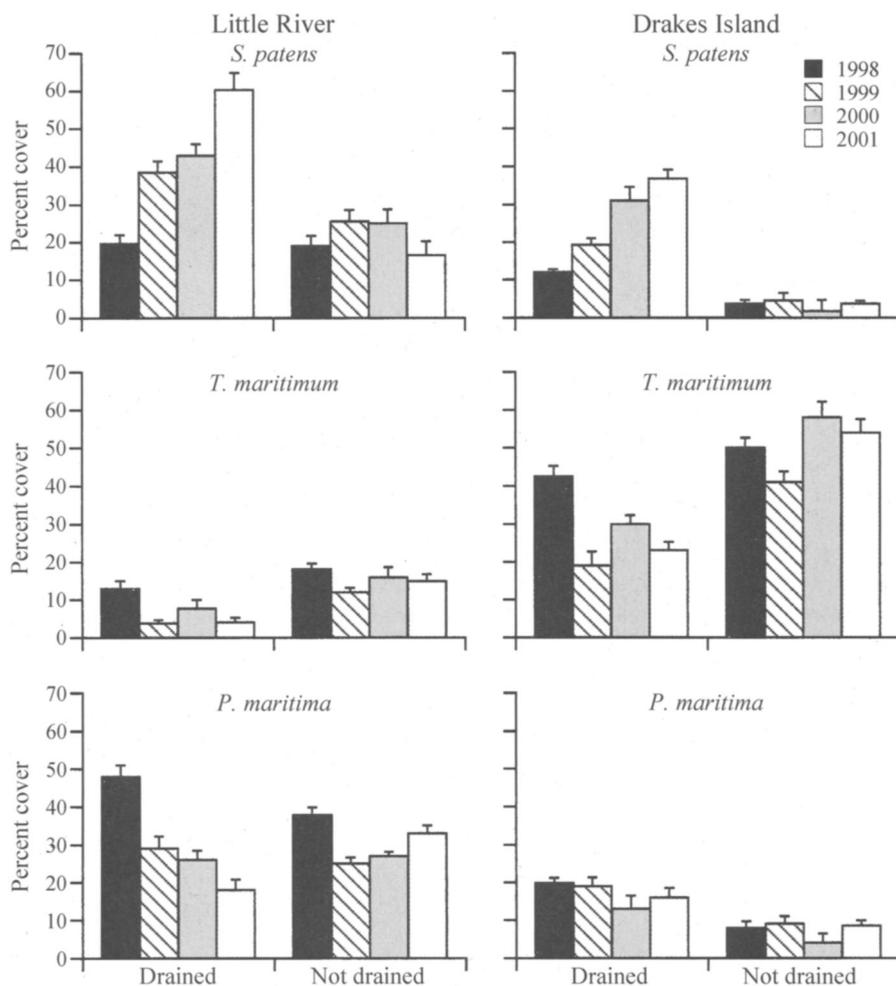


FIG. 1. Percent cover of the dominant species (*Spartina patens*, *Triglochin maritimum*, *Plantago maritima*) in the drained and not drained plots at the end of each growing season (1998–2001). Data shown are the means (± 1 SE) of each treatment for each marsh. Other forb panne species (*A. maritima*, *A. patula*, *G. maritima*, *L. nashii*, *S. europaea*, *S. linearis*) showed a decline in percent cover with draining treatment.

cantly increased in our drained plots from 20% to 60% at L.R. and from 10% to 40% at D.I. (Fig. 1, Table 1). The rate of *S. patens* increase was similar at both sites (Fig. 1). No change in the cover of *S. patens* was observed in the control plots (Fig. 1). The increase in *S. patens* corresponded to a decrease in the cover of many of the forb panne species, which is consistent with our previous transplant experiments (Ewanchuk and Bertness 2004). The two dominant forb panne species (*Triglochin maritimum* and *Plantago maritima*) both showed declines in cover over the course of the experiment (Table 1, Fig. 1). Species richness of the drained plots also decreased during the experiment (initial mean richness = 8.37 ± 0.32 , final = 6.75 ± 0.41 [all data expressed as mean ± 1 SE]).

S. patens biomass showed a correlated response to the percent cover data (Table 1, Fig. 2). At the end of the fourth year, the biomass of *S. patens* in the drained plots had increased by $>300\%$ at L.R. and 500% at

D.I. (Table 1, Fig. 2). Although both *T. maritimum* and *P. maritima* showed significant increases in biomass in the drained plots at both sites (Table 1, Fig. 2), previous experiments indicate that they will eventually be out-competed (Ewanchuk and Bertness 2004). Our estimate of the whole community response, overstory, and understory abundance, also indicated that *S. patens* increased in the drained plots over the experiment (*S. patens* in 1998 = $10.90 \pm 2.26\%$, 2001 = $41.85 \pm 3.06\%$; $P < 0.001$). At the same time, although the biomass of *P. maritima* did increase (Fig. 2), its abundance in the community declined (1998 = $43.29 \pm 2.23\%$, 2001 = $35.92 \pm 2.84\%$; $P < 0.001$).

Lifting experiment

Our elevation treatments produced responses in the panne plant community similar to those in the drainage experiment. Percent cover data showed that all plots had similar plant communities at the start of the ex-

TABLE 1. Statistical results from the nested ANOVA testing the effect of site (S) and drainage (D) on the percent cover and biomass at the end of the experiment (August 2001).

Species and effect	df	Percent cover		Biomass	
		MS	F	MS	F
<i>Spartina patens</i>					
S	1, 4	0.03	0.87	0.13	7.98**
D	1, 4	0.28	8.73*	0.15	9.00**
S × D	1, 4	<0.00	0.13	<0.00	0.05
Plot [site, drainage]	4, 24	0.06	4.39**	0.26	3.082*
<i>Triglochin maritimum</i>					
S	1, 4	0.07	4.25	0.12	8.03**
D	1, 4	0.16	9.80*	<0.00	0.04
S × D	1, 4	<0.00	0.19	<0.00	0.42
Plot [site, drainage]	4, 24	0.03	3.46*	0.01	0.50
<i>Plantago maritima</i>					
S	1, 4	<0.00	0.01	<0.01	0.52
D	1, 4	0.08	4.47	<0.00	0.04
S × D	1, 4	<0.00	0.31	<0.00	0.06
Plot [site, drainage]	4, 24	0.03	2.82*	<0.01	0.51

* $P < 0.05$; ** $P < 0.01$.

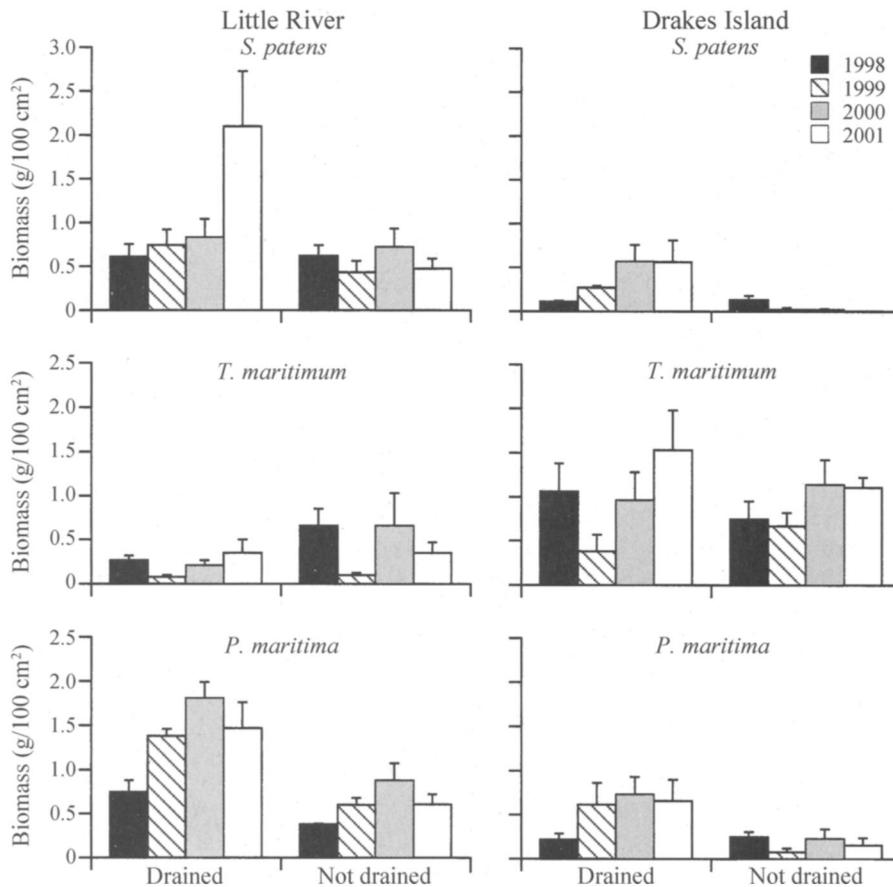


FIG. 2. End-of-season (1998–2001) biomass of the dominant species in the drained and not drained plots. Data shown are mean biomass (+1 SE) in each of the marshes.

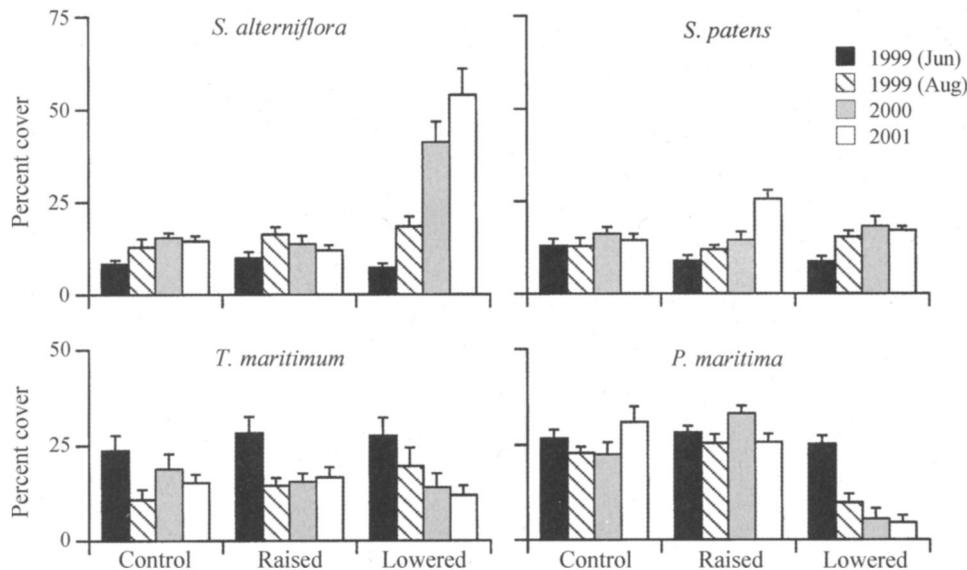


FIG. 3. Percent cover of the dominant species in the control, raised, and lowered plots at the end of each season (1999–2001). Data shown are the means (+1 SE) of each treatment.

periment (Fig. 3). Over the next three years however, our lifting manipulation resulted in dramatic changes in the cover of the dominant turf and forb species (Fig. 3). In addition, lifting significantly altered the redox potential, with higher redox values in our lifted treatment than in either the controls or lowered plots (control = 86.80, lowered = -45.19, raised = 139.65; Wilks' lambda = 0.11, df 2, 21, $P = 0.03$). Lowering the forb panne community resulted in a rapid conversion from panne species to plots dominated by *Spartina alterniflora* at the end of the experiment in August 2001 (Fig. 3). Both percent cover and biomass of *S. alterniflora* showed significant treatment effect (percent cover, $F_{2,21} = 30.20$, $P = 0.001$; biomass, $F_{2,21} = 27.02$, $P = 0.001$). Conversely, raising plots led to an increase in the percent cover of the *S. patens* ($F_{2,21} = 11.50$, $P = 0.004$).

Although the raised plots have not completely converted to *S. patens*, the conversion is well underway (Fig. 3). The response of the whole plant community again indicated that *S. patens* increased in the lifted plots over the experiment (*S. patens* in 1999 = $9.02 \pm 1.03\%$, 2001 = $20.56 \pm 1.0\%$, $P < 0.001$). Although biomass of *P. maritima* increased with the reduced waterlogging stress (Fig. 4), its total abundance in the community declined (1998 = $33.16 \pm 1.89\%$, 2001 = $7.37 \pm 3.06\%$; $P < 0.001$). Biomass of the clonal turfs increased by greater than 300% in both the raised and lowered treatments, indicating that, as in previous experiments, they will eventually outcompete the panne forbs (Ewanchuk and Bertness 2004).

DISCUSSION

Our results show that alleviating waterlogging stress in northern New England marshes likely leads to the

replacement of the panne community by more typical mid-marsh vegetation. When the harsh edaphic conditions of the pannes are reduced either by draining or raising the marsh elevation, panne forbs are outcompeted by the clonal turfs. In addition, increasing waterlogging by lowering marsh elevation resulted in a shift in the community structure and loss of many of the forb species. Changes in the plant community associated with our manipulations suggest that forb pannes are maintained by soil waterlogging.

Physical stress maintenance of forb pannes

The harsh abiotic conditions of the pannes appear to provide a refuge from competition for many of the forbs. Previous experiments have shown that many of these forbs are competitively displaced to these physiologically harsh panne habitats by *S. patens*, but that *S. patens* survivorship and growth is limited by the physical conditions of the panne habitats (Ewanchuk and Bertness 2004). When soil waterlogging is either experimentally increased or decreased in the forb pannes, the endemic plant community is quickly altered (Figs. 1 and 3). Soil waterlogging affects a number of soil abiotic factors that could potentially limit the encroachment of *S. patens*. A number of other important edaphic factors (salinity, redox, hydrogen sulfide concentration, and nutrient availability) may play a role in the maintenance of forb pannes.

Reducing soil waterlogging strongly affected the soil redox potential in both our manipulations. The increase in soil redox potential indicates that when waterlogging is reduced the amount of oxygen available for plant root respiration is increased. These changes in soil oxygen may not only directly affect plant respiration, but also may indirectly change the availability of soil nu-

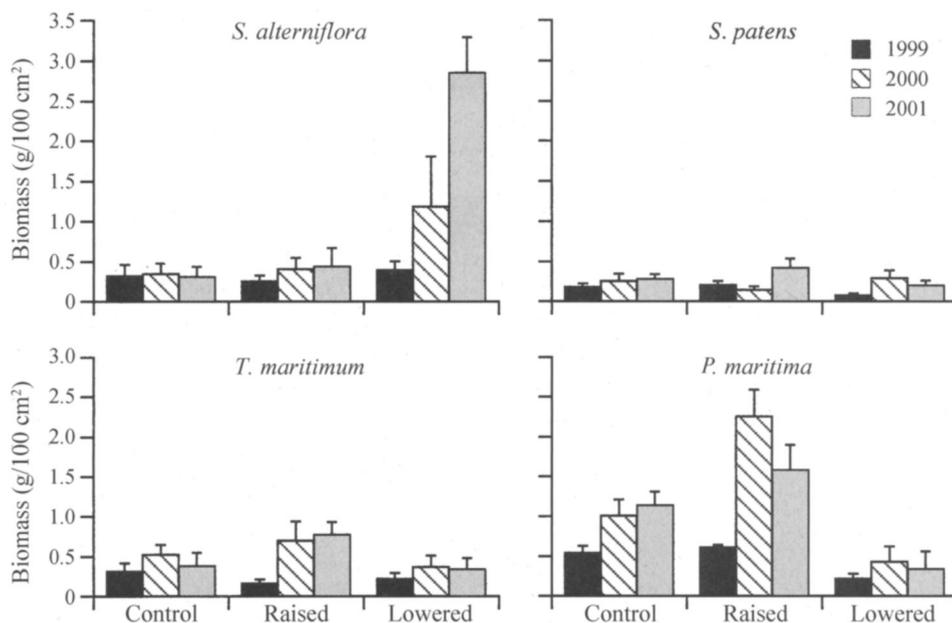


FIG. 4. End-of-season (1998–2001) biomass of the dominant species in the control, raised, and lowered plots at the end of each season (1999–2001). Data shown are the means (+1 SE) of each treatment.

trients (Bradley and Morris 1990, Mendelsson and Morris 2000). The increased levels of soil waterlogging found in forb pannes may increase, for example, the amount of available soluble phosphorus (Patrick and Mahapatra 1968). Higher levels of phosphorus may provide the forb species with an advantage over the clonal turfs, specifically if any of the forbs are P limited (Paludan and Morris 1999, Theodose and Roths 1999). Soil saturation also reduces the rate at which oxygen is able to diffuse into the soil, which limits the amount of oxygen available for plant root and microorganism respiration (Gambrell and Patrick 1978). Reduced soil oxygen level also increases the hydrogen sulfide concentration, which reduces the availability of nitrogen to plant roots (Bradley and Morris 1990). Therefore, waterlogging may limit the overall availability of certain nutrients in the pannes. Limited nutrient availability may reduce the ability of clonal turfs to invade or compete within the panne habitats. Competition experiments in the panne community suggest that competition shifts to belowground, further indicating the possibility of nutrient limitation (Ewanchuk and Bertness 2004).

Conservation and management implications

Waterlogging as the primary mechanism in maintaining forb pannes has important implications for the conservation, restoration, and management of New England marshes. Human alteration through ditching and draining over the last 350 years has likely eliminated forb pannes from most marshes in southern New England. These marshes have undergone extensive ditching as a result of farming of salt marsh hay, live-

stock grazing, and insect control. As a result, the classic descriptions of New England salt marshes may be largely descriptions of anthropogenically altered marshes, and the lack of forb pannes in southern New England may be an artificial state (Miller and Egler 1950, Redfield 1965, Nixon 1982, Bertness 1992).

Increased waterlogging results in large areas that are dominated by annual and perennial forbs, consequently forb pannes are the centers of marsh plant diversity. Understanding how forb pannes are created and maintained is vital, not only because they contain a large proportion of marsh plant richness and diversity, but because they may also be important to other trophic levels (Hacker and Gaines 1997). In addition, forb pannes may represent the historically “pristine” marsh condition, which to this point has not yet been adequately appreciated.

Increased marsh drainage resulting from human activities in southern New England has possibly led to the loss of forb pannes. Studies suggest that, over the last 150 years, sea-level rise in New England has increased at unprecedented rates (Gehrels 1999). Rapid increase in sea level may now lead to increased waterlogging of marshes and possibly to the temporary conversion of mid-marsh elevations to forb pannes (Warren and Niering 1993). As sea level increases, it will bring more water onto the surface of the marsh at higher elevations and for longer periods of time, resulting in large areas of mid-marsh elevations becoming increasingly more waterlogged. However, just as we currently see a latitudinal gradient in the occurrence of forb pannes, the impact of sea-level rise on New England marshes may also vary across latitude. Sea-

level rise in areas where marsh hydrology has been significantly altered may result in a temporary increase of the occurrence of forb pannes. However, since most marshes are totally surrounded by human development, there is no upland habitat available for plants to migrate to. As a result, these areas will eventually be converted to monocultures of *S. alterniflora* and then to mud flats. In northern New England marshes, where forb pannes occur naturally, sea-level rise and slow rates of peat accretion in forb pannes may result in the conversion of these areas to *S. alterniflora* or mud flats. The net result in either location would be significant loss of species diversity within our New England marsh plant communities. By continuing to develop a mechanistic understanding of how these high diversity forb pannes are generated and maintained, we can develop effective strategies for the conservation of these ecologically important habitats.

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