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Recovery of a northern New England salt marsh plant community from winter icing

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Abstract High latitude salt marsh plant communities are frequently exposed to conspicuous winter ice disturbances, which trigger secondary succession. In this paper, we document the recovery of a northern New England salt marsh from a severe winter icing event in 1998. Ice disturbances that killed plants but that left the underlying peat intact recovered rapidly. However, ice damage that killed plants and removed the underlying peat, led to areas of physiologically harsh edaphic conditions, specifically waterlogged and anoxic soils that limited plant recolonization. A transplant experiment revealed that only the most stress-tolerant plants were capable of invading the most stressful portions of ice disturbances. A second experiment that artificially dried disturbance patches accelerated patch recovery. These data suggest that recovery from intense ice disturbance is dependent on stress-tolerant plants invading edaphically harsh disturbances, eventually facilitating the recolonization of the community. This process likely takes longer than a decade for full recovery to occur in the areas where both plants and the peat base are removed.

Keywords Anoxia · Competition · Facilitation · Plant ecology · Redox

Introduction

Disturbance plays a major role in the vegetation dynamics of many aquatic and terrestrial ecosystems (Sousa 1984, 2001; Pickett and White 1985). Ecological disturbance is generally defined as a removal of plant and/or animal biomass creating discrete openings or patches within a community (Grime 1977). As a result of biomass removal, disturbance events can produce communities that contain a number of patches in different successional stages (Paine and Levin 1981; Sousa 1984). The extent to which these habitat patches appear at different stages of succession depends on a number of attributes of the disturbance regime (Pickett and White 1985; Farrell 1991). Characteristics of the disturbance regime such as intensity, frequency, size and shape all affect the degree to which a community is impacted (Sousa 1979, 2001; Pickett and White 1985; Farrell 1991). Many of these attributes also affect the environmental conditions of disturbance patches, which may affect the subsequent colonization and succession (Bazzaz 1979; Bertness et al. 1992). Understanding how these changes in patch quality affect recovery and the pattern of succession is vital to our understanding of the generation and maintenance of mosaic communities.

Recovery from a disturbance event through succession consists of a series of colonization and species replacements that occur in a predictable fashion (Connell and Slayter 1977). Connell and Slayter (1977) defined three models of succession that vary in the effect early successional species have on the establishment of later colonizers. All three models of succession (facilitation, tolerance, and inhibition), have received considerable attention from ecologists (e.g., Clements 1936; Davis and Cantlon 1969; Sousa 1979; Farrell 1989, 1991; Bertness and Shumway 1993). However, to understand how communities recover from disturbance events it is important not only to document the pattern of recovery or succession, but also to understand the mechanisms that drive the different models of succession. Although a community may recover from a disturbance by a given model of succession, the underlying mechanisms on which the model depends may differ with disturbance type or habitat. For example, facilitative succession may occur through the amelioration of harsh physical conditions in the disturbance patch (Bertness and Shumway 1993), or through early colonizers protecting later arrivals from herbivores (Lubchenco 1983; Sousa and Connell 1992).

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Salt marsh plant communities provide an ideal system for investigating variation in the underlying mechanisms of secondary succession. New England salt marshes are subjected to a number of common physical disturbances that generate variation in marsh plant community structure (Miller and Egler 1950; Hardwick-Witman 1985; Bertness and Ellison 1987; Hartman 1988). In addition to variation in disturbance, a number of physical factors (e.g., salinity, redox potential, waterlogging) vary across marshes (Howes et al. 1981; Adam 1990). Many of these physical factors can strongly affect the ability of species to colonize and/or survive in a given habitat (Bertness et al. 1992; Bertness and Shumway 1993). Salt marsh disturbances (e.g., terrestrial runoff, wrack, ice, deposition of sand and mud, herbivory and even fire), commonly act over a number of spatial scales, affecting a number of different species within a marsh (Miller and Egler 1950; Bertness and Ellison 1987; Hik et al. 1992; Ford and Grace 1998; Pennings and Bertness 2001). Many of these disturbances, such as sand deposition from storm overwash and grazing by waterfowl may also require amelioration of harsh abiotic factors in order for recovery to occur (Smith and Odum 1981; Jefferies 1988; Hik et al. 1992; Gough and Grace 1998). Recovery following wrack disturbance in southern New England high marshes is relatively rapid and highly dependent on facilitation local edaphic conditions (Bertness and Ellison 1987; Bertness and Shumway 1993). Disturbance events may not only affect the environmental conditions of the disturbance site itself, but may also alter environmental conditions in adjacent areas (Bazzaz 1979; Bertness et al. 1992). The different environmental conditions of these areas may lead to different mechanisms and rates of recovery.

In addition to the disturbances described above, northern New England salt marshes are subjected to severe winter ice annually (Dionne 1969; Mathieson et al. 1982; Hardwick-Witman 1985). Winter ice regularly damages the low marsh in many salt marshes in Maine. These yearly disturbances reduce low marsh vegetation, *Spartina alterniflora*, so that this zone is limited to vegetative ramets annually reinvading low marsh habitat before being killed back the following year (Bertness 1999). Ice disturbances that result in severe damage and large scale removal of middle and high marsh vegetation are less common. However, during winters of heavy icing areas of both the middle and high marsh are impacted by two common forms of ice disturbance, sediment deposition and ice scouring. Sediments incorporated into ice sheets can be deposited on the marsh surface when the ice comes to rest and melts. Scouring of the salt marsh by ice blocks carried during tidal flows can remove both plant material and sediment, leaving behind a marsh surface pitted with shallow depressions (ice scars), which modify the microrelief of the salt marsh (Dionne 1969; Bélanger and Bédard 1995). The depressions of these ice scars can persist for several years on the marsh (Dionne 1969, 1974). This loss of marsh peat changes many edaphic factors: (inundation, redox potential, salinity and the amount of waterlogging) due to changes in drainage patterns. As a result of these changes, many of the larger ice scars develop what appear to be rings or halos of dead vegetation around them. The loss or reduction of live plant cover in the halos is assumed to be a result of the changes in some underlying edaphic factor resulting from the direct disturbance. One possibility for this loss of vegetation may be changes in salinity resulting from the loss of neighboring aboveground vegetation, which is known to lead to high soil evaporation rates and subsequent high salinities (Bertness et al. 1992). However, in the halo areas the aboveground vegetation is still present although dead and may be able to buffer the higher salinities. Another suggestion is that the decrease in live plant biomass may lower the transpirational leaf area and may promote soil waterlogging (Mitsch and Gosselink 1993). Recovery of the ice scars and halos may proceed at different rates and by different mechanisms because of changes in the underlying edaphic conditions caused by the disturbance.

Removal of peat by these icing events effectively removes the history of bioengineering by the plants (Redfield 1972; Adam 1990; Mitsch and Gosselink 1993). As a result, the recovery of these disturbances may occur through a process more similar to primary than secondary succession. The removal of the peat base might return these patches to edaphic conditions more similar to an unvegetated mud flat than to wrack or other disturbance patches. Therefore recovery may require the plants to rebuild the peat through a recovery process similar to primary succession or marsh creation described by Redfield (1972).

In this paper, we examine the recovery of winter ice disturbances in a northern New England salt marsh plant community. We start by describing the natural recovery process of vegetation after a severe winter disturbance and document the consequences of the disturbance on local edaphic conditions. We then present the results of experimental studies that test the hypothesis that the harsh edaphic conditions in disturbance patches limit the rate of secondary succession following severe ice disturbances. Together our results suggest that intense ice disturbances that remove the peat foundation of northern New England marshes lead to harsh edaphic conditions, specifically anoxic soils that limit plant recolonization and require facilitative succession for the community to recover entirely.

Materials and methods

Our studies were conducted on the Little River marsh at the Wells National Estuarine Research Reserve in Wells, Maine, USA. The Little River marsh is a large (245 ha) coastal salt marsh that exhibits vegetation zonation typical of other New England marshes (Bertness 1991a, 1991b; Bertness and Ellison 1987). The striking vertical zonation pattern of the dominant vegetation has been the focus of extensive research (see Penning and Bertness 2001 for a review).

One of the most severe ice storms in recent history struck much of New England and southeast Canada in early January 1998 (Eichorn et al. 2001). More than 5 cm of freezing rain fell over a 3-

day period, leaving much of Maine under at least 2 cm of ice. Ice from this storm generated extensive tree damage (Irland 1998; Eichorn et al. 2001; Rhoads et al. 2002). In addition, a thick layer of ice covered many coastal marshes and subsequent break-up and movement caused extensive damage to marsh surfaces. Although this icing event resulted in the creation of a large number of disturbance patches, evidence of relatively frequent past icing events is present across mid-marsh elevations (Ewanchuk, personal observation)

In spring 1998, we identified 50 large ice disturbances in the *Spartina patens* and *Juncus gerardi* zones of the marsh. The ice-disturbed areas were easily distinguished from other disturbances because in the area of direct impact, vegetation had been removed and underlying sediments exposed. Each disturbance area contained both the direct site of the disturbance where the peat base had been removed (ice scar) and the associated area of dead vegetation around them (scar halo). Disturbances were measured and individually marked with re-bar and numbered flags. The ice disturbances were mapped and the length and width of each disturbance was measured to approximate the area (m^2). The area of each halo was calculated by subtracting the scar area from the total disturbance area.

We monitored recovery of each disturbance by measuring each patch at the end of the growing season for 4 years (1998–2001). To examine the recovery of both ice scar and halos, we installed two permanent quadrats (0.5×0.5 m) in each marked disturbance patch: one located in the halo area and the other at the border of the halo and the ice scar. These quadrats were photographed at the end of each growing season (1998–2001). Photographs were then projected and analyzed for plant cover using the point intercept method (100 point).

To examine whether ice disturbances markedly altered marsh edaphic conditions that could influence recolonization we quantified soil salinity, redox potential, and depth to water table in the marked patches in June, July and August of 1998–2001. We measured edaphic conditions in three areas in each disturbance patch: ice scar, halo and undisturbed vegetation. Soil salinity measurements were taken by extracting a core of peat 3 cm in diameter ×3 cm deep. We extracted pore water from the core by squeezing the core through cotton gauze: salinity of the pore water was then quantified using a hand-held NaCl refractometer. Soil redox potentials were measured by removing a soil plug (1 cm diameter ×3 cm deep) from the substrate and inserting a redox electrode into the hole (Orion Research, Beverly, Mass., USA). To examine the potential degree of waterlogging plant roots are exposed to, the depth to the water table was measured in well holes cored in each of three areas. Depth to the water table was measured approximately three hours after high tide in each well hole. These measurements were taken daily for a month through an entire lunar tidal cycle to assess flooding and drainage differences among these habitats.

Soil moisture content was quantified by determining the difference between wet weight and dry weight of the soil core samples. In July 1998, soil cores (10 cm diameter ×15 cm deep) were extracted from each of the three areas disturbance in during low tide. Cores were placed in plastic zip-loc bags and brought back to the laboratory for analysis. Aboveground plant biomass was clipped from each core and cores were then weighed. Cores were then dried in an oven at 65°C until sample weight no longer changed. The difference in before and after weight expressed as a percentage of wet soil weight was used as a measure of soil moisture content.

Soil percolation, a measure of how easily water moves through the soil, was measured with percolation tubes. Percolation tubes were inserted into the marsh surface in each of the three habitats. Tubes were then filled to a fixed level with water. After 45 min the amount of water remaining in the tubes was recorded. The volume of water that drained into the soil was used as an indicator of soil percolation.

To assess the ability of marsh plants to recolonize and live in ice disturbances it is important to understand what species are able to survive in the disturbed areas with altered edaphic conditions. To examine the hypothesis that edaphic conditions in ice scars limit plant recolonization, a transplant experiment was performed. Transplants were done in late May just as the plants were emerging from either over-wintering rhizomes or seeds. Four clonal turf species were transplanted; *Spartina patens*, *Juncus gerardi*, *Distichlis spicata*, and *Puccinellia maritima* (hereafter *Puc. maritima*), while the following forb species were transplanted; *Salicornia europaea*, *Triglochin maritimum*, *Plantago maritima*, *Glaux maritima* and *Limonium nashii*. These are the most common and abundant species at the middle marsh elevation where the ice disturbance impacted the marsh. Transplant material was collected from the clonal turfs by using 7.5 cm diameter cores and extracting a transplant plug 10–15 cm deep. For the forb species we used 2- to 3-week-old seedlings. Cores of the turf species were removed with a standard corer and seedlings along with 3 cm diameter peat plug were extracted from the marsh using a sharp knife, taking care to include as much intact root material as possible. All transplant material was collected within 100 m of the transplant site and randomly assigned to treatments. Transplants were planted within an hour of collection into each of the three areas (ice scars, ice scar halos and undisturbed vegetation) and marked with numbered flags. Five large disturbance areas were used to allow for adequate spacing between transplants. Each disturbance was treated as a replicate block with five individuals of each species transplanted within each of the three disturbance areas. Transplants were then scored every 2 weeks for survival. Differences in survivorship of each species were analyzed with an ANOVA of survivorship at the end of the experiment. All surviving transplants were harvested at the end of the growing season by clipping all aboveground vegetation. Samples were then cleaned and sorted to remove any dead vegetation and dried to a constant weight in a drying oven at 60°C, and then weighed. Biomass data for each species was transformed using log $(x+1)$, and then analyzed using an ANOVA with block and transplant location as the main factors. All post hoc comparisons when necessary were performed using the linear contrast feature of JMP (SAS 1995).

To test the hypothesis that the limited plant colonization found in disturbance patches is the result of waterlogging caused by the absence of vegetation, a wicking experiment was performed. Four quadrats (30×30 cm) were set up in each of the five large disturbance areas. Two quadrats were placed on the edge of the ice scar, and the other two were placed in the halo area close to the untouched vegetation around the disturbance. To artificially increase the evaporation of water, nine Playtex tampons were inserted on 10 cm centers in each of the quadrats (30×30 cm). Tampons were inserted half way into the marsh substrate so the top half was open to the air to allow evaporation. This manipulation was done to mimic the drying caused by active leaf transpiration of live vegetation. Tampons were changed at the beginning of each growing season. Quadrats were then monitored for changes in rate of colonization and in the percent cover of colonizers for the next two years. Edaphic conditions (salinity, redox) were monitored monthly during the growing season in each of the quadrats.

Results

Disturbance recovery

The harsh winter icing event that occurred at the Little River marsh in January 1998 resulted in large areas of the high marsh impacted by ice scour. The most conspicuous and damaging effects of the ice were the ice scars created when portions of the peat were torn from the marsh as part of ice sheets and/or ice sheets gouged the marsh surface. In either case this not only killed the marsh vegetation, but also removed surface peat foundation under the marsh plant community. The size of ice scars

Table 1 Mean size of ice scars and halos on the Little River marsh following the severe winter ice storm January 1998. Disturbances are broken down into the two components of the disturbance event, the ice scar and halo area. The mean size of the remaining unvegetated areas at the end of the 2001 growing season is also included. Mean area (m^2) ± SE (n=50 disturbances)

Disturbance area	Mean size 1998	Minimum	Maximum	Mean size 2001
Scar	5.33±0.9	0.18	24.24	2.81±0.8
Halo	11.44±3.19	0.13	142.95	0
Total	22.36±4.75	0.39	151.84	2.81±0.8

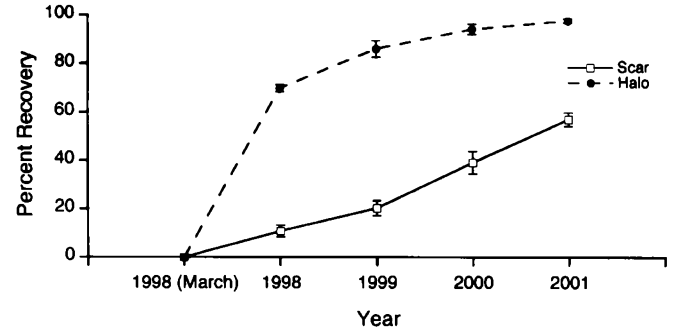


Fig. 1 Recovery of ice disturbance in Little River marsh. Percent recovery of vegetation in both ice scars and scar halo areas over the 4 years of the study (mean percent recovery ±SE, n= 50)

Table 2 Summary of the repeated measures analysis of variance on substrate salinity and redox in each of the three disturbance areas (Fig. 3). For each year the repeated measures ANOVA was done that considered the disturbance location (ice scar, scar halo, and undisturbed vegetation) as a fixed effect and sampling time (month) the repeated effect

Year	Salinity (‰)		Redox (mV)	
	df	Wilks' λ	*df*	Wilks' λ
1998				
Time (T)	2, 26	0.05***	2, 26	0.43***
Treatment × T	4, 52	0.33***	4, 52	0.19***
1999				
Time (T)	2, 26	0.20***	2, 26	0.60**
Treatment × T	4, 52	0.50**	4, 52	0.39***
2000				
Time (T)	2, 26	0.16***	2, 26	0.63**
Treatment × T	4, 52	0.44**	4, 52	0.17***
2001				
Time (T)	2, 26	0.25***	2, 26	0.68**
Treatemtn × T	4, 52	0.51**	4, 52	0.07***

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

caused by the harsh winter icing event ranged from less than 1 m^2 to greater than 20 m^2, with the average size of an ice disturbance scar approximately 5.33 m^2 (Table 1). These ice scars were highly visible on the marsh surface because of the loss of vegetation and peat associated with their generation. The removal of biomass and associated peat base resulted in a lowering of the surface elevation in the ice scar by approximately 4 cm (mean =3±0.76 cm, n=50). The scar halo around the perimeter of each scar was approximately twice the size of the ice scar. All the vegetation in these areas was dead, but the marsh peat was still intact and undamaged.

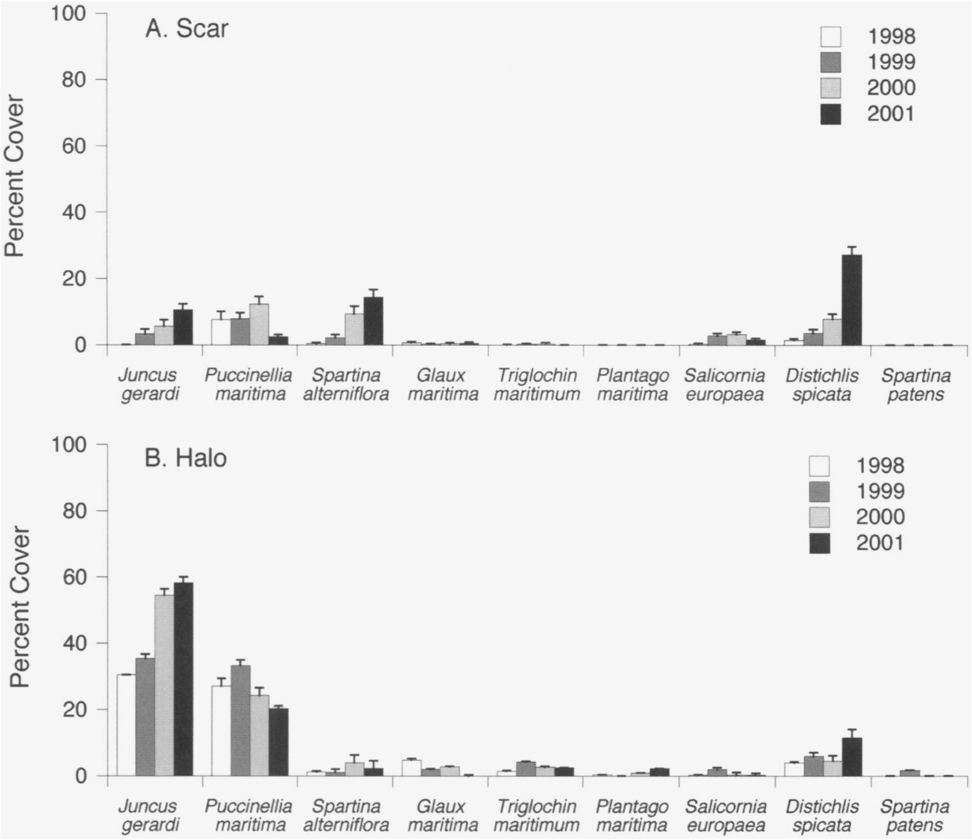
Quantification of the natural recovery of the marked ice scars revealed that ice scar and ice scar halos recover very differently. The recovery of vegetation in the halos was rapid, but in the ice scar vegetation recovery was very slow. Over the 4 years of our study the halo areas were completely revegetated (Table 1). In contrast, the scar areas showed a much slower revegetation. Only the perimeters of the scars have begun to recover and the centers remain unvegetated. Vegetation cover data from the permanent quadrats placed in scars and halos show a similar pattern to the area data (Fig. 1). In 4 years the halo areas are 97% covered by vegetation, while quadrats on the edges of the scars are only 60% vegetated (Fig. 1).

The plant species colonizing ice scars and ice scar halos also differed (Fig. 2). Ice scar halos were rapidly recolonized by *J. gerardi*, *Puc. maritima*, and *D. spicata*. Most of this colonization was from belowground rhizomes invading vegetatively from the surrounding undisturbed vegetation. Seedlings of forb species (*Salicorina europaea*, *Triglochin maritimum*, *Plantago maritima*, and *Glaux maritima*) were also able to colonize the scar halos (Fig. 2). Four years after the ice disturbance event the halo areas had rapidly returned to the species composition of the surrounding vegetation. In contrast, the ice scar areas remained relatively unvegetated (Figs. 1, 2) and were only being recolonized by the most stress-tolerant plants in the community. The scar areas were starting to be recolonized vegetatively by *Spartina alterniflora* and *D. spicata* ramets and by *Salicornia europaea* seedlings. Even after four years there was no evidence of any of the other common salt marsh species colonizing the ice scar areas (Fig. 2). In particular, neither *J. gerardi* nor *Puc. maritima* which dominate the surrounding vegetation, had been able to reestablish in the ice scars.

Variation in edaphic conditions

Edaphic conditions in the ice scars and ice scar halos differed in many ways from the surrounding undisturbed vegetation. Soil salinity was lower in the ice scars than in either the scar halos or the surrounding vegetation (Fig. 3, Table 2). This was likely due to the fact that the scars are at a lower tidal elevation, remaining flooded for longer periods of time which limits the evaporative build up of salinity. Soil redox was markedly lower in ice scars than in halos or undisturbed vegetation (Fig. 3, Table 2). This likely reflects the role that live plants and porous peat

Fig. 2 Results of the recovery of permanent quadrats in both the ice scars (**A**) and scar halo (**B**) following the 1998 winter ice storm. Quadrats were followed for 4 years (1998–2001, mean percent cover ±SE)



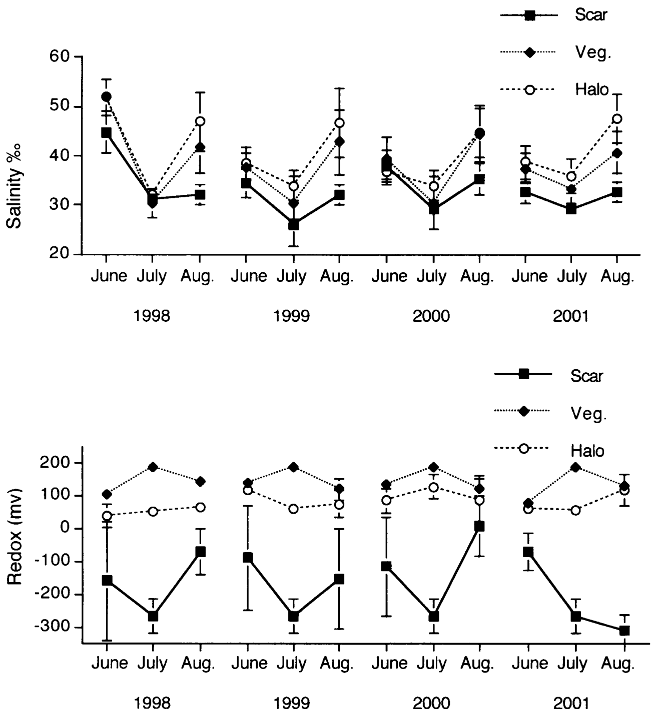


Fig. 3 Monthly substrate salinity and redox from the three areas of around each disturbance patches (ice scars, scar halos, and undisturbed vegetation); mean ±SE of 25 samples

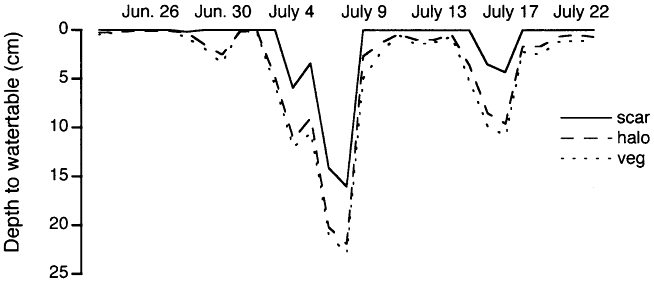


Fig. 4 Depth to the water table in each of the three areas generated by ice disturbance. Data from summer 1998 are shown, although a similar pattern was found for both years for which water table data were collected

play in oxygenating marsh substrate (Howes et al. 1986; Bertness 1991b).

Water table levels were consistently different between scar, halo, and undisturbed areas (Fig. 4). Over a month-long tidal cycle the water table was higher in scar areas in comparison to the adjacent halo and undisturbed areas (Fig. 4). For most of the tidal cycle water was within 5 cm of the surface in the scars, well within the potential root zone of most marsh species. The water table in halos was slightly higher than the vegetated areas, which is consistent with halos having lower soil redox potentials than undisturbed vegetation. The soil moisture data from each location indicate a similar pattern. Cores from the scars contained almost 60% water (57.21±7.45%) significantly

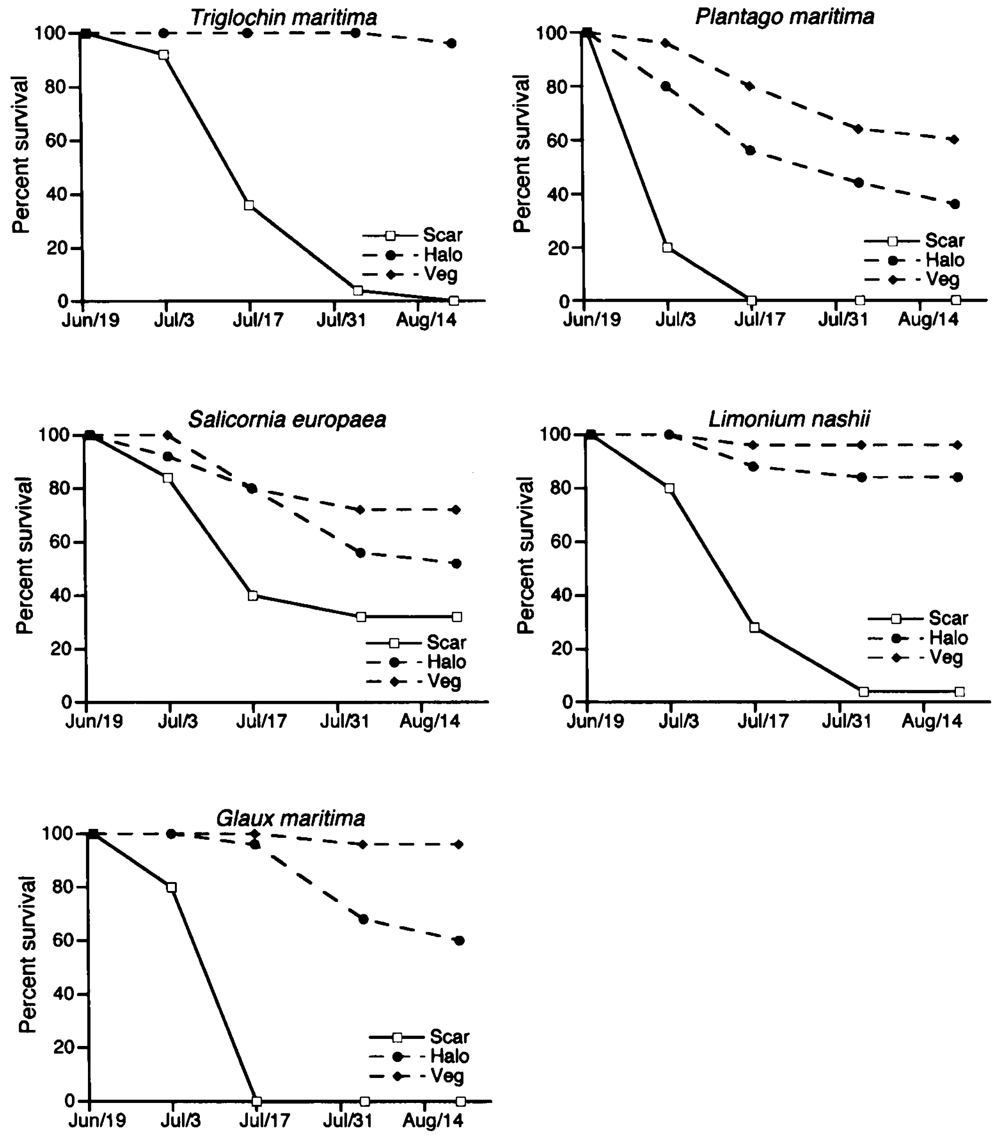


Fig. 5 Transplant survivorship in each of the disturbance areas. Mean percent survivorship for each of the forb species, (*Triglochin martimum*, *Plantago maritima*, *Salicornia europaea*, *Limonium nashii*, and *Glaux maritima*)

greater than either the halos or undisturbed areas (halos: 48.26±1.89%, vegetation: 45.21±2.79, ANOVA, $F_{2,14}$= 7.21; P<0.01).

Soil percolation in the scar, halo, and undisturbed vegetation was also consistent with the water table and redox data (Figs. 3). The amount of water that percolated into each habitat differed significantly (ANOVA, $F_{2,27}$= 22.14; P<0.001). Post hoc analyses indicated that the scar habitats had the lowest soil percolation (40.6±9.8 ml / h) compared to the halo and background vegetation (64.8±23.7 and 110.1±35.2 ml / h respectively, linear contrast, P<0.001).

Transplant experiment

Transplant experiments of the most common marsh plants showed that survivorship and biomass production varied among the scar, halo and undisturbed vegetation (Figs. 5, 6, Table 3). For most species transplanted, survivorship and growth were lowest in the scar habitat (Figs. 5, 6). The results of ANOVA on the percent survivorship to the final sampling date for each species indicated that transplant survivorship varied significantly among the three areas (ANOVA, P>0.05 for all species). *Salicornia europaea* was the only forb species that survived in the scar areas (Fig. 5). All of the other forbs experienced 80–100% mortality within 4 weeks of being transplanted into ice scars (Fig. 5). The biomass response of each species was used as an indication of the health of a given species in each environment. Only *D. spicata* grew better in the scar areas than in either the halo or in the background vegetation (Fig. 6, Table 3, P>0.01 linear contrast). Biomass production of *Salicornia europaea* and *Puc. maritima* were affected by transplant location (Fig. 6). Both species increase production in the halo areas compared to vegetated background areas, although growth of both species were impacted by the physical conditions of the scars (Fig. 6, Table 3). Both *J. gerardi* and *Spartina patens*, the dominant plants in undisturbed

Fig. 6 Results of the biomass production at the end of the transplant experiment. Biomass (g) ±SE are given for all species in each of the three disturbance areas

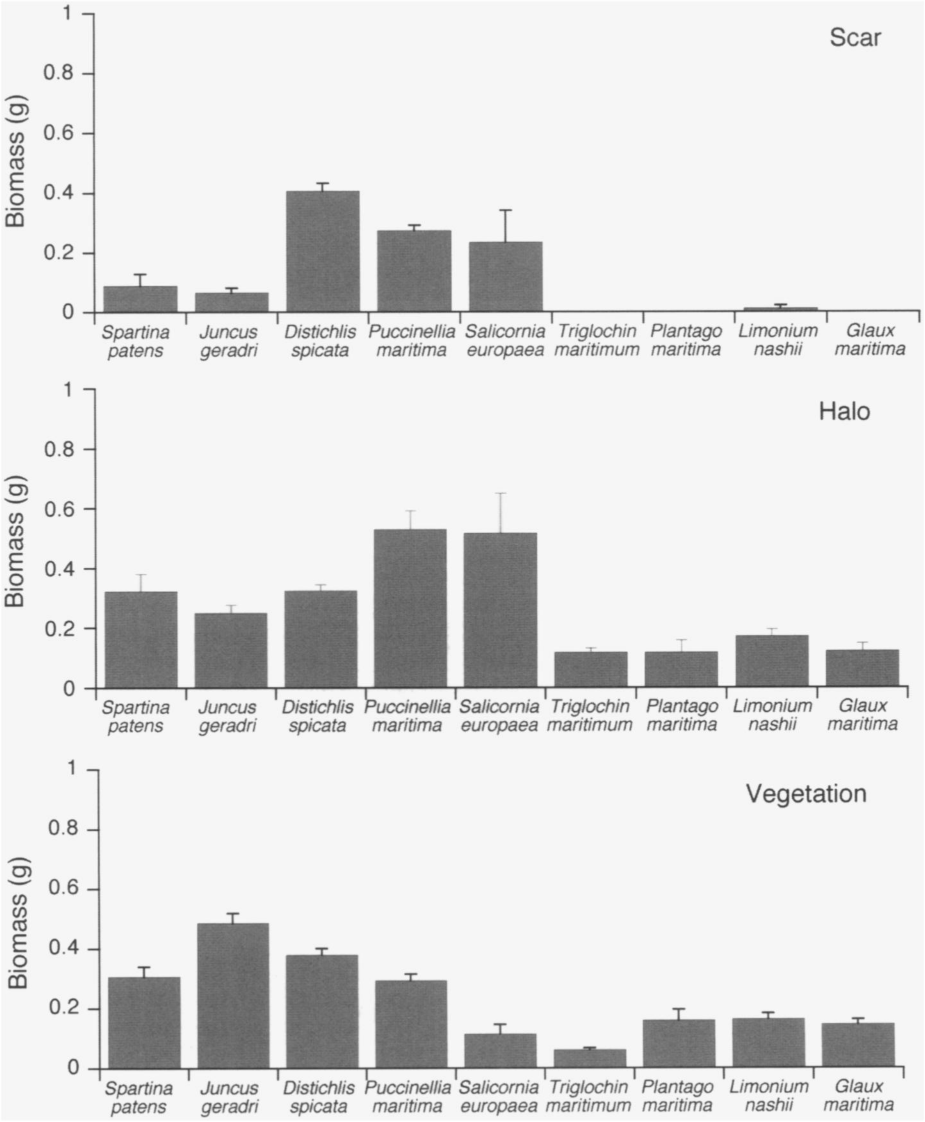


Table 3 Summary of the analysis of variance on the end of season biomass for each transplant species (Figs. 6, 7). For each species the data are the result of a 2-way (Block × Location) ANOVA on log transformed biomass data. *df*=2,8 for all tests

Species	Block	Treatment (scar, halo, veg)	Interaction
Spartina patens	*P*>0.234	*P*<0.001	*P*>0.511
Juncus gerardi	*P*<0.050	*P*<0.001	*P*<0.003
Distichlis spicata	*P*<0.202	*P*<0.020	*P*<0.044
Puc. maritima	*P*>0.828	*P*<0.001	*P*>0.925
Salicornia europaea	*P*>0.139	*P*<0.013	*P*>0.584
Triglochin maritimum	*P*>0.234	*P*<0.001	*P*>0.536
Plantago maritima	*P*<0.001	*P*<0.001	*P*<0.004
Limonium nashii	*P*<0.014	*P*<0.001	*P*>0.266
Glaux maritima	*P*>0.125	*P*<0.001	*P*>0.495

vegetation, survived in the scar areas, but biomass was strongly suppressed (Fig. 6, Table 3). Although significant block effects were found for three species (*J. gerardi*, *P. maritima*, and *L. nashii*), the effect of treatment location was consistent with only changes in magnitude of the effect.

Wicking experiment

Adding absorbent wicking elements to the edge scar decreased the water content of the soil, increased soil redox and accelerated the colonization (Fig. 7, Table 4). Wicking significantly increased the redox potential by approximately 100% on the edge of each scar, whereas little change occurred in the disturbance halo (Fig. 7,

Fig. 7A, B Substrate salinity and redox in the wicking experiment. Data are shown for both the manipulated (*with*) and control (*without*) plots in both locations. **A** Scar edge and **B** halo

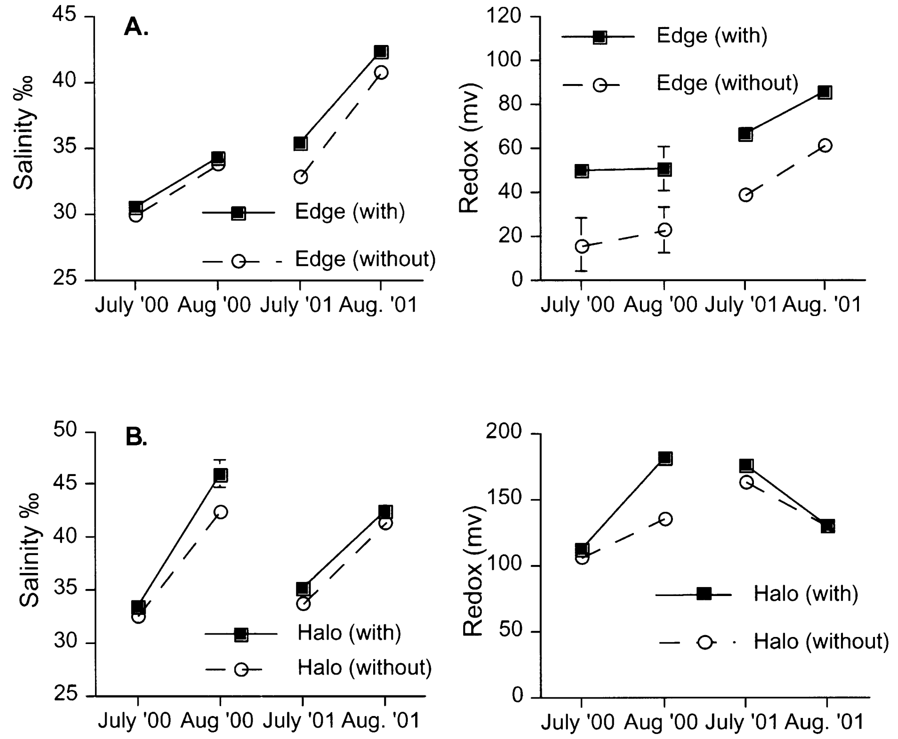


Table 4 Summary of the repeated measures analysis of variance on substrate salinity and redox on wicking experiment (Fig. 8). For each year the repeated measures ANOVA was done that considered the Location (Edge, Halo) and Treatment (with wicking elements or control) and as fixed effects and sampling time (month) the repeated effect

Year	Salinity (‰)		Redox (mV)	
	df	Wilks' λ	*df*	Wilks' λ
2000				
Time	1, 36	0.11***	1, 36	0.45***
Time × Location (L)	1, 36	0.34 ***	1, 36	0. 53***
Time × Treatment (T)	1, 36	0.94	1, 36	0.90
Time × L × T	1, 36	0.93	1, 36	0.83**
2001				
Time	1, 36	0.03***	1, 36	0.77**
Time × Location (L)	1, 36	0.99	1, 36	0.23***
Time x Treatment (T)	1, 36	0.93	1, 36	0.93
Time × L × T	1, 36	0.99	1, 36	0.98

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

Table 4). The decreased soil waterlogging and increased soil oxygen levels led to 30% more plant colonization of wicked areas than unmanipulated control. In both experimental and control plots virtually all of the plants reinvading were either *J. gerardi* and/or *Puc. maritima* (Fig. 8).

Discussion

Our results show that ice disturbance in New England high marsh plant communities generates unvegetated

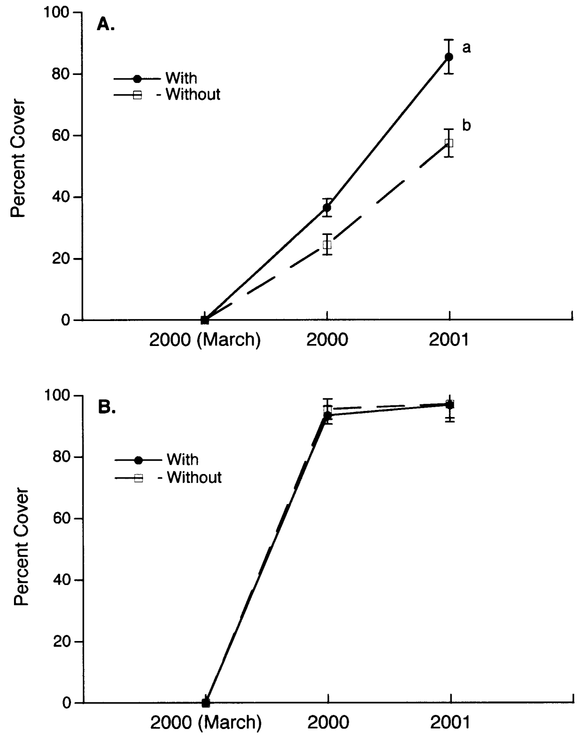


Fig. 8A, B Recovery of the scar edge with and without the wicking manipulation. Percent cover of vegetation is shown for both 2000 and 2001 in both the locations (scar edge **A** and halo **B**). Results of 2-way ANOVA on year 2001 data indicate significant differences among treatments. Different letters indicate significant differences among treatments ($F_{1,\,31}$=6.69 $P<0.01$)

patches with harsh edaphic conditions that limit recolonization by most marsh plant species. Harsh physical conditions in these disturbance patches slow patch recovery and likely lead to secondary succession that requires plant amelioration of harsh conditions for disturbance patches to recover to the plant species composition of undisturbed vegetation.

Disturbance in New England salt marshes

New England salt marshes are exposed to two natural disturbance processes that play an important role in shaping plant communities. Wrack disturbance occurs when floating plant debris (wrack) is washed by tides to high marsh elevations where it is stranded. If wrack stays in place long enough it can kill underlying vegetation leaving unvegetated substrate that then undergoes secondary succession (Reidenbaugh and Branta 1980; Bertness and Ellison 1987; Hartman 1988; Brewer and Bertness 1996; Brewer et al. 1998). In New England the high aboveground production of the cordgrass (*Spartina alterniflora*), the winter die back of cordgrass leaving a large amount of dead plant material, and the high tidal amplitude make wrack disturbance common. Wrack disturbance, however, is largely restricted to high marsh habitats since tides typically prevent wrack accumulation from staying in place long enough to kill underlying vegetation in low marsh habitats.

Winter ice is arguably the second most important natural disturbance agent in New England marshes. In contrast to wrack disturbance which primarily impacts high marsh habitats, ice disturbance most strongly impacts low marsh habitats that are exposed to daily tidal water movement (Dionne 1969; Hardwick-Witman 1985; Bélanger and Bédard 1994). In southern New England (Rhode Island) winter ice incorporated into low marsh cordgrass can rip free large 1–3 m^2 portions of the marsh and raft them from the marsh on ice during high tides. This can leave low marsh habitats a mosaic of patches recovering from disturbance (Bertness and Ellison 1987; Brewer et al. 1998). Further north winter ice becomes more pervasive and severe (Mathieson et al. 1982; Bélanger and Bédard 1994; Hardwick-Witman 1995). Typically in many tidal salt marshes of Maine winter ice regularly entirely destroys the low marsh so that low marsh vegetation (that part of the marsh daily covered and uncovered by tides) is limited to cordgrass ramets annually reinvading before being killed back the following year (Bertness 1999).

In northern New England marshes winter ice also impacts middle and high marsh areas. The common type of middle and high marsh ice disturbance occurs when ice sheets rest on the high marsh surface, melt and deposit sediments incorporated into the ice on the high marsh surface. This commonly leaves discrete mounds of sediment 5–10 cm high by 0.5–2.0 m^2 on the marsh surfaces that are colonized by surrounding plants. This sediment deposition leads to mounds or isolated patches of plants.

Mechanisms of secondary succession

Salt marsh plant community secondary succession following wrack has been studied in southern New England high marshes and has been shown to be relatively rapid and highly dependent on local edaphic conditions (Bertness and Ellison 1987; Bertness and Shumway 1993; Brewer and Bertness 1996). Unvegetated bare patches generated by wrack cover typically are entirely recolonized in 3–5 years (Bertness and Ellison 1987). The mechanisms of secondary succession, however, are dependent on patch physical conditions. Bare patches in the high marsh can become hypersaline because of the evaporation of pore water leaving surface soil salinities up to 150 ppt (Bertness 1992). The degree of patch hypersalinity is dependent on patch size (and shading), tidal height, and yearly climate variation (Bertness 1992; Bertness and Ewanchuk 2002). Secondary succession in saltier bare patches has been shown to be facilitative, while in patches that are not hypersaline the interaction among colonizing plants is entirely competitive (Bertness 1991a; Bertness and Shumway 1993).

We have recently shown that in the marshes of southern Maine the secondary succession of wrack bare patches is not characterized by facilitation because cooler summers lead to conditions that do not result in hypersaline patches (Bertness and Ewanchuk 2002). Our results suggest that middle marsh secondary succession patterns may also be slowed by low soil oxygen. In ice scars with the vegetation and peat removed, the substrate was waterlogged and had low redox (Fig. 3). This is likely due to the loss of plants that oxygenate marsh soils with their aerenchyma (Howes et al. 1986) and possibly the loss of the underlying peat which is very porous and thus drains water preventing the development of anoxic soil conditions (Armstrong et al. 1995). Anoxic conditions in ice scars limit plant colonization to highly tolerant marsh plants that invade the anoxic scars vegetatively; *D. spicata* and *Spartina alterniflora*. By invading vegetatively, these plants may be supported by ramets outside the patches (sensu Alpert 1990, 1991; Pennings and Callaway 1992; Shumway 1995; Amsberry et al. 2000). Once in the patches, however, both these plants have well-developed aerenchyma to oxygenate the soils. Over time substrate oxygenation of these patches by the initial invaders appears to lead to facilitation of the less tolerant high marsh plants that dominate nearby undisturbed habitats. Given that we could find no evidence of old ice scars on the marsh, and the unscarred high marsh was dominated by monocultures of *Spartina patens* and *Juncus gerardi*, we predict that these areas will ultimately recover to these monocultures.

Our results suggest that middle marsh secondary succession in northern New England salt marshes following intense icing events may be limited by anoxic soil conditions, but facilitated by aerenchymous stress-tolerant invaders. This suggests that disturbance recovery of marsh plant communities may provide two examples of facilitative succession, one driven by hypersalinity, the other by anoxia.

Ice disturbance and the structure of northern New England salt marsh plant communities

Winter ice disturbance plays a major role in determining the structure of the mid-marsh plant community. Scouring by ice blocks carried during high tides in the winter removes sediment and changes the microrelief of the marsh surface (Dionne 1969). In northern New England marshes these recurring icing events generate a mosaic pattern of vegetation cover across the marsh. The recovery from these ice disturbances is a much slower process than previous documented cases of disturbance on marsh vegetation (Figs. 1, 2) (Bertness and Ellison 1987; Brewer and Bertness 1996). Disturbances in southern New England marshes are generally caused by wrack and are fundamentally different in their frequency and intensity and generally recover within 3 years (Bertness and Shumway 1993). Winter ice disturbances in Maine marshes, although not as frequent as wrack disturbances, are stronger in the intensity with which they change the vegetation structure of the marsh. Not only are large areas of the mid-marsh vegetation affected by each ice disturbance but large areas of the marsh peat are also affected. In addition to the actual disturbance site, the areas around them also are impacted. These multiple areas affected by the ice disturbance result in the recovery process for the whole disturbance occurring in two distinct ways.

The most significant difference between the areas impacted by ice disturbance is the rate at which they recover. The halo areas that surround the scar areas where the peat base was removed recover within 3 years of the disturbance event (Fig. 1). This rate of recovery is similar to recovery rates found in marshes with other disturbances (Bertness and Ellison 1987). However, in contrast to wrack disturbances that produce similar areas of dead vegetation (Bertness and Shumway 1993), the recovery of the halos does not require facilitative mechanisms for closure of the disturbance patch. Salinities in the halos do not build up to the point at which they would inhibit the recruitment and or survival of plant species. However, our transplant results indicate that survivorship of many of the forb species is affected by the disturbance. These changes in survivorship suggest that the changes in redox and soil water content may reduce their survivorship but not to the point of exclusion.

The ice scars that result from the ice disturbance event follow a much slower and very different pattern of recovery than their adjacent halos. Because of the changes to the peat surface, these areas undergo a recovery that is similar to primary succession or marsh creation described by Redfield (1972). The decrease in redox and increase in soil water content make these areas on the marsh surface similar in soil chemistry found in the lower *Spartina alterniflora* zone. The slow recovery observed after 4 years suggests that these areas will eventually close, if not impacted by another disturbance before full recovery.

Only three species were able to survive and grow in the reduced sediments of these scars. Although not tested in this transplant study, *Spartina alterniflora* seemed to rapidly colonize the scar areas from belowground rhizomes. It appears that the removal of the approximately 4 cm of peat does not affect the deep rhizomes of *Spartina alterniflora*. The other two species, *D. spicata* and *Salicornia europaea*, are known to be able to tolerate these physical stresses. In fact, both of these species play a major facilitative role in the closure of disturbance patches in other marshes (Bertness and Shumway 1993). Only *D. spicata* and *Spartina alterniflora* have the roots and rhizomes necessary to bind the sediments and rebuild the peat base, indicating that the recovery of these scar areas will first require the colonization by one or both of these species to facilitate the scar recovery by changing redox potential and soil water content.

The results of this study of winter ice disturbance on northern New England salt marshes suggest that marsh disturbance recovery is a slow process. In addition, the patterns of recovery are dictated by how the disturbance event affects the soil chemistry of the marsh. The resultant changes in salinity, redox potential, and soil water content suggest that these edaphic variables strongly dictate the plant community and in particular the number of species able to recolonize the different disturbances.

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