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Effects of Warming and Altered Precipitation on Plant and Nutrient Dynamics of a New England Salt Marsh.

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Effects of warming and altered precipitation on plant and nutrient dynamics of a New England salt marsh

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Abstract. Salt marsh structure and function, and consequently ability to support a range of species and to provide ecosystem services, may be affected by climate change. To better understand how salt marshes will respond to warming and associated shifts in precipitation, we conducted a manipulative experiment in a tidal salt marsh in Massachusetts, USA. We exposed two plant communities (one dominated by *Spartina patens–Distichlis spicata* and one dominated by short form *Spartina alterniflora*) to five climate manipulations: warming via passive open-topped chambers, doubled precipitation, warming and doubled precipitation, extreme drought via rainout shelter, and ambient conditions. Modest daytime warming increased total aboveground biomass of the *S. alterniflora* community (24%), but not the *S. patens–D. spicata* community. Warming also increased maximum stem heights of *S. alterniflora* (8%), *S. patens* (8%), and *D. spicata* (15%). Decomposition was marginally accelerated by warming in the *S. alterniflora* community. Drought markedly increased total biomass of the *S. alterniflora* community (53%) and live *S. patens* (69%), perhaps by alleviating waterlogging of sediments. Decomposition was accelerated by increased precipitation and slowed by drought, particularly in the *S. patens–D. spicata* community. Flowering phenology responded minimally to the treatments, and pore water salinity, sulfide, ammonium, and phosphate concentrations showed no treatment effects in either plant community. Our results suggest that these salt marsh communities may be resilient to modest amounts of warming and large changes in precipitation. If production increases under climate change, marshes will have a greater ability to keep pace with sea-level rise, although an increase in decomposition could offset this. As long as marshes are not inundated by flooding due to sea-level rise, increases in aboveground biomass and stem heights suggest that marshes may continue to export carbon and nutrients to coastal waters and may be able to increase their carbon storage capability by increasing plant growth under future climate conditions.

Key words: altered precipitation; climate change; decomposition; Distichlis spicata; *ecosystem services; nutrient cycling; open-topped chamber; salt marsh;* Spartina alterniflora; Spartina patens.

INTRODUCTION

Salt marsh ecosystems are highly productive, and provide valuable services; they export biomass and nutrients, filter pollutants and runoff, protect coastlines from flooding and erosion, and sequester carbon. How will these important ecosystems respond to climate change? Warmer air, soil, and water, and changes in the timing and amount of incoming freshwater could strongly affect salt marshes (Scavia et al. 2002). Although salt marshes are highly vulnerable to sea-level rise, and studies related to climate change predominant-

ly focus on this threat, the effects of climate change on marshes are likely to be interactive. For example, while sea-level rise is likely to lead to marsh flooding and inundation in the mid-Atlantic, precipitation-induced shifts in stream flow could increase allochthonous sediment delivery to marshes, enhancing the ability of some marshes to accrete and keep pace with sea-level rise (Najjar et al. 2000). However, if marshes do not keep pace, they will be more susceptible to erosion by storm surges, which are likely to be enhanced by increases in storm frequency and intensity associated with climate change. The ability of marshes to keep pace with sea-level rise also depends on peat formation, and thus primary production (Patrick and Delaune 1990, Morris et al. 2002). Temperature can have important effects on primary production, physiological processes, and plant community composition. In addition, there is evidence to suggest that warming could increase accretion rates by increasing soil organic matter production, and that warming could also affect the carbon storage capabilities of marshes (Najjar et al.

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2000). Finally, sea-level rise is often correlated with global temperature rise, though not always tightly coupled to it, especially given shorter term fluctuations in tidal ranges, and marsh subsidence (e.g., Varekamp et al. 1992, Donnelly 2006).

Only a handful of researchers have examined the impacts of experimental temperature increases on salt marshes (Gray and Mogg 2001, Bertness and Ewanchuk 2002, Loebl et al. 2006). Their research suggests that increasing temperatures could be enhancing the spread of invasive plants (e.g., *Spartina anglica*), altering plant interactions and plant community composition, and affecting plant growth. To our knowledge, there are no published studies in which temperature was experimentally increased in salt marshes to specifically simulate future climate conditions, as has been done in various other ecosystems (Shaver et al. 2000), and no studies experimentally addressing the interactive effects of warming and precipitation.

In many ecosystems, precipitation manipulations have evoked strong community-level and ecosystem-level responses (e.g., Hanson et al. 2001, Davidson et al. 2004, English et al. 2005). However, extrapolating these results to salt marshes, with their unique abiotic stresses, is problematic. Models suggest that precipitation may have regional scale impacts on marshes by altering estuarine salinities and the amount and timing of river discharge (Saenger 2006). Interannual variation in precipitation leads to variation in salinity and soil moisture in marshes, and consequently affects marsh species composition, germination, and/or biomass (Allison 1992, Dunton et al. 2001, Noe and Zedler 2001, Alexander and Dunton 2002). In some cases, wet years have been linked with the spread of invasives (e.g., less salt-tolerant *Phragmites australis*; Minchinton 2002). Large-scale manipulative experiments have focused on precipitation as a physical disturbance and a mechanism by which recently deposited sediment and nutrients are mobilized and redistributed on the marsh surface (Mwamba and Torres 2002). This could be significant for the biota, since rainfall can redistribute a disproportionate amount of sediment relative to flooding by tides, and rainfall preferentially mobilizes nitrogen over organic carbon, leading to lower nutrient concentrations and organic matter on the marsh surface, and in some cases increased export from the marsh (Torres et al. 2003, Voulgaris and Meyers 2004). Although fewer studies have artificially increased rainfall in a marsh to assess plant population or community responses, results suggest that biomass and species abundances can be affected by additional precipitation (Nestler 1977, Callaway and Sabraw 1994). We are unaware of published studies that have artificially decreased precipitation in marshes. In addition, precipitation studies on marshes in the northeastern United States are lacking in the literature.

Global climate models now project mean global surface temperature increases of 1.8–4.0°C by the end of the 21st century (relative to the period from 1980 to 1999), and sea-level rise ranging from 0.18 m to 0.59 m (IPCC 2007). On a regional scale, annual surface temperature is projected to increase by 2.9–5.3°C in the northeastern United States by the end of the century (relative to the period from 1961 to 1990), depending on future emissions scenarios, with summer warming being greater than or equal to winter warming (Hayhoe et al. 2007). Annual precipitation is projected to increase by 7–14%, with winter increases of 12–30% and essentially no change in summer precipitation, also depending on future emissions scenarios. The anticipated intensification of the hydrologic cycle will lead to more frequent episodes of heavy precipitation and more frequent droughts, particularly in summer and autumn (Hayhoe et al. 2007). To address the gaps in research on climate change in salt marshes, and considering the climate predictions for the northeastern United States, we conducted a manipulative experiment in which we increased temperature and altered precipitation (both increased and decreased vs. ambient) in two salt marsh plant communities dominated by perennials (see Plate 1). By including two very different precipitation treatments, we hoped to elucidate the significance of rainfall to this marsh.

We hypothesized that warming would promote aboveground plant growth by increasing photosynthetic rates. However, we also expected that warming would increase soil salinity by accelerating evaporation from the marsh surface, which might decrease plant growth. We expected that warming would increase microbial activity and thus accelerate decomposition and nutrient cycling, leading to higher nutrient availability. Since sulfate reduction dominates microbial stages of decomposition in salt marshes (Howarth and Teal 1979), we expected warming to increase pore water sulfide concentrations. Valiela et al. (1985) found that warmer water accelerated salt marsh decomposition, a finding we sought to extend to air temperatures. We also expected that warming would advance flowering and delay senescence, as has been seen in other warming experiments (Shaver et al. 2000, Cleland et al. 2007).

We suspected that increasing precipitation would decrease soil salinities enough to alleviate salt stress on the marsh plants, and anticipated that these effects would be most significant in poorly drained areas (depressions), or infrequently flooded areas (high marsh), and might increase the germination success of annual fugitive species (e.g., *Salicornia europea*). We also predicted that productivity would be positively correlated with precipitation, as has been shown in other studies (e.g., Nestler 1977). Reduced precipitation could also slightly offset waterlogging stress due to anoxia. Finally, we speculated that there could be interactive effects of warming and precipitation as has been shown in other experiments (Norby et al. 2007) if, for example, warming increased evapotranspiration and led to salinity stress, which was then offset by increased
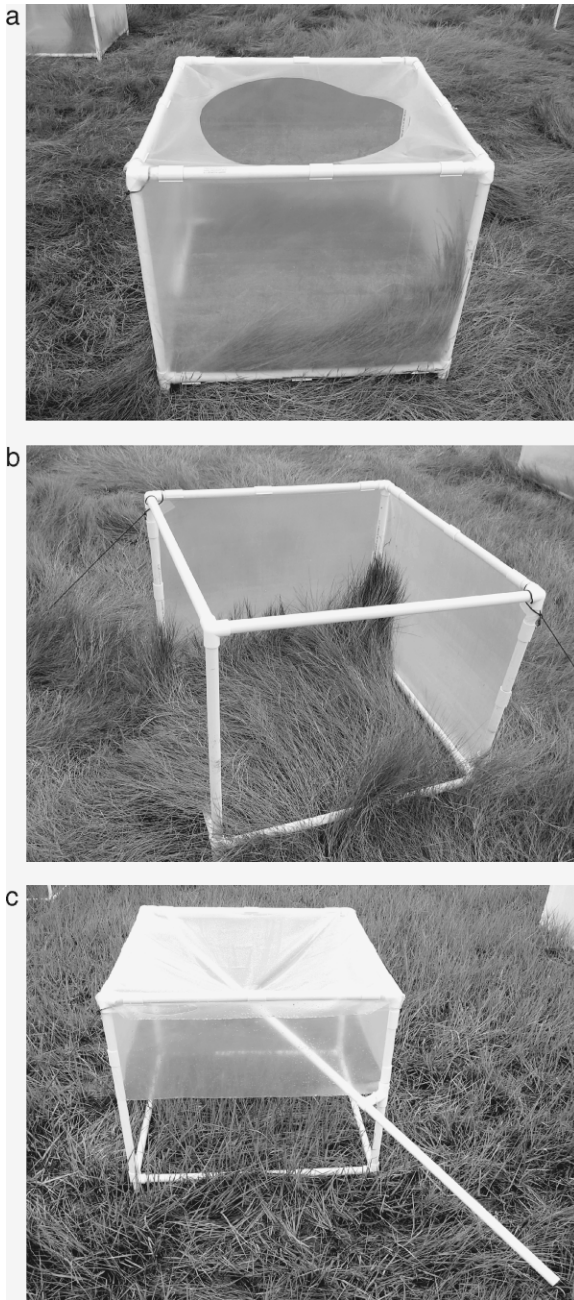
FIG. 1. Experimental design infrastructure. (a) Open-topped chamber for warming marsh plots, (b) control frame, and (c) rainout shelter for diverting rainfall from marsh plots.

precipitation. We tested these hypotheses in two salt marsh plant communities.

METHODS

Study site and timeframe

The experiment took place in a tidal salt marsh in the Plum Island estuary in Rowley, Massachusetts, USA (70°51′ W, 42°43′ N). The site is located adjacent to the Rowley River, within the Plum Island Ecosystem (PIE) Long Term Ecological Research site (LTER). The marsh vegetation in this area is typical for New England salt marshes with patterns of plant zonation based predominantly on salinity and waterlogging, due to differences in elevation, frequency of tidal inundation, and soil drainage. Mean tidal range for the estuary is 2.9 m. Experimental plots were all located in the high marsh at a mean elevation of 2 m, where the marsh is only flooded about twice per month during spring tides, to a mean depth of 10 cm. One set of plots was established in a mixed community comprised exclusively of *Spartina patens* (marsh hay) and *Distichlis spicata* (spike grass; hereafter simply *Distichlis*), typical of the high marsh in this area. Mean percent cover was 85% for *S. patens*, 90% for *Distichlis*, and 100% for standing dead (numbers add to >100% due to overlapping canopy layers). Another set of plots was established in slight depressions in the high marsh, where salinities are high and waterlogging causes the dominant *Spartina alterni-flora* (cordgrass) to grow in a stunted "short form." *Spartina alterniflora* also dominates the low marsh since it is one of the few species that can tolerate daily tidal flooding. The semidiurnal tides reduce salt and toxin buildup in this zone, allowing *S. alterniflora* to grow in a tall form (Bertness et al. 2002). In the high marsh community, mean percent cover was 75% *S. alterniflora*, 15% *Salicornia europea*, 3% *S. patens*, <1% *Atriplex patula*, 75% standing dead, and 10% bare ground. Monthly estimates of the percent cover of all species showed no significant differences between treatments (ANOVAs, $P > 0.20$), or over the time course of the experiment, with the exception of an increase in standing dead late in the growing season. Experimental manip-ulations occurred during five months of the 2006 growing season, from the beginning of June until the end of October.

Experimental design

The experimental design consisted of five main treatments: control, increased precipitation, decreased precipitation, warming, and warming plus increased precipitation. In addition, open plots with no infra-structure were established for comparison to framed controls. We were not able to include an effective treatment of decreased precipitation plus warming due to the limitations of our experimental infrastructure. We constructed five replicates of each treatment in each of the two plant communities for a total of 50 framed plots and 10 open plots. Plot locations were chosen for their uniformity, and treatments were randomly assigned to plots.

Each experimental plot was enclosed in a cube-shaped PVC (polyvinyl chloride) frame, 83×83 cm in footprint and 70 cm in height (Fig. 1), including a gap of 4–5 cm between the base of the structures and the marsh surface, which allowed normal tidal flow over the plots. Warming was accomplished by wrapping "greenhouse plastic" around the sides and partially covering the top

of the PVC frames (Fig. 1a) to form passively warmed open-topped chambers. The section of plastic on top of the structures was added on 20 June 2006 to increase the warming effect. Greenhouse plastic (Dura-Film Thermax, AT Plastics, Edmonton, Alberta, Canada) is transparent 6 mil polyethylene (1 mil = 0.001 inch = 25.4 μm) that is coated to retain infrared radiation. The whitish tinge (Fig. 1) is an anticondensate coating that affects the clarity of the film, but not the light transmission (91% of photosynthetically active radiation, PAR). The gap at the base of the structures and the circular opening on top (~48 cm diameter) minimized unwanted side effects of closed chambers, such as retention of water vapor and excessive warming under certain conditions (Marion et al. 1997). The plastic on top was sloped slightly downward to allow rainfall to drip into the plots. Although these chambers did not allow for precise temperature control or significant nighttime warming, they increased temperatures enough to reasonably simulate the lower end of the range of expected future conditions in New England, particularly during the summer months (Hayhoe et al. 2007; Fig. 2).

We designed control frames (Fig. 1b) with polyethylene on two sides of the PVC frame to control for shading without warming the plots. All experimental frames and plots were oriented with corners on a north–south axis, and control frames had plastic on the southeast and southwest sides to maximize their shading effect and thus their accuracy as controls.

Decreased precipitation plots were covered by a rainout shelter consisting of a PVC frame, topped by a funnel of polyethylene (Dura-Film, Super 4) not coated to retain infrared radiation, and which transmitted 92% of PAR (Fig. 1c). The funnel directed rain into a PVC pipe that diverted it away from the plot. The top half of these structures was covered with uncoated plastic to keep out rain while maximizing air circulation.

To increase precipitation, we sprinkled well water on the plots with a watering can, with the same quantity of water that fell during each rainfall event; thus, each plot received double normal rainfall in total. Natural rainfall amounts were obtained from the PIE-LTER weather station <4 km away in South Byefield, Massachusetts, USA. We attempted to follow the natural temporal variation in rainfall in our watering schedule (Fig. 3), though this was not always feasible. We watered the plots predominantly in between low and high tide or at low tide. While we watered several times at high tide, it was not always safe to access the site in these conditions. Plots were watered in increments, instead of all at once, to more closely mimic natural rainfall. Increased precipitation treatments had the same infrastructure as control plots, and increased precipitation plus warming treatments had standard warming chambers. After a relatively dry April, May and June were unusually wet, and rain accumulated at normal rates between July and October. Precipitation treatments began on 1 June and ended the last week of October (Fig. 3). Decreased
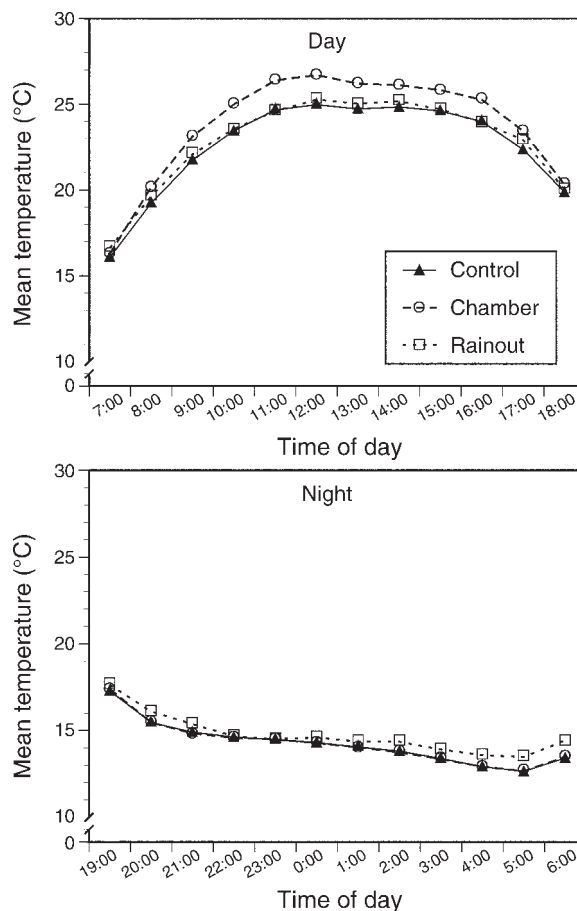

FIG. 2. Mean hourly air temperatures for control frames, open-topped chambers, and rainout shelters from (a) 07:00 to 18:00 and (b) 19:00 to 07:00 hours over the course of the experiment. Open-topped chambers were significantly warmer than controls or rainout shelters during daytime hours, and rainout shelters were slightly warmer than controls or chambers during nighttime hours. See *Results: Temperature, precipitation, salinity and light* for statistical results.

precipitation plots received very little rainfall after 1 June, though occasional high winds and a few structural failures allowed small amounts of rain to reach these plots.

Monitoring manipulations

Temperature sensors were positioned in 10 of the plots at a time and rotated over the course of the experiment. They consisted of a HOBO pendant data-logger (Onset Computer Corporation, Buzzards Bay, Massachusetts, USA) that recorded temperature at a set interval (every 5–15 min) inside a small solar radiation shield (Spectrum Technologies, Plainfield, Illinois, USA). Sensors were attached to a corner of the PVC frame and were positioned in or just above the plant canopy, about 30 cm from the ground, and extending about half of the diagonal distance to the center of the plots, on a section of PVC pipe. We measured salinity of
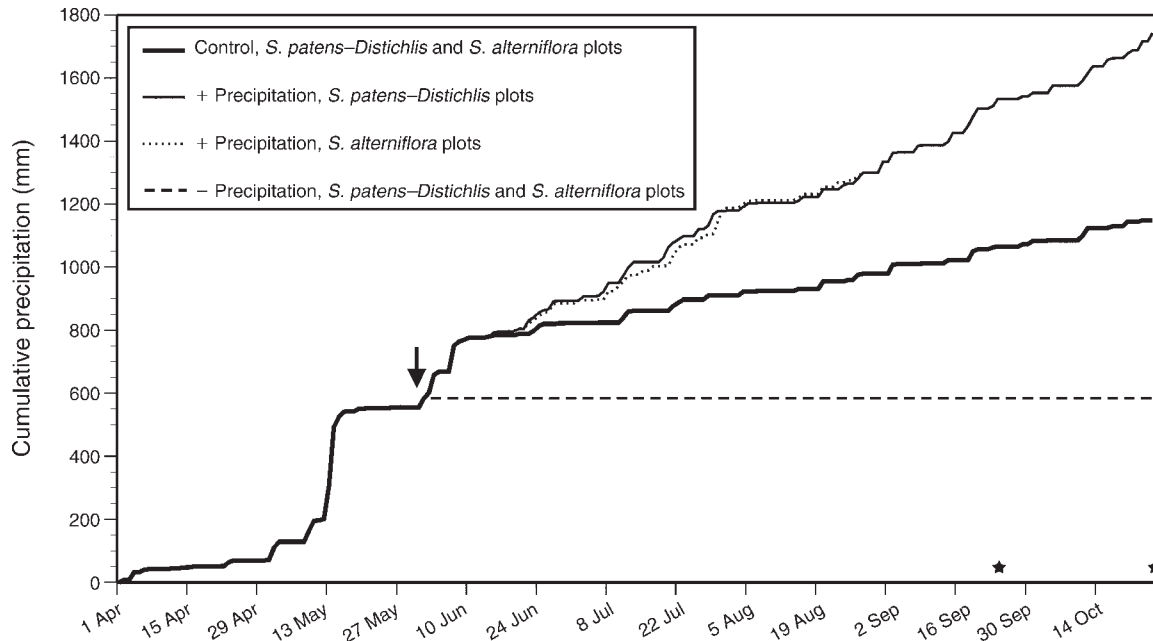
FIG. 3. Cumulative precipitation received by plots during the 2006 growing season via rainfall and/or watering. In the legend, "+ precip." refers to increased precipitation and "− precip." refers to decreased precipitation. The arrow indicates the start of experimental treatments. Stars indicate biomass harvest dates.

water on the marsh surface several times prior to and following watering, using a handheld salinity refractometer, and we measured chloride concentrations in pore water. We assessed shading due to greenhouse plastic by measuring the amount of light passing through the plastic, and actual light levels inside the various plots using a ceptometer (AccuPAR, model LP-80, Decagon Devices, Pullman, Washington, D.C., USA). These measurements were made at the same height in each structure (approximately halfway to the top) to assess the light reaching the top of the plant canopy.

Response measurements

We measured aboveground productivity by harvesting plants in a 20 × 20 cm subplot near the time of peak biomass after new growth had ceased in September (Valiela et al. 1975) and in a second subplot in October. Subplots were positioned at least 10 cm from the edges of the plots, in fixed, predetermined locations in each plot. Plants in *S. alterniflora* plots were clipped as close as possible to the marsh surface, whereas *S. patens–Distichlis* were clipped just above the horizontal layer of dead plant matter. Dead plant matter was not harvested since it included litter from previous years. Live and dead plant biomass was weighed after drying at 60–65°C in a forced-air oven. We also measured heights of the 10 tallest stems of each species on a monthly basis from July to September, and averaged them for analyses. The number of flowering stems of each species was counted in each plot every two to four weeks when plants were flowering (July to September). Percentage of flowering

stems was then estimated using stem density data from September; thus for earlier time points, these are conservative estimates.

We measured decomposition using litter bags. Recently senesced tall-form *S. alterniflora* and mixed *S. patens–Distichlis*–forbs were collected the previous fall and air-dried. Fiberglass mesh litter bags (11 × 11 cm with 2 mm mesh size) were filled with 2 ± 0.03 g of either *S. patens* or *S. alterniflora* (50% leaves and 50% stems, approximately). Each *Spartina alterniflora* plot received two litter bags containing *S. alterniflora*, since this is the dominant species normally decomposing in this community. Each *S. patens–Distichlis* plot received two *S. alterniflora* and two *S. patens* litter bags. This simulated decomposition of wrack, comprised largely of tall form *S. alterniflora*, which is sometimes found in the high marsh. Litter bags were tethered to the marsh surface and were positioned vertically to simulate decomposition of standing dead stems. One set of each type of litter bag was retrieved after three months in the field, and the other set was retrieved after five months. Litter was gently rinsed with distilled water while still in litter bags. Bags and litter were then dried in a forced air oven, and litter was removed and weighed. Control and decomposed samples were ground in a Wiley mill (Thomas Scientific, Swedesboro, New Jersey, USA) and again in a custom made ball mill, dried overnight at 60°C, and cooled in a desiccator before weighing. Sediment samples from each of the plant communities were also obtained and dried. Carbon and nitrogen contents of litter and sediment were determined with an elemental

analyzer (ECS 4010 Elemental Combustion System, Costech Analytical Technologies, Valencia, California, USA), and litter mass was corrected for the presence of any sediment by assuming a constant carbon content (Franck et al. 1997). Mass remaining at each time point was calculated using corrected weights, and decomposition constants (k) were calculated by plotting ln(mass remaining/initial mass) against time, where k is the slope of the regression (Austin and Vivanco 2006).

Nutrient availