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An Investigation of Salt Marsh Dieback in Georgia Using Field Transplants

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ABSTRACT: In 2001 and 2002, Georgia salt marshes experienced a dieback event that affected more than 800 ha throughout the coastal zone. The dieback event was unprecedented in the state and affected both *Spartina alterniflora* and *Juncus roemerianus*. A transplant study was conducted from May to October 2003 to determine if healthy plants could survive in dieback areas. Transplants were carried out at two locations on the Georgia coast in areas of *S. alterniflora* dieback along the banks of tidal creeks, an area of *S. alterniflora* dieback in the mid marsh, and a *J. roemerianus* dieback area in the mid marsh. Transplant survival was nearly 100% and growth (measured as increases in the height of the 5 tallest stems and the number of stems per experimental pot) was observed in both healthy (control) and dieback areas. *J. roemerianus* grew more slowly than *S. alterniflora*, with no observed increase in stem height and an average 38% increase in stem density as compared to an average 57% increase in stem height and 137% increase in stem density in *S. alterniflora*. Differences in growth were inconsistent but in most cases no significant differences were observed between healthy and dieback areas. Soil characteristics measured over the course of the experiment were generally comparable between healthy and dieback areas (redox potential averaged 69 $\pm$ 123 [SD] across all observations at all sites, pH averaged 6.7 $\pm$ 0.3, and salinity averaged 24.9 $\pm$ 4.4), but porewater ammonium (NH_4) concentration was often higher in dieback areas (overall mean NH_4 concentration was 138 $\pm$ 127 μM in dieback areas versus 33 $\pm$ 40 μM in healthy areas). These results suggest that the cause of dieback was no longer present at the time of this study and that transplants are a possibility for restoring affected areas.

Introduction

In 2001, dieback began affecting portions of the salt marshes of coastal Georgia, leading to the largest salt marsh dieback event ever recorded in the state. Affected areas were characterized by loss of aboveground vegetation, resulting in large expanses of bare mud. The two dominant plants in Georgia salt marshes, *Spartina alterniflora* and *Juncus roemerianus*, were both affected. Rhizomes were present in the sediment, but chlorotic or standing dead vegetation was rarely, if ever, observed. Previously described causes of vegetative dieback in Georgia salt marshes, such as causeway construction, accumulation of *Spartina* wrack, or herbivory (Basan and Frey 1977; Edwards and Frey 1977) were rarely associated with the 2001–2002 dieback. By March 2002, aerial surveys conducted by the Coastal Resources Division of the Georgia Department of Natural Resources showed that extensive dieback of over 240 ha had already occurred at a single site, and subsequent surveys revealed that approximately 800 ha were affected in total. Areas of salt marsh dieback varied greatly in size, with three areas of extensive dieback ($>$ 40 ha) and numerous smaller areas. Each of the large dieback areas was located in a nonriverine estuary, occurred at the boundary between *S. alterniflora* and *J. roemerianus* marshes, and encompassed extensive dieback of both species. Smaller dieback areas were distributed throughout the coastal zone (Ogburn 2004).

The Georgia salt marsh dieback event was characterized by four distinctive patterns of vegetation loss (Fig. 1). The most striking and most common pattern of dieback (based on field surveys, Ogburn 2004), referred to as creek bank dieback, occurred in 1–3 m wide strips parallel to the banks of both large and small tidal creeks. Barren areas were typically located on the top of the levee that borders the creek as well as the side leading down to the creek edge, with healthy vegetation often observed in the creek at the base of the levee. Mid marsh dieback areas, the second most common dieback pattern, were usually small and were reminiscent of panne dieback described at other locations wherein bare or sparsely vegetated patches are observed in inland areas (Goodman et al. 1959; Linthurst and Seneca 1980; Mendelssohn and McKee 1988; de Souza and Yoch 1997). Berm dieback was characterized by the formation of scallop-shaped barren areas on or behind the creek bank levee. These scallop-shaped areas were actually raised berms located at a higher elevation than the rest of the marsh. The surface of the berms was often dry and cracked or covered with precipitated salt nodules and was almost always heavily disturbed by fiddler crabs. The least common pattern of

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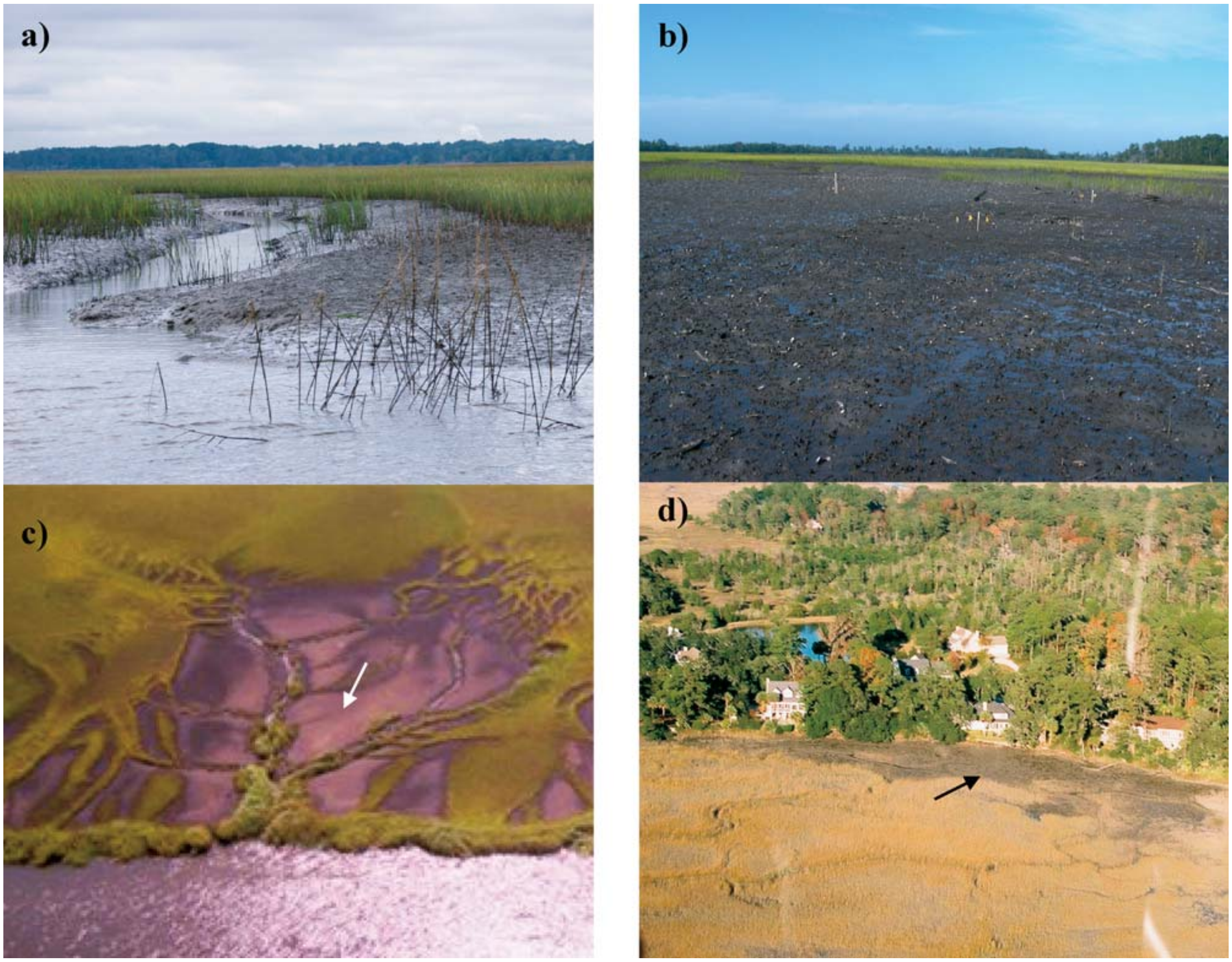

Fig. 1. Patterns of salt marsh dieback in Georgia (photos by M. Ogburn): a) creek bank dieback, b) mid marsh dieback, c) berm dieback, and d) upland dieback. Arrows indicate dieback areas.

dieback was upland dieback, with barren areas occurring adjacent to the upland border of the marsh where wrack disturbance is common. Wrack was not always present at these sites.

Although this is the first report of extensive salt marsh dieback in Georgia, the phenomenon has been observed in a variety of other locations. Sustained loss of fresh and salt marshes has occurred throughout the Mississippi River delta since as early as the 1960s (Smith 1970; Mendelssohn and McKee 1988; Turner 1990). Such historical dieback events may be different from the more recent acute dieback that occurred in Louisiana in 2000 in which more than 100,000 ha of *S. alterniflora* became chlorotic and died over the course of several months (McKee et al. 2004). Other cases of salt marsh dieback have been observed that affected *S. alterniflora* in North and South Carolina (Linthurst and Seneca 1980; de Souza and Yoch 1997). *Spartina townsendii* in Great Britain has also been known to suffer dieback (Goodman et al. 1959). Most recently, *S. alterniflora* dieback was reported at several sites in Connecticut and Massachusetts in spring 2004 (Rozsa unpublished data), and there have also been observations of brown marsh at sites in Virginia (Christian, personal communication). Diebacks may be naturally-occurring events, but these recent reports suggest that it can be extensive and that it occurs in both subtropical and temperate marshes.

The causes of salt marsh dieback are likely varied and remain unclear in most cases. The historical dieback in Louisiana is attributed to sustained inundation due to sea level rise that results in soil water-logging and elevated porewater sulfide concentrations (Mendelssohn and McKee 1988). Goodman and Williams (1961) proposed a similar mechanism for *S. townsendii* dieback in Great Britain but lacked the analytical techniques to isolate sulfide as the primary stressor. Acute salt marsh dieback in Louisiana was not caused by water logging, as it occurred during a period of severe drought and low water levels (McKee et al. 2004). McKee et al. (2004) suggested that it was caused by soil desiccation resulting in periods of low pH and increased bioavailability of toxic metals including iron and aluminum. The causes of dieback events in North Carolina, South Carolina, Massachusetts, and Virginia have not been determined.

