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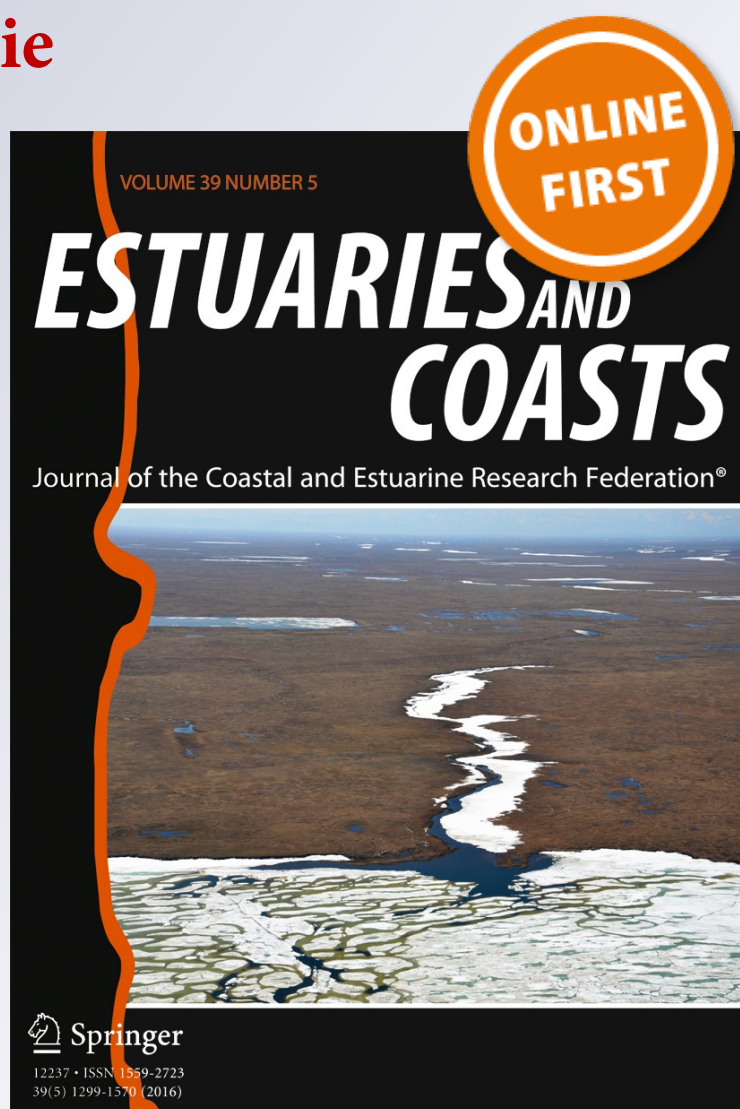
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Spartina alterniflora Biomass Allocation and Temperature: Implications for Salt Marsh Persistence with Sea-Level Rise

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Abstract To predict the impacts of climate change, a better understanding is needed of the foundation species that build and maintain biogenic ecosystems. *Spartina alterniflora* Loisel (smooth cordgrass) is the dominant salt marsh-building plant along the US Atlantic coast. It maintains salt marsh elevation relative to sea level by the accumulation of aboveground biomass, which promotes sediment deposition and belowground biomass, which accretes as peat. Peat accumulation is particularly important in elevation maintenance at high latitudes where sediment supply tends to be limited. Latitudinal variation in *S. alterniflora* growth was quantified in eight salt marshes from Massachusetts to South Carolina. The hypothesis that allocation to aboveground and belowground biomass is phenotypically plastic was tested with transplant experiments among a subset of salt marshes along this gradient. Reciprocal transplants revealed that northern *S. alterniflora* decreased allocation to belowground

biomass when grown in the south. Some northern plants also died when moved south, suggesting that northern *S. alterniflora* may be stressed by future warming. Southern plants that were moved north showed phenotypic plasticity in biomass allocation, but no mortality. Belowground biomass also decomposed more quickly in southern marshes. Our results suggest that warming will lead northern *S. alterniflora* to decrease belowground allocation and that belowground biomass will decompose more quickly, thus decreasing peat accumulation. Gradual temperature increases may allow for adaptation and acclimation, but our results suggest that warming will lower the ability of salt marshes to withstand sea-level rise.

Keywords *Spartina alterniflora* · Salt marsh · Smooth cordgrass · Climate change · Biomass · Elevation

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Introduction

Increasing rates of sea-level rise have the potential to dramatically alter coastal ecosystems. Ecosystems that are intrinsically limited to specific elevations relative to the sea are particularly vulnerable, such as seagrass and coral reefs that require exposure to light, and intertidal wetlands whose species can only withstand periodic submergence (Fitzgerald et al. 2008). These shallow subtidal and intertidal ecosystems must be able to maintain their relative elevation and keep pace with sea-level rise to resist habitat loss. Understanding the impact of sea-level rise on these ecosystems is critical for predicting where and when they may be lost, along with the ecosystem services they provide.

Salt marshes are particularly at risk to increasing sea-level rise (Gedan et al. 2011). They fringe temperate coastlines along a narrow range of elevations, limited at lower elevations by their ability to survive submergence (Armstrong et al. 1985; Bertness and Ellison 1987; Morris et al. 2002; Voss et al. 2013). Salt marshes are dynamic ecosystems, expanding and contracting as sea level has changed over the millennia. However, most contemporary salt marshes were formed over the last 4000 years as glacial retreat slowed and the rate of sea-level rise decreased (Redfield 1972). It is not known if these systems will be able to keep pace with the rates of sea-level rise predicted for this century (Stocker et al. 2013).

Salt marshes are highly valued because they provide storm protection and nursery habitat, prevent erosion, and reduce pollution of estuaries (Teal and Howes 2002; Day et al. 2007; Costanza et al. 2008; Gedan et al. 2009). Marsh drowning would cause the loss of these societal benefits. Salt marshes are also one of the most dense carbon storage ecosystems on the planet and are important to the global carbon cycle (Chmura et al. 2003). The human health and economic repercussions of potential salt marsh loss are substantial (Barbier et al. 2011). Thus understanding where and when they might be converted to other habitat types (e.g., open water or mudflats) will allow people to anticipate the loss of these services.

Salt marsh elevation is maintained by the growth of salt- and submergence-tolerant plants. On the US Atlantic and Gulf coasts, the foundation species (sensu Dayton 1972) *Spartina alterniflora* Loisel (smooth cordgrass) plays a central role in salt marsh establishment, persistence, and recovery from disturbance (Bertness and Ellison 1987; Bertness 1991). Since many salt marshes cannot migrate upland due to human development, maintaining their elevation relative to sea level is critical for their persistence. Whether salt marshes will keep pace with the rate of sea-level rise will depend on rates of (1) sea-level rise, (2) organic accretion, and (3) sediment delivery and retention. Aboveground, *S. alterniflora* stems and leaves slow tidal flow, increasing sediment deposition (Redfield 1965; Redfield 1972; Stumpf 1983). Belowground, *S. alterniflora* roots and rhizomes accumulate, increasing the

subsurface marsh volume (Redfield 1972; Turner et al. 2000; Nyman et al. 2006). Increases in marsh elevation are a function of sedimentation and plant growth and can be offset by decomposition, compaction, and local groundwater withdrawal. The fate of salt marshes with increasing sea-level rise is thus strongly tied to *S. alterniflora* growth.

Along the US Atlantic coast, there is a latitudinal gradient in the amount of peat (accumulated belowground plant biomass) in tidal salt marshes (Pennings and Bertness 2001). Northern marshes have more peat and are thought to maintain elevation primarily through accumulation of belowground biomass, whereas southern marshes have less belowground biomass and rely primarily on sediment capture. Previous studies on latitudinal relationships in *S. alterniflora* growth have shown an increase in annual aboveground biomass production with decreasing latitude (Turner 1976; Kirwan et al. 2009). Belowground biomass has been primarily studied at local to regional scales (Valiela et al. 1976; Ellison et al. 1986; Turner et al. 2004; Darby and Turner 2008), with fewer studies of belowground patterns across broad latitudinal ranges (Gallagher and Plumley 1979; Gross et al. 1991). At higher latitudes, cold winter conditions might select for greater belowground allocation because plants must withstand freezing and store carbon reserves belowground over the winter to generate new stems in the spring (Gallagher 1983). Freezing also slows decomposition, thus decreasing the loss of organic matter. In contrast, lower latitude populations of *S. alterniflora* typically do not experience prolonged freezing and salt marshes in the southeast are able to maintain aboveground biomass year-round (Turner 1976). However, variability in sediment supply exists along the US east coast that may also contribute to differences in how salt marshes keep pace with sea level. Geographic signatures such as local geology, geomorphology, tidal range, drainage basin size, riverine discharge, land use patterns, and urbanization can impact sediment loading (Roman et al. 2000). For example, Pleistocene glaciers scoured northern latitudes of soft sediments, while many shorelines south of Long Island remained unscoured and sediment rich (Meade 1982). Northeastern marshes also tend to have small watersheds and low riverine discharge relative to southern coastal plains (Roman et al. 2000). Bedrock substrates and upland forest cover also contribute to the lower sediment loading typically observed in northern marshes (Roman et al. 2000). These differences in sediment supply may impact salt marsh accretion rates and elevation gain mechanisms.

The apparent latitudinal gradient in biomass allocation provides an opportunity to explore mechanisms of marsh plant growth and the potential response of a foundation species to global change. One valuable approach to explore this gradient is transplant experiments. Despite limitations, transplant experiments have the potential to inform our understanding of ecological dynamics (Connell 1961; Bertness and Ellison

1987; Menge et al. 1994; Scheepens et al. 2010; Agren and Schemske 2012). Transplant experiments can be used to predict how *S. alterniflora* growth will change under altered environmental conditions, enabling better predictions of future marsh elevation.

Using a latitudinal gradient as a proxy for future climate, surveys and experiments were conducted on *S. alterniflora* in eastern US marshes from Massachusetts to South Carolina. The study included (1) latitudinal field surveys of plant biomass and stem properties, (2) a fully factorial reciprocal transplant experiment of *S. alterniflora* among a subset of marshes, and (3) quantification of decomposition rates across the latitudinal gradient. We hypothesized that northern and southern marshes differed in *S. alterniflora* stem properties, biomass allocation, seasonality, and rates of belowground decomposition. The goal of this study was to understand whether plant responses to increasing temperatures would make these northern marshes more or less likely to keep pace with the simultaneously increasing rates of sea-level rise.

Methods

Study Area

Eight sites along a natural latitudinal gradient on the US Atlantic coast from Massachusetts to South Carolina were studied, spanning a range of latitudes from 32° to 41° N (Fig. 1). Field sites included salt marshes in Falmouth, MA (Waquoit Bay National Estuarine Research Reserve, NERR); Prudence Island, RI (Prudence Island NERR); Fire Island

National Seashore, NY (National Park Service, NPS); Dover, DE (St. Jones River NERR); Lewes, DE (Canary Creek); Assateague Island National Seashore, MD (NPS); Beaufort, NC (Rachel Carson NERR); and Bennett's Point, SC (ACE Basin NERR). Data from National Oceanic and Atmospheric Administration (NOAA) weather stations near each site (National Climate Data Center; Table S1) were used to quantify mean growing season air temperatures (average of data collected 10 times per hour from March 15–October 15, 2010), total growing season precipitation (using monthly total precipitation data from March–October), and the mean tidal range of those sites. Salinity measurements were collected at each of the sites in May, July, and October 2010 and April and October 2011 using an YSI salinometer (Model 85) in the creek nearest the sampling area.

Sampling was conducted in monospecific stands of *S. alterniflora* with similar peak field stem heights (40–50 cm) that were at least 1 m from tidal creeks. Sampling areas were standardized by plant height form and submergence frequency across sites to avoid confounding effects of inundation on biomass and growth (Morris et al. 2002; Voss et al. 2013). All eight sites have semi-diurnal tides, and the specific areas sampled within each marsh experienced submergence <20 % of the duration of each tidal cycle. Submergence frequency was determined by measuring the height of the water at high tide at multiple places on the marsh surface in the sampling area, comparing those water heights to the nearest tide gauge and using this relationship and tide gauge data to calculate the percentage of time that the marsh was submerged. Therefore, all study sites experienced similar tidal exposure even when the mean tidal range differed across marshes.

Latitudinal Surveys

Field surveys of plant characteristics at the eight sites were conducted in March, May, July, August, and October of 2010 and April and October of 2011. Aboveground biomass (from 0.25 m² clip plots, $n = 8$ per site), live stem density (per 0.25 m², $n = 8$ per site), height of 5 stems per 0.25 m² quadrat to the tip of the tallest leaf ($n = 8$ quadrats per site), diameter of 5 stems per 0.25 m² quadrat at the first node ($n = 8$ quadrats per site), and belowground biomass (from sediment cores) were quantified. Belowground biomass was sampled with an 8-cm diameter serrated-edge aluminum manual corer to a depth of 20 cm ($n = 8$ per site). The corer was lowered to the marsh surface around the stems and twisted into the marsh to minimize compaction, after which the top of the corer was plugged to pull intact cores out of the marsh. Each core contained several stems, and the core size was selected to minimize the impact on the marshes studied while providing a sufficient number of stems for the experiment. While transplant core diameters vary among studies, the diameter in this experiment was similar to that used in previous studies (e.g.,

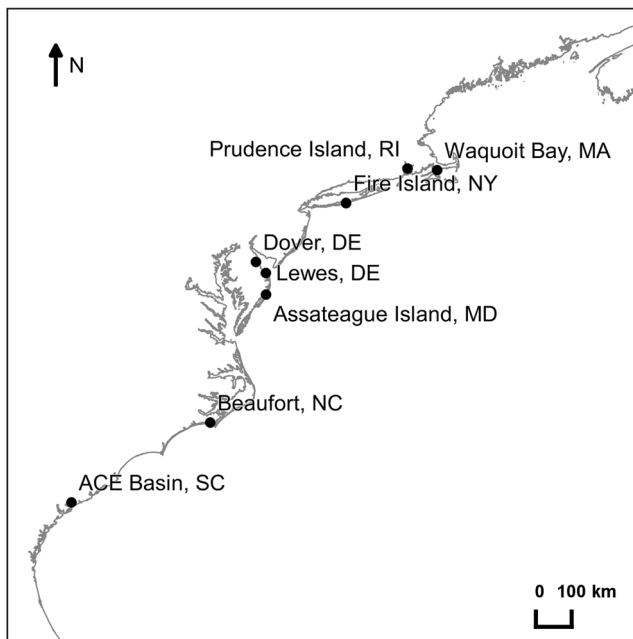


Fig. 1 Location of salt marshes included in the study

Bertness and Ewanchuk 2002; Castillo et al. 2008; Holdredge et al. 2009). Biomass samples were stored on ice, transported to the lab, and frozen until analysis.

Latitudinal Transplant Experiment

A reciprocal transplant study was conducted in March 2010 at the two most northern (MA and RI) and two most southern (NC and SC) study sites, in the same areas where the latitudinal surveys were done. *S. alterniflora* was reciprocally transplanted among study sites in a fully factorial design. Aboveground and belowground material (8-cm diameter to 20-cm depth) was collected using the corer. Samples were taken before emergence of live aboveground biomass for the northern sites, while southern sites had emergent stems. Forty cores were collected from each source site and transplanted to each of the four sites ($n = 8/\text{site/source}$), including eight cores from each marsh replanted locally as transplant controls. Each marsh thus contained cores from four different marshes: eight from each of the three other sites and eight from that marsh. During transport, the cores were kept cool and wet using water-saturated cloths draped over the bins containing the samples. They were kept in ambient local air temperature conditions overnight (which were cool in March 2010) and inside an air-conditioned vehicle during transit. The plants showed no visible signs of stress (no wilting or discoloration of the leaves and no obvious desiccation or stem damage). Macrofauna (such as snails and crabs) were removed from the cores prior to transplantation. Within each marsh, cores were planted >50 cm apart with a 15-cm border of stems clipped around each core with water-permeable garden cloth secured to the sediment to limit initial mortality from neighbor shading. The experiment was conducted for the duration of the northern growing season (March–October). In May, July, August, and October 2010, stem height and diameter ($n = 3$ stems/core) and the densities of live and dead stems were counted in each core. After the October 2010 sampling, cores were removed and frozen until analysis. The genotypes of transplants were not known.

Belowground Decomposition

Belowground litterbags were used to quantify growing season belowground decomposition at all eight marshes. Litterbags ($n = 8/\text{site}$) were deployed in July 2010 and retrieved in October 2010. Pre-weighed (3.0 g) dried (at 60 °C) rhizomes from each site were buried 10 cm below the surface in 3-mm mesh plastic bags. Rhizomes used were collected from that site where they were deployed. Organic material remaining in October was washed over a 2-mm mesh sieve, dried to a constant weight (60 °C), and reweighed to quantify mass loss. Mass loss was divided by days of deployment to estimate decomposition rate (grams dry weight lost per day).

Biomass Sample Analysis

For all biomass samples, stems and leaves were separated from cores at the surface, and then the belowground biomass was cut into 0–10 and 10–20 cm depth sections. Aboveground and belowground samples were gently washed over a 2-mm mesh sieve to remove sediment. Care was taken washing belowground samples to retain fine roots. After washing, the plant components were separated into live and dead fractions (determined using color and turgor), dried to a constant weight (60 °C), and weighed (± 0.01 g). Analysis and sorting followed procedures as described in Darby and Turner (2008). All biomass processing and sorting were conducted by or directly overseen by S.C. Crosby. When reported, “total” biomass is the mass of the combined live and dead components.

Data Analysis

Data were tested for statistical assumptions and analyzed using JMP (Version 11.0, SAS Institute Inc., Cary, NC, 1989–2014). For data where the statistical test assumptions were not met, non-parametric methods were used (e.g., Wilcoxon tests, Kruskal-Wallis/Mann-Whitney U tests, also performed in JMP). Throughout the text, means $\pm$ standard errors are reported. Statistical significance was assessed at the $p = 0.05$ level. Linear regression was used to test for relationships between latitude and mean aboveground to belowground biomass ratio (log transformed), between latitude and mean belowground decomposition rate, and between latitude and local environmental conditions (mean temperature, total precipitation, mean tidal range, and mean salinity). A Kruskal-Wallis test was used to test for differences in mean aboveground to belowground biomass ratio among transplant controls. Data were pooled between northern- and southern-sourced transplants, and a Wilcoxon test was used to test for differences in the change of multiple parameters (mean live and dead stem density, biomass, stem height, and stem diameter) relative to the transplant controls from their respective sites. An analysis of covariance (ANCOVA) was used to test for differences in mean live and dead belowground biomass (at two depths 0–10 and 10–20 cm) with latitude between 2 years of sampling in October (2010 and 2011).

Results

Study Area

Mean growing season air temperature varied along the latitudinal gradient from 15 to 24 °C (Table 1), with a significant negative relationship between temperature and site latitude ($R^2 = 0.88$, $F = 42.01$, $p = 0.0006$, $df = 1, 7$).

Table 1 Basic characteristics of the eight marshes studied

Study site	Latitude (°N)	Longitude (°W)	Mean tidal range (m)	Total precip (cm)	Mean salinity (ppt)	Mean air temp (°C)
Waquoit Bay, MA	41.580	70.521	0.55	99.2	25.1	17.1
Prudence Island, RI	41.625	71.324	1.14	78.0	26.6	17.8
Fire Island, NY	40.689	72.992	0.58	72.8	25.8	15.4
Dover, DE	39.089	75.437	1.62	82.1	10.7	20.1
Lewes, DE	38.788	75.167	1.24	71.0	24.1	19.5
Assateague Island, MD	38.201	75.162	0.67	67.3	27.5	19.4
Beaufort, NC	34.723	76.675	0.95	96.6	32.3	23.0
Bennett's Point, SC	32.558	80.439	1.90	65.8	26.4	24.2

There was a significant negative relationship between mean growing season air temperature and site latitude ($y = -0.84x + 51.73$; $R^2 = 0.88$, $F = 42.01$, $p = 0.0006$, $df = 1, 7$). There was no relationship between latitude and total precipitation ($y = 0.82x + 47.79$; $R^2 = 0.04$, $F = 0.27$, $p = 0.62$, $df = 1, 7$), mean tidal range ($y = -0.09x + 4.41$; $R^2 = 0.33$, $F = 2.91$, $p = 0.14$, $df = 1, 7$), or mean salinity ($y = -0.52x + 44.78$; $R^2 = 0.07$, $F = 0.48$, $p = 0.52$, $df = 1, 7$). Weather stations from which air temperature, precipitation, and tidal range data were obtained can be found in Table S1

There was no relationship between latitude and total precipitation ($R^2 = 0.04$, $F = 0.27$, $p = 0.62$, $df = 1, 7$), mean tidal range ($R^2 = 0.33$, $F = 2.91$, $p = 0.14$, $df = 1, 7$), or mean salinity ($R^2 = 0.07$, $F = 0.48$, $p = 0.52$, $df = 1, 7$). Total precipitation ranged from 65.8 to 99.2 cm, mean salinity ranged from 10.7 to 32.3 ppt, and mean tidal ranges were between 0.55 and 1.90 m (Table 1).

Latitudinal Surveys

The ratio of live aboveground to belowground biomass decreased with latitude when measured during the middle of the growing season (Fig. 2; $R^2 = 0.67$, $F = 10.0$, $p = 0.025$, $df = 1, 6$). Northern marshes had less live aboveground biomass per gram live belowground than southern marshes. End-of-season comparisons in October 2010 and 2011 indicated no statistically significant differences in belowground biomass with latitude between years (Fig. 3; ANCOVA). Across years, a positive relationship with latitude was found between shallow (0–10 cm) live belowground biomass ($R^2 = 0.23$, $F = 3.67$, $p = 0.080$, $df = 1, 13$), deeper (10–20 cm) live belowground biomass ($R^2 = 0.36$, $F = 6.83$, $p = 0.023$, $df = 1, 13$), and deeper dead belowground biomass ($R^2 = 0.50$, $F = 12.0$, $p = 0.0047$, $df = 1, 13$). This suggests that northern marshes are both producing and retaining more belowground biomass. Differences in seasonal patterns were observed between the most northern (Massachusetts and Rhode Island) and southern (North Carolina and South Carolina) marshes, where the transplant experiment was conducted (Fig. 4). Greater variation was observed in both live and dead biomass over the season in the northern sites. In particular, in MA and RI, a greater decrease in belowground live biomass was seen at the start of the

growing season and a greater range in live belowground biomass was observed (Fig. 4).

Latitudinal Transplant Experiment

Northern transplant controls had a lower ratio of aboveground to belowground biomass (less live aboveground biomass per gram of live belowground biomass) at the end of the growing season (MA 0.19 ± 0.03 ; RI 0.11 ± 0.02) than the southern transplant controls (NC 0.45 ± 0.05 ; SC 0.75 ± 0.25). There was a significant difference between the transplant controls for MA and SC and between RI and SC, with a lower

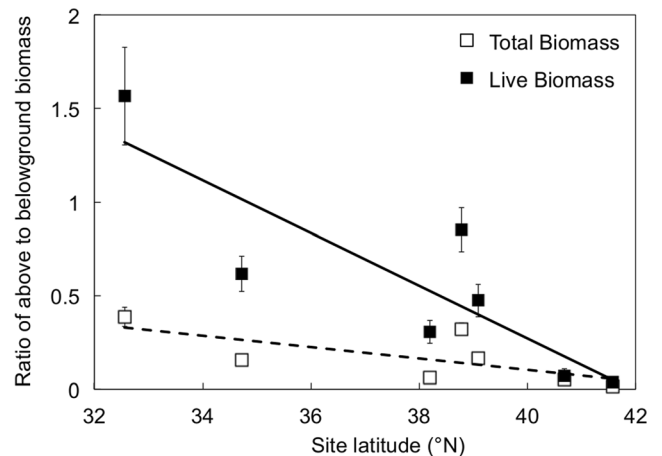


Fig. 2 Biomass allocation ratio (g dry weight aboveground/belowground biomass) in July 2010 ($n = 8$ per site). A log transformation was applied to both the live and total (live plus dead) biomass ratios for analysis. A relationship between the live biomass allocation ratio and the latitude was observed using linear regression ($y = -0.14x + 5.91$; $R^2 = 0.67$, $F = 10.0$, $p = 0.025$, $df = 1, 6$). A marginally significant relationship was also observed using linear regression between the total (live plus dead) biomass allocation ratio and the latitude ($y = -0.03x + 1.32$; $R^2 = 0.51$, $F = 5.26$, $p = 0.070$, $df = 1, 6$). Error bars represent standard error

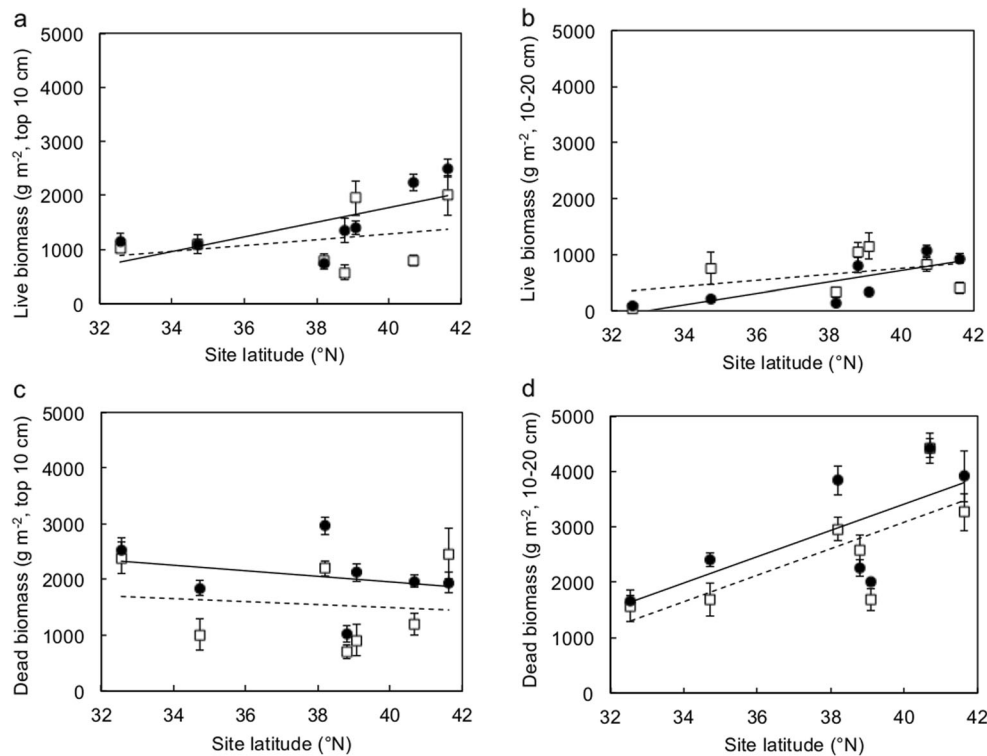
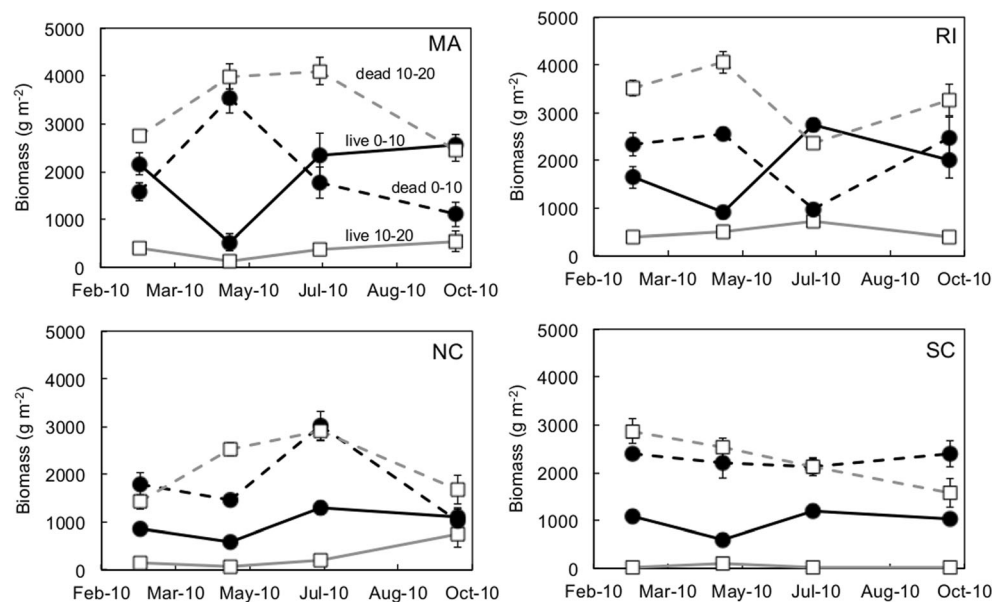


Fig. 3 Live and dead belowground biomass (dry weight, g) measured for two depths below the marsh surface (0–10 and 10–20 cm). Biomass data shown by year for **a** 0–10 cm live, **b** 10–20 cm live, **c** 0–10 cm dead, and **d** 10–20 cm dead. Open squares and dashed lines indicate data from October 2010 ($n = 8$), while filled circles and solid lines indicate data from October 2011 ($n = 7$). Massachusetts was excluded from analysis because only 1 year of data was available. No difference was observed between 2010 and 2011 using linear regression and analysis of covariance (**a–d**, ANCOVA, $p > 0.05$). A relationship between biomass and latitude was observed using linear regression for **b** 10–20 cm depth live biomass

(2010 $y = 53.59x - 1388.4$, 2011 $y = 102.08x - 3365.5$; $R^2 = 0.36$, $F = 6.83$, $p = 0.023$, $df = 1, 13$) and **d** dead biomass (2010 $y = 239.72x - 6503.8$, 2011 $y = 237.82x - 6099.6$; $R^2 = 0.50$, $F = 12.0$, $p = 0.0047$, $df = 1, 13$) across the 2 years of data. The relationship between **a** 0–10 cm depth live biomass and latitude was marginally significant using linear regression (2010 $y = 53.56x - 856.07$, 2011 $y = 135.72x - 3652.5$; $R^2 = 0.23$, $F = 3.67$, $p = 0.080$, $df = 1, 13$). There was no relationship between **c** 0–10 cm depth dead biomass and latitude (2010 $y = -26.67x + 2566$, 2011 $y = -49.854x + 3953.8$). Error bars represent standard error

Fig. 4 Within-season belowground biomass (g m⁻², dry weight, $n = 8$) in 2010 for Massachusetts (MA), Rhode Island (RI), North Carolina (NC), and South Carolina (SC) salt marshes. Black lines and filled circles indicate 0–10 cm depth, while gray lines and open squares indicate 10–20 cm depth. Solid lines indicate live biomass, and dashed lines indicate dead biomass. Error bars represent standard error



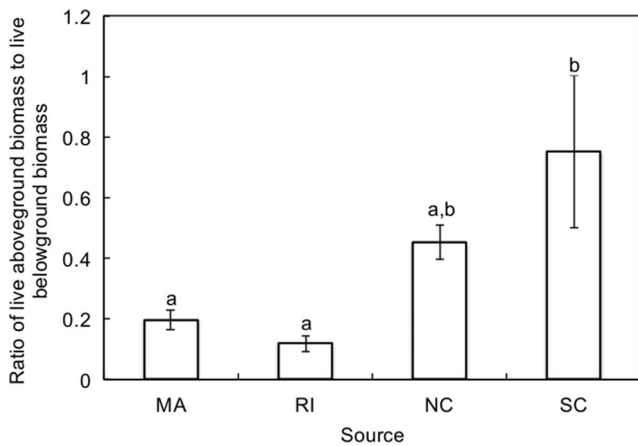


Fig. 5 Biomass allocation ratio (live aboveground biomass/live belowground biomass) for Massachusetts (MA), Rhode Island (RI), North Carolina (NC), and South Carolina (SC) transplant controls ($n = 8$ per site). Northern plants had less aboveground biomass per unit belowground at the end of the growing season (Kruskal-Wallis, $p = 0.0011$, $\chi^2 = 16.01$, $df = 3$). Significantly different results are indicated by letters ($p < 0.05$). Error bars represent standard error

aboveground to belowground biomass ratio at the northern marshes (Fig. 5; Kruskal-Wallis, $p = 0.0011$, $\chi^2 = 16.01$, $df = 3$). In the transplant controls, aboveground live biomass ranged from 333 to 655 g m^{-2} (MA 336.2 ± 62.4 , RI 333.4 ± 42.7 , NC 634.6 ± 79.3 , SC $654.5 \pm 153.3 \text{ g m}^{-2}$), while the belowground live biomass in the top 20 cm ranged from 1208 to 3096 g m^{-2} (MA 1738.5 ± 182.3 , RI 3096.2 ± 299.9 , NC 1419.1 ± 101.5 , SC $1208.4 \pm 332.9 \text{ g m}^{-2}$).

Multiple shifts in aboveground and belowground traits were observed in northern and southern transplants. Data were pooled between the northern source (MA and RI) and southern source (NC and SC) marsh transplants and are labeled as “north to south” and “south to north” transplants, respectively. When southern plants were moved north, a 29 % (± 9 %) increase in belowground biomass relative to the transplant controls was observed. For northern plants transplanted south, a 34 % (± 6 %) decrease in belowground biomass relative to the transplant controls was observed (Fig. 6). A decrease relative to the transplant controls in live stem density, height, and diameter was also observed for northern plants moved south (Fig. 6). Increases relative to the transplant controls in height and diameter were observed for the southern plants moved north but were of smaller magnitude than the decreases observed for the northern plants (Fig. 6). Both transplant directions (north to south and south to north) also had an increased density of dead stems (Fig. 6).

Decreased survival was observed in northern plants moved to southern marshes. At the end of the growing season, 100 % of the south to north transplants survived, while northern plants moved to the south were less successful (Fig. 7). A stepwise pattern was observed for both MA source and RI source plants, where MA plants experienced lower survival in SC than NC (0 % in SC and 50 % in NC), and RI plants

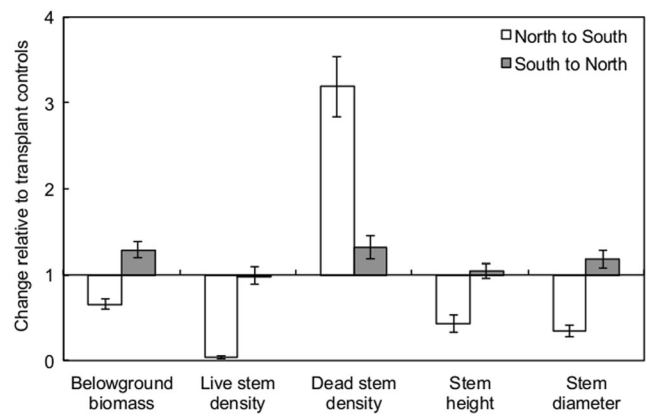


Fig. 6 Proportion of belowground biomass and stem properties relative to the transplant controls from their source marsh at the end of the growing season. Values greater than 1 indicate a positive change in that parameter with transplantation relative to the transplant control mean. “North to south” indicates pooled results of both Massachusetts (MA) and Rhode Island (RI) plants moved to both North Carolina (NC) and South Carolina (SC), and vice versa ($n = 32$ transplants). “Belowground biomass” includes live biomass in the top 20 cm. Differences were observed using a Wilcoxon test between North to South and South to North transplants’ responses in all measures: belowground biomass ($p < 0.001$, $\chi^2 = 21.90$, $df = 1$), live stem density ($p < 0.001$, $\chi^2 = 48.63$, $df = 1$), dead stem density ($p < 0.001$, $\chi^2 = 16.66$, $df = 1$), stem height ($p = 0.0016$, $\chi^2 = 9.92$, $df = 1$), and stem diameter ($p = 0.0002$, $\chi^2 = 13.82$, $df = 1$). Error bars represent standard error

showed a similar pattern but exhibited greater survival than MA plants in the southernmost growing location (12.5 % survival in SC and 50 % in NC; Fig. 7).

Belowground Decomposition

Mean growing-season belowground decomposition rate (expressed as grams per day) was negatively related to site latitude (Fig. 8; $R^2 = 0.86$, $F = 37.2$, $p = 0.0009$, $df = 1, 7$),

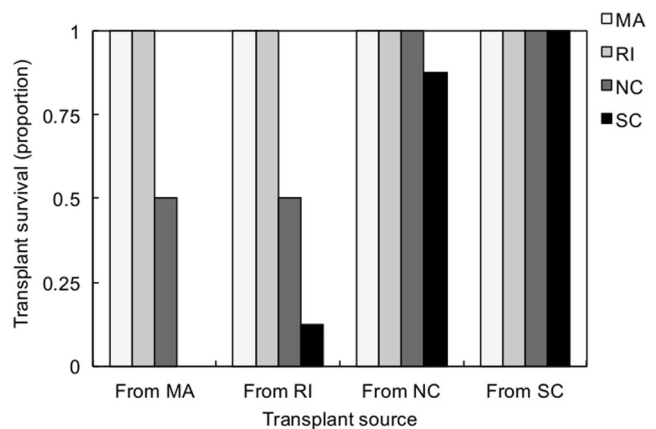


Fig. 7 Proportion of transplants ($n = 8$) with live stems at the end of the experiment (value of 1 indicates that all transplants survived) for Massachusetts (MA), Rhode Island (RI), North Carolina (NC) and South Carolina (SC). Bar colors indicate the location where the transplant was grown (i.e., black bar plants were grown in SC). None of the transplants from MA survived in SC

with belowground biomass in the south decomposing more rapidly than in the north. A positive relationship was also observed between the percent mass remaining and site latitude ($R^2 = 0.61$, $y = 0.77x + 52.88$), and similarly, a negative relationship was observed between the percent mass remaining and the air temperature ($R^2 = 0.54$, $y = -1.16x + 109.32$).

Discussion

Differences among northern and southern *S. alterniflora* biomass allocation and rates of decomposition suggest that increasing temperatures with climate change will make northern marshes less likely to keep pace with sea-level rise. *S. alterniflora* allocated relatively more biomass belowground in northern than southern marshes (Figs. 2 and 5) and had more total biomass belowground in northern marshes at the end of the growing season (Fig. 3). This allocation in belowground biomass is consistent with the “peat-based” and “sediment-based” descriptions of northern and southern systems (Pennings and Bertness 2001), which in turn rely on different mechanisms to withstand sea-level rise. Live belowground biomass increased with latitude (Fig. 3), and allocation to belowground biomass changed with transplantation (Fig. 6). Our study also showed that latitudinal trends in belowground biomass were conserved interannually (Fig. 3) and was consistent with previous studies of both local interannual variability (Teal and Howes 1996) and latitudinal trends in aboveground growth (Turner 1976; Kirwan et al. 2009). Our findings are also consistent with previous findings (Gross et al. 1991) that southern marshes had less belowground biomass per gram aboveground.

We also found decreased survival when northern plants were transplanted to southern marshes (Fig. 7). Plants from

all four transplant study sites grown in a greenhouse in RI (data not shown) all survived through the growing season, thus we do not believe that the mortality in the field study was due to the transplantation process itself. This implies that northern *S. alterniflora* may be unable to tolerate future warmer temperatures. Our transplantation was an abrupt change rather than the gradual change that plants will experience with climate change, so there may be adaptation in growth or stress tolerance to changing conditions (Hoffmann and Sgro 2011). However, the frequency of extreme heat events is also expected to increase with climate change even as mean growing season temperatures rise more slowly. So, the step changes in temperature experienced by the plants in our experiment may also demonstrate the inability of northern populations to withstand the anticipated increase in extreme heat events during the growing season even if populations are able to adapt to the more slowly increasing changes in mean temperature.

Charles and Dukes (2009) found an increase in aboveground growth in experimentally warmed plots in a northern marsh but did not quantify belowground growth or peat accumulation. Our transplants also showed increased allocation to aboveground biomass and changes in aboveground stem traits in northern plants moved to warmer locations (Fig. 6). Northern marshes typically have a lower sediment supply than southern marshes (Meade 1982), thus a shift in allocation by *S. alterniflora* in northern marshes could exacerbate marsh loss to drowning. Additionally, if extreme heat events drive increases in plant mortality, sediment retention will be further reduced. The supply of sediment to salt marshes is decreasing (Weston 2014), but this sediment deficit could be offset by episodic sediment supply during increased storms predicted with climate change; increases in the frequency or intensity of storms have been shown to increase salt marsh accretion and persistence with sea-level rise (Schuerch et al. 2013). In some salt marshes, *S. alterniflora* growth may deviate from these patterns, due to microtidal, highly eutrophic, nutrient-starved, brackish conditions, and other factors (Anisfeld and Hill 2012; Deegan et al. 2012; White et al. 2012; Morris et al. 2013).

Seasonal differences were also observed with latitude. In northern but not southern marshes, a decrease in live belowground biomass was seen at the start of the growing season, potentially reflecting belowground to aboveground translocation during spring green-up. Connor and Chmura (2000) also found initial decrease in live belowground biomass coincident with the onset of aboveground growth in the Bay of Fundy. Gross et al. (1991) found no seasonal change in belowground biomass in Delaware marshes, consistent with our data from southern marshes (NC and SC). A greater range in live belowground biomass during the growing season was also observed in northern marshes (Fig. 4). These differences suggest that the variability in belowground biomass during the growing season may change in northern marshes with climate. Changing seasonal

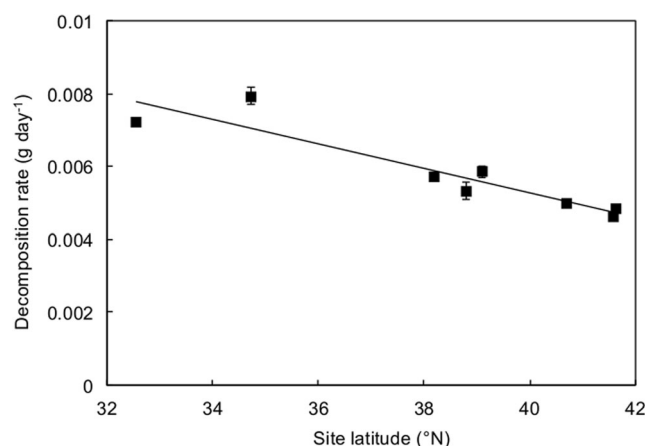


Fig. 8 Litter bags ($n = 8$) containing pre-weighed dry rhizomes, deployed at eight marshes from March–October 2010, showed decreasing decomposition rate with increasing latitude using linear regression ($y = -0.0003x + 0.0188$; $R^2 = 0.86$, $F = 37.2$, $p = 0.0009$, $df = 1, 7$). Error bars represent standard error

patterns of growth could impact temporal patterns in the microbial community, nutrient and carbon cycling, and other processes in which plant translocation of resources and decomposition of belowground material play a role.

The primary process counteracting *S. alterniflora* dead belowground biomass accumulation is microbial decomposition (Benner et al. 1991). We found that the belowground decomposition rate was higher in southern than northern marshes (Fig. 8), consistent with studies of decomposition and temperature at local scales (Howes et al. 1985; Valiela et al. 1985; Kirwan and Blum 2011). This relationship may be complicated by differences in plant nutrient content across marshes, which can also affect rates of decomposition (Newell et al. 2000). Our results are also complementary to recent studies of salt marsh biomass allocation. Darby and Turner (2008) found that the ratio of production to standing stock was higher at lower latitudes, indicating that southern marshes produce more biomass per unit time to reach a given standing stock of biomass than do northern marshes, consistent with the decomposition relationship we observed. While the rate of loss and decomposition of new belowground growth (and how it varies with latitude) is not known, roots in a closely related species, *S. anglica*, have been shown to live for nearly 1 year (Bouma et al. 2002). However, it is not known to what extent within-season turnover may have contributed to the differences observed in belowground biomass allocation with latitude.

Temperature increases associated with climate change will also increase the length of the growing season and the frequency of warmer days, potentially stimulating further decomposition in salt marshes. Similar effects have been observed in other ecosystems (Aerts 2006). In northern marshes, decomposition is also slowed or halted in the winter, suggesting that annual differences along this gradient could be even more dramatic than those observed during this study. As more belowground biomass is broken down through microbial processes, the subsurface marsh volume will decrease. Increasing decomposition will thus be a driver of elevation loss and must be made up for by other elevation-increasing mechanisms including allocation to belowground biomass.

The interplay of local adaptation and plasticity in driving latitudinal variation in our study is unclear. Within a single marsh, *S. alterniflora* exhibits plasticity in aboveground stem traits. This variation is thought to be a plastic response to environmental stress (Shea et al. 1975; Valiela et al. 1978), although others have shown that short and tall form plants can be distinct ecotypes (Gallagher et al. 1988). Our transplant data provide evidence of plasticity, although the relative importance of plasticity versus potential ecotypic differences is unknown. While latitudinal genetic differences in *S. alterniflora* have been found that are indicative of isolation by distance, there is also some overlap in haplotypes between northern and southern marshes (Blum et al. 2007). These

genetic differences, however, have not been associated with specific plant traits. If genetic differences exist and northern populations of *S. alterniflora* do not survive with warming, southern genotypes could migrate north. Since southern populations currently have less belowground biomass and higher rates of decomposition, we might see a similar outcome to that of our transplant study with northward migration. In addition, shifts in dominant genotypes may occur on local scales to favor more heat-tolerant forms, which could dampen some of these effects.

While the accumulation of peat has allowed northern systems to keep pace historically, the combination of altered biomass allocation (Fig. 6), lower supply of sediment (Meade 1982; Weston 2014), and rising rates of decomposition (Fig. 8) may ultimately cause these marsh systems to be submerged. Salt marshes protect people and cities from storms, provide nursery habitat for wildlife, reduce nutrient pollution of estuaries, and form the base of estuarine food chains. Salt marshes also play an important role in carbon sequestration globally (Chmura et al. 2003). If northern marsh plants sequester less carbon belowground, then more marsh-produced carbon will enter the atmosphere as CO₂, further driving global change. The fate of these ecosystem services with sea-level rise will depend on the response of *S. alterniflora* to rising temperatures. Current predictions of salt marsh loss do not include the implications of a temperature response by marsh plants (e.g., Craft et al. 2009), and our data suggest that changes in biomass allocation with warming may cause greater loss of salt marshes than is currently predicted.

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Compliance with ethical standards

Conflict of Interest The authors declare that they have no conflict of interest.

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