In Georgia, greenhouse experiments were carried out to determine the viability of plant tissue and suitability of soil for plant growth from a dieback area (Ogburn 2004). Plugs of *S. alterniflora* from a completely denuded area (rhizomes still present) did not sprout, whereas those from a small area of live vegetation located within the dieback area continued to grow. This result was supported when rhizomes from dieback areas were analyzed for viability by staining them with 2,3,5 triphenyltetrazolium chloride; those that appeared dead did not take up the stain (Franklin personal communication). In a second experiment, healthy young shoots of *S. alterniflora* (14 ± 6 cm tall) exhibited similar growth rates over the course of 3 mo when planted into pots containing soil from a dieback area and a nearby healthy marsh (the source of the shoots). These results suggested that soil from dieback areas was viable and that the dieback was a short-term event.

This study was designed to investigate the responses of healthy *S. alterniflora* and *J. roemerianus* to transplanting into dieback areas in the field. The purpose of these efforts was to determine whether healthy *S. alterniflora* or *J. roemerianus* plants could survive and grow in dieback areas under field conditions and whether differences in soil chemistry between dieback and healthy areas could be related to transplant survival and growth.

Methods

Study Sites

Transplant experiments were carried out using four paired experimental plots at two locations on the Georgia coast. Study sites exhibited two of the common patterns of dieback: creek bank and mid marsh dieback. The first site (referred to as the Sapelo creek bank site—31°23′40″N 81°17′16″W) was located on the southern end of Sapelo Island in McIntosh County, Georgia, near the University of Georgia Marine Institute. This barrier island site is approximately 50 m from Doboy Sound and is submerged at high tide except during neap tides. Only *S. alterniflora* occurs at this site. Dieback occurred in the creek bank pattern, affecting a 1–3 m wide strip along the upper end of a small tidal creek where tall form *S. alterniflora* occurs. A healthy reference area (and source of transplants) was located about 20 m from the dieback area along the same small creek, closer to Doboy Sound. The site is located near an old dike but has been relatively undisturbed in recent years. Dieback was first reported at this site in the late fall of 2002.

The three other sites were located approximately 15 km inland from Sapelo Island on Dickinson Creek at Melon Bluff Plantation in Liberty County, Georgia (31°43′43″N 81°17′41″W). Dieback at Melon Bluff Plantation is reported to have begun during summer and fall 2001. The Melon Bluff creek bank site is a creek bank dieback of tall form *S. alterniflora* comparable to the site on Sapelo Island. This site is also submerged at high tide except during neap tides. At this site, *S. alterniflora* died on the top and sides of the creek bank in a strip 1–3 m wide, although there were some small patches of live *S. alterniflora* at the bottom of the creek. A healthy reference site was located approximately 5 m from the creek directly behind the dieback area. The second site at Melon Bluff was a patch of dieback in an area of short form *S. alterniflora* (referred to as the mid marsh *Spartina* site). This site was located near the upper extent of moderate high tides. Dieback occurred in an area of saturated soils and was characteristic of the mid marsh dieback pattern. The marsh surface at this site was composed of a dense, spongy mat of roots about 10–15 cm thick with very soft, wet mud underneath. The healthy control site was located about 5 m from the edge of the dieback area in an area with similar elevation and soil saturation. At the third Melon Bluff site, patches of *J. roemerianus* occurred within an area dominated by short form *S. alterniflora* (referred to as the *Juncus* site). This site was slightly higher in elevation than the high marsh *Spartina* site and was only flooded during spring tides. Dieback in this area affected both *S. alterniflora* and *J. roemerianus* (although only *J. roemerianus* dieback areas were used) and occurred in the mid marsh pattern. The marsh surface at this site was a thick mat of roots similar to the mid marsh *S. alterniflora* site. A healthy reference site was located approximately 1 km south of the dieback area (31°42′51″N 81°16′57″W) because live *J. roemerianus* closer to the dieback site only remained in very small clumps or as individual stems at the edges of some former patches. The reference area, which was still located on Dickinson Creek, was the closest available source of healthy transplants.

Experimental Design

A series of reciprocal transplants was set up at each site, wherein plants from the healthy area were transplanted into either the healthy or dieback zone. When possible, plants from the dieback area were likewise transplanted. In each healthy site, 24 swards (plants and the surrounding soil) of *S. alterniflora* or *J. roemerianus* were dug up and placed into 20-cm diameter × 20-cm tall plastic pots. *S. alterniflora* swards averaged 7 ± 3 stems per pot, whereas *J. roemerianus* swards averaged 14 ± 5 stems per pot. There were no significant differences between treatments at any site in initial stem count or height of the 5 tallest stems. Each pot had numerous 3-cm diameter holes drilled in both the sides and bottom to allow free exchange of interstitial water between the transplant and its external environment. Of these 24 pots, 12 were randomly planted into new holes in the dieback area and the remaining 12 were randomly placed back into holes in the healthy area as controls. At two of the sites (Sapelo creek bank and mid marsh *Spartina*), a second set of 24 swards was dug up in or at the edge of the dieback area and treated similarly. At the other two sites (Melon Bluff creek bank and *Juncus*), there were no remaining live plants in the dieback area with which to carry out these treatments. In these cases, only healthy plants were transplanted.

The transplant study was initiated at the three Melon Bluff sites between May 3 and 9, 2003. Initial measurements (described in detail below) were made immediately after transplanting was completed. Measurements were subsequently made on June 14, July 15, and October 12, 2003. At Sapelo Island, transplanting was carried out and initial measurements were made on May 28, 2003. Subsequent measurements were made on July 6 and October 4, 2003.

Transplant Growth Responses

On each sampling date, the total number of stems per pot and height of all stems were recorded. Gain or loss of individuals was calculated as the difference between the initial and final number of stems in each pot, expressed as a proportion of the initial number. The average height of all stems in a pot could not be used because increases in the number of new stems caused average plant height to decrease even though individual plants increased in height. To eliminate this effect, the height of the 5 tallest stems in each pot was used as an indicator of plant height. Change in height was calculated as the difference between the initial and final height of the 5 tallest stems in each pot, expressed as a proportion of initial observations.

Plant tissue samples were collected by removing one or two outer green leaves from a randomly chosen plant in each pot on each sampling date. Tissue samples were placed in plastic bags and kept on ice for several hours (no more than 24 h), rinsed in deionized water, dried at 60°C, and pulverized (ball grinder). Samples collected in May and October at the Sapelo creek bank and *Juncus* sites were chosen for preliminary analyses of carbon (C), nitrogen (N), and sulfur (S) concentrations (CE Elantech Flash Elemental Analyzer 1112) to determine if differences in elemental composition could be observed between healthy and dieback areas for either species.

Porewater Analysis

On each sampling date, soil pore water was sampled at rooting depth (15 cm) and analyzed for redox potential, pH, salinity, and ammonium (NH_4) concentration. Redox potential was measured using a Mettler-Toledo Combination Redox Electrode (Pt4805-SC-DPAS-K8S/200) attached to a Fisher Scientific accumet AP62 portable pH/mV meter. A correction factor of +225 mV was added to measured values to account for the potential of the Ag/AgCl reference electrode. To obtain porewater samples for the remaining analyses, shallow wells (measuring 5 cm in diameter and 15 cm deep) were dug into the marsh surface at five locations within the transplant area in both the dieback and healthy areas at each site. (Wells were dug outside the transplant pots to prevent destruction of transplants.) Interstitial water was allowed to percolate into wells for several minutes prior to sampling. Water samples were extracted using a large pipette and stored in 30-ml plastic bottles on ice. Within several hours of collection, samples were filtered through Whatman GF/F 47-μM filters and approximately 15 ml of filtrate was stored frozen (0°C) in ashed 20-ml glass scintillation vials for later analysis of NH_4 concentration (analyzed colorimetrically and measured with a Shimadzu UV-1601 spectrophotometer; Koroleff 1983). The remaining filtrate was used to determine salinity (Leica model 10419 temperature-compensated refractometer) and pH (Fisher Scientific accumet pH probe 13-620-AP50).

Statistical Analyses

Pairwise *t*-tests were used to compare soil characteristics in healthy versus dieback areas. p values were adjusted using the Dunn-Šidák method to achieve an overall alpha of 0.05 ($\alpha' = 1-[1-\alpha]^{1/k}$), where α is the overall alpha, α' is the adjusted alpha used for each test, and k is the total number of *t*-tests carried out. *t*-tests also were used to compare changes in height and plant abundance at sites where only plants from healthy areas were transplanted (Melon Bluff creek bank and *Juncus*). Plant growth metrics were square-root transformed prior to analysis when necessary to meet the assumptions

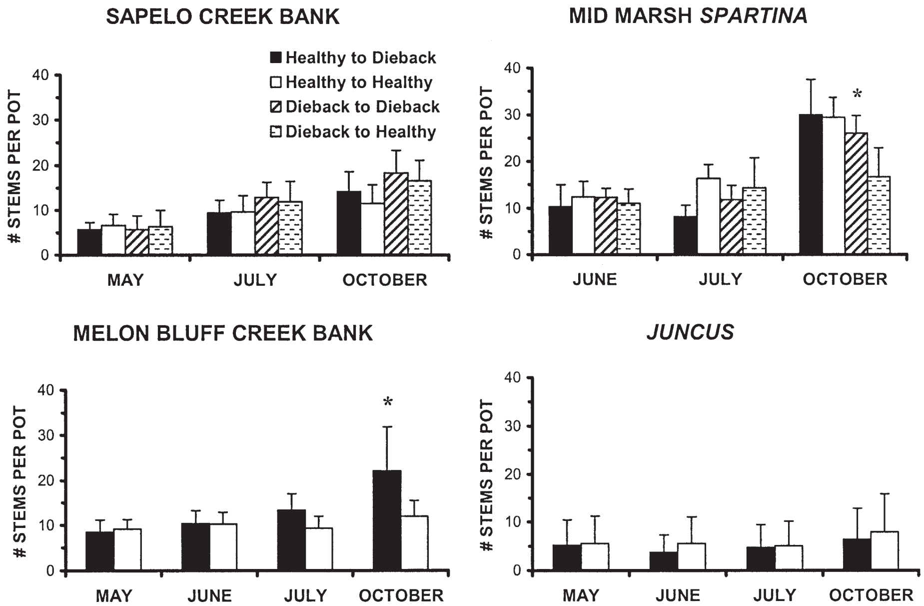

Fig. 2. The number of stems per pot over the course of the experiment of healthy *Spartina alterniflora* (Sapelo creek bank, mid marsh *Spartina*, Melon Bluff creek bank) and *Juncus roemerianus* (*Juncus*) transplanted into dieback (black bars) and healthy (white bars) areas and of *S. alterniflora* at the edge of a dieback area transplanted into dieback (hatched bars) and healthy (dashed bars) areas. Asterisks indicate a significant difference in the proportionate increase in stem density over the course of the experiment between plants from the same source transplanted to healthy as compared to dieback areas. Error bars represent standard deviations (n = 12).

of normality and equal variance. For sites where reciprocal transplants were carried out (Sapelo creek bank and mid marsh *Spartina* sites), two-way analyses of variance were used to compare changes in height and plant abundance by source and destination (healthy versus dieback) using transplant source and transplant destination as fixed effects. Square-root transformed data were again used when necessary. In cases where destination was significant, *t*-tests were used to examine differences in growth at the two destinations within each source category.

Results

Transplant Growth Responses

Survival of live transplants was high in both dieback and healthy areas at all sites. Although occasional stem death occurred early in the experiment in some pots, live stems survived throughout the course of the experiment in every pot (Fig. 2). By March 2004 (10 mo after the experiment was initiated), roots and rhizomes of both *S. alterniflora* and *J. roemerianus* had extended through holes in most pots, and live stems sometimes sprouted up next to the pots.

At the Sapelo creek bank site (where tall form *S. alterniflora* occurs), plants in all treatments survived and grew over the course of the experiment (Figs. 2 and 3). The transplant source had a significant effect on plant growth (Table 1): plants originating in dieback areas exhibited proportionately greater increases in terms of both the total number of stems per pot (from 6 ± 3 to 17 ± 5 stems) and the height of the 5 tallest stems (from 59 ± 20 to 98 ± 27 cm) than those originating in healthy areas (which increased from 6 ± 3 to 13 ± 4 stems and 72 ± 12 to 84 ± 12 cm, respectively). Transplant destination did not significantly affect growth.

At the Melon Bluff creek bank site (tall form *S. alterniflora*) all plants survived, but plants moved from the healthy area to the dieback area had significantly larger proportionate increases in the number of stems per pot over the course of the experiment (from 8 ± 3 to 22 ± 10 stems) than those that remained in healthy areas, which increased from 9 ± 2 to 12 ± 3 stems ($t = 3.60$, $p = 0.002$; Fig. 2). The proportionate increase in average height of the 5 tallest stems was also significantly higher in the dieback area (from 48 ± 5 to 76 ± 10 cm) as compared to the healthy site, which increased from 46 ± 6 to 52 ± 2 cm ($t = 7.92$, $p < 0.001$; Fig. 3).

At the mid marsh *Spartina* site (short form *S. alterniflora*), there were significant differences in both the source of the transplants and their destination (Table 1), but the growth responses were inconsistent (Figs. 2 and 3). Plants from dieback areas exhibited a proportionately greater

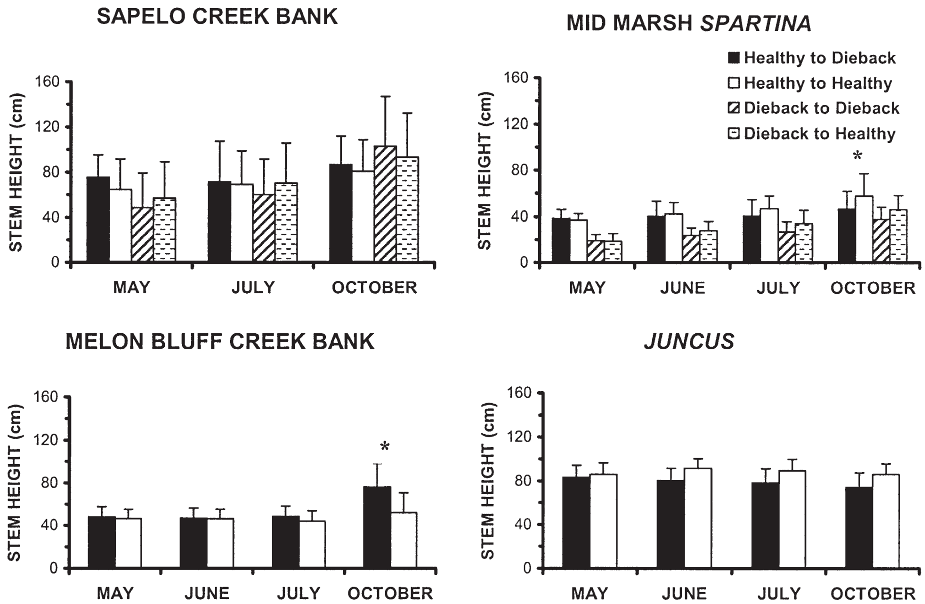

Fig. 3. Average height of the 5 tallest stems in each pot over the course of the experiment of healthy *Spartina alterniflora* (Sapelo creek bank, mid marsh *Spartina*, Melon Bluff creek bank) and *Juncus roemerianus* (*Juncus*) transplanted into dieback (black bars) and healthy (white bars) areas and of *S. alterniflora* at the edge of a dieback area transplanted into dieback (hatched bars) and healthy (dashed bars) areas. Asterisks indicate a significant difference in the proportionate increase in the stem height over the course of the experiment between plants from the same source location transplanted to healthy as compared to dieback areas. Error bars represent standard deviations (n = 12).

increase in stem height over the course of the experiment (from 19 ± 5 to 42 ± 10 cm versus 38 ± 4 to 52 ± 12 cm) but a smaller increase in the number of stems per pot (from 12 ± 3 to 21 ± 8 stems versus 11 ± 4 to 30 ± 7 stems). In terms of destination, plants transplanted to dieback areas exhibited a smaller increase in stem height (from 29 ± 11 to 42 ± 10 cm versus 28 ± 11 to 52 ± 12 cm) but a greater increase in stem density (from 11 ± 4 to 28 ± 7 stems versus 12 ± 3 to 23 ± 9 stems). Post-hoc comparisons revealed a significantly greater increase in stem height in plants from the healthy area transplanted to the healthy area as compared to the dieback area (t = 3.70, p = 0.001) and a greater increase in stem density in plants from the dieback area transplanted to the dieback area (t = 3.42, p < 0.002).

At the *Juncus* site *J. roemerianus* transplants survived, but they did not exhibit as much growth as *S. alterniflora* transplants. There were no significant differences in either the proportionate increase in the number of stems per pot or average height of the 5 tallest stems between plants moved to the dieback area as compared to those moved to the healthy area (Figs. 2 and 3). There was a net decrease in average height of the 5 tallest stems of plants in the dieback area (from 83 ± 9 to 74 ± 9 cm; Fig. 3), which was the result of the death of a few tall stems in some pots. This mortality may have occurred because plants moved into the

TABLE 1. Results of two-way ANOVAs for the change in height of the 5 tallest stems and number of stems per pot (stem count) at both the Sapelo Creek bank and the Mid Marsh Spartina site. Source is the source of transplants (healthy or dieback area) and destination is the location where plants were transplanted (healthy or dieback area). * = p < 0.05

	Sapelo Creek Bank				Mid Marsh Spartina			
Source of variation	Sum of squares	df	F ratio	p level	Sum of squares	df	F ratio	p level
5 tallest stems								
Transplant source	3.36	1	34.35	< 0.001*	4.36	1	48.73	< 0.001*
Transplant destination	0.02	1	0.16	0.069	1.12	1	12.53	< 0.001*
Source × destination	0.85	1	8.6	0.005*	0.02	1	0.16	0.687
Stem count								
Transplant source	3.14	1	11.29	0.002*	11.51	1	26.80	< 0.001*
Transplant destination	0.96	1	3.44	0.070	5.49	1	12.77	< 0.001*
Source × destination	0.34	1	1.21	0.277	0.05	1	0.11	0.744

TABLE 2. Soil salinity, pH, redox potential (Eh), and NH_4 concentration measured [average values (SD), n = 5] in dieback and healthy areas at each experimental site. SI denotes Sapelo Island, and MB denotes Melon Bluff. * indicates significantly higher values in either the healthy area or dieback area for a given month and porewater measurement (*t* tests evaluated at the 0.05 level using adjusted p values). nd denotes not detectable.

Site	Salinity (psu)		pH		Eh (mV)		NH_4 (μM)	
	Dieback	Healthy	Dieback	Healthy	Dieback	Healthy	Dieback	Healthy
Creek Bank *Spartina*—SI								
May	21 (1)	24 (3)	6.8 (0.1)	6.9 (0.6)	259 (14)	199 (93)	89 (36)	54 (60)
July	22 (1)	26 (3)	6.5 (0.1)	6.9 (0.4)	109 (33)	86 (86)	81 (72)	22 (10)
October	28 (0)	30 (1)	6.5 (0.2)	6.3 (0.3)	7 (16)	75 (120)	73 (31)*	8 (8)
Creek Bank *Spartina*—MB								
May	14 (2)	26 (4)*	6.8 (0.3)	No data	235 (40)	273 (114)	81 (11)*	10 (6)
June	20 (1)	23 (2)	6.2 (0.5)	6.1 (0.4)	210 (68)	144 (86)	182 (78)*	23 (7)
July	18 (4)	25 (4)	6.4 (0.2)	6.3 (0.3)	144 (85)	220 (41)	113 (50)*	13 (7)
October	23 (2)	26 (2)	6.4 (0.3)	6.4 (0.3)	181 (37)	152 (73)	167 (84)*	13 (13)
Mid Marsh *Spartina*—MB								
May	25 (1)	26 (2)	7.5 (0.2)	7.2 (0.1)	−82 (15)	−74 (7)	21 (17)	16 (12)
June	25 (1)	26 (1)	7.2 (0.1)	7.1 (0.4)	−73 (11)	−65 (10)	12 (17)	1 (2)
July	26 (1)	27 (1)	6.7 (0.1)	6.8 (0.1)	−85 (40)	−105 (4)	20 (24)	nd
October	24 (1)	24 (1)	7.0 (0.2)	7.0 (0.2)	−70 (48)	−49 (31)	10 (17)	4 (11)
Juncus—MB								
May	31 (3)*	18 (5)	7.1 (0.2)	No data	−35 (18)	152 (66)*	261 (29)*	92 (53)
June	33 (3)*	24 (2)	6.8 (0.1)	6.7 (0.2)	−34 (14)	126 (88)	440 (92)*	144 (109)
July	34 (3)*	22 (4)	6.7 (0.1)*	6.4 (0.1)	−54 (16)	172 (68)*	198 (45)*	66 (12)
October	32 (3)	25 (2)	6.8 (0.1)	6.6 (0.1)	−24 (42)	85 (42)*	316 (39)*	26 (15)

dieback area had to be carried between sites by car, whereas those moved to the healthy area were carried a short distance by hand.

The fact that significant differences in plant growth were rarely observed in these experiments led us to further analyses to determine whether we had adequate power to detect differences between healthy and dieback areas (i.e., by transplant destination). Where significant differences in growth were observed, there was an average 41% difference in the proportionate increase in stem height and 87% difference in the proportionate increase in stem density. In cases where no significant differences were observed, our experiments could have detected differences of half this size (i.e., 20% difference in height and 43% difference in density) with a power of 0.8 or greater for all comparisons at all sites except for the change in density at the mid marsh *Spartina* site. Note that in most cases (including density at the mid marsh *Spartina* site) the average increase was actually greater in the dieback area as compared to the healthy site, so it is highly unlikely that we would have detected significantly better growth in healthy areas with improved power.

Elemental analyses were carried out on tissue samples collected in May and October at the Sapelo creek bank and *Juncus* sites. No significant differences were observed between healthy and dieback areas for any metric at either site. Values for *S. alterniflora* that originated in both healthy and dieback areas averaged 44.1 ± 1.2% C, 1.2 ± 0.3% N, and 0.4 ± 0.2% S, with an average C:N ratio (atomic) of 46 ± 10. *J. roemerianus* (from healthy areas only) averaged 46.7 ± 0.7% C and 1.6 ± 0.2% N (sulfur was below the detection limit of 0.19%), with an average C:N ratio of 35 ± 5. These values are similar to those previously reported for *S. alterniflora* and *J. roemerianus* in southeastern salt marshes (Gallagher 1975).

Porewater Analysis

In the three experimental sites with *S. alterniflora*, soil pore water varied from 11 to 31 psu and averaged 24 ± 4 psu (Table 2). Salinities were generally comparable between dieback and healthy areas and through time, although they were significantly higher in the healthy area than the dieback area at the Melon Bluff creek bank site in May (Table 2). In the *Juncus* site, salinities in the dieback area average 32 ± 3 psu as compared to 24 ± 3 psu in the healthy areas and were significantly higher during 3 of the 4 sampling times (Table 2).

Soil pH ranged from 5.69 to 7.75 and averaged 6.72 ± 0.40 across all sites, with no differences between dieback and healthy areas or through time except for a small but significant decrease in pH in the healthy area at the *Juncus* site in July (Table 2).

Redox potential at 15 cm depth varied both within and among sites (Table 2). Redox potential values were positive in both healthy and dieback areas at the 2 creek bank *Spartina* sites, whereas they were negative in both areas at the mid marsh *Spartina* site. The *Juncus* site was the only place where significant differences in redox potential were observed between dieback and healthy areas: redox potential was positive in the healthy area and negative in the dieback area.

The concentration of NH_4 in pore water was often significantly higher in dieback areas than in healthy areas (Table 2). NH_4 concentrations were significantly higher at all 4 sampling times at both the Melon Bluff creek bank and *Juncus* sites and at 1 of the 3 sampling times at the Sapelo creek bank site. No significant differences were observed at the mid marsh *Spartina* site (Table 2).

Discussion

This study demonstrated that both *S. alterniflora* and *J. roemerianus* could survive and grow when transplanted to salt marsh dieback areas along the Georgia coast, with very few differences in plant growth between healthy and dieback sites. No significant differences in growth (based either on the proportionate increase in the number of stems per pot or average height of the 5 tallest stems) were observed at the Sapelo creek bank or *Juncus* sites. At the mid marsh *Spartina* site, differences in growth between healthy and dieback areas were inconsistent. The Melon Bluff creek bank site was the only site where consistent differences were observed, with plants in the dieback area growing better as compared to the healthy area. This unexpected difference may indicate a release from competition in dieback areas and is potentially related to the observation that NH_4 concentrations were significantly higher in the dieback area, which would have provided a ready source of nutrients. These results are not consistent with what would have been expected if dieback had been continuing during the course of the experiment.

Soil conditions were rarely different between dieback and healthy areas. Salinity, pH, and redox potential were similar in dieback and healthy areas at all sites except the *Juncus* site. At this site, the dieback and healthy areas were separated by a much greater distance (approximately 1 km) than at the other three sites and may have been subject to different hydrologic regimes. The lack of difference in soil characteristics observed here is consistent with field surveys indicating that soil porewater characteristics (salinity, pH, redox potential, and temperature) and faunal densities (*Littoraria irrorata*, *Geukensia demissa*, and crab holes) were similar between adjacent dieback and healthy areas during summer 2003 (Ogburn 2004). The concentration of NH_4 was often higher in dieback areas, but this was likely a result of decomposition and reduced nutrient uptake in these areas as opposed to a cause of plant death and has been observed in dieback areas at other locations (Linthurst and Seneca 1980; Mendelssohn and McKee 1988; de Souza and Yoch 1997).

The Georgia dieback has some similarity to the recent acute salt marsh dieback in Louisiana. As in Louisiana, this event was unprecedented, ephemeral (lasting only a few months), and occurred during severe drought conditions. The 3-yr period leading up to the dieback, from 1999–2001, was the driest 3-yr period in 108 yr of record keeping (http://lwf.ncdc.noaa.gov/oa/climate/research/2002/aug/st009dv00pcp200208.html). Differences between the two states include the fact that there were no observations of standing dead plants in Georgia, and *J. roemerianus* was highly affected in Georgia but was not affected in Louisiana (McKee et al. 2004). McKee et al. (2004) have suggested that in Louisiana soil desiccation may have led to reduced water availability, increased soil salinity, or soil acidification, as evidenced in part by elevated levels of metals in leaf tissue. This may be true in Georgia as well, but there were no dying plants available for analysis of metal concentrations.

Dieback areas remained bare over the course of this experiment but there are now signs of recovery. By March 2004 some small patches (including areas at both the Melon Bluff and Sapelo creek bank sites) showed limited natural recolonization by way of rhizome extension from surrounding healthy plants, and ongoing monitoring coordinated by the Georgia Coastal Research Council (http://www.marsci.uga.edu/coastalcouncil/marsh_monitoring.htm) has documented regrowth in some (but not all) sites. Although natural recolonization may be occurring, the expansion may be too slow to revegetate large areas within a reasonable amount of time. Expansion of *S. alterniflora* into bare patches created by wrack disturbance has been measured at a rate of 12 cm yr^{-1} (Hartman 1988). In North Carolina and Louisiana, *S. alterniflora* has recolonized some dieback areas rapidly via seedling growth (Linthurst and Seneca 1980; Mendelssohn personal communication), but seedling growth has rarely been observed in Georgia. It is also possible that *J. roemerianus* dieback areas will be overtaken by *S. alterniflora*. There was a shift in the *Spartina*-*Juncus* border towards dominance by *S. alterniflora* observed in some Georgia marshes concurrent to this study (Pennings unpublished data), and one of the dieback monitoring sites that had been dominated by *J. roemerianus* is being recolonized by *S. alterniflora*. *S. alterniflora* grows more rapidly than *J. roemerianus* and is known to colonize bare areas (Pennings and Callaway 2000; Pennings et al. 2005), so this is not surprising.

The results from this study suggest that the causative agent of the Georgia dieback is no longer present and that transplanting is a potentially viable strategy for restoration. Transplant source (whether from a healthy area or from a dieback area) played a significant role in determining growth, which is consistent with previous studies of transplant success in dieback areas in which transplant source was related to survival (Linthurst and Seneca 1980; Carlson et al. 2001). Hester et al. (1996, 2001) showed that under short-term sublethal salinity stress *S. alterniflora* exhibits intraspecies genetic variation in salt tolerance, so it would be useful to track strains if transplants are attempted.

The recent salt marsh dieback events in Louisiana and Georgia, along with new reports of dieback in Massachusetts, Connecticut, and Virginia, may represent a new phenomenon facing salt marshes throughout the Atlantic and Gulf coasts of North America. The ephemeral nature of these events have limited our ability to determine their causes or whether they are shared among sites. In Louisiana, an extensive wetland monitoring program has been set up that will provide baseline data on variability and hopefully capture the early stages of future dieback events (http://www.lacoast.gov/watermarks/2004-04/3crms/index.htm). In the face of global warming, increasing climate variability, and rapid development, all of which have the potential to affect coastal environments, it would be useful to be in a position to understand what initiates such rapid degradation of salt marsh ecosystems.

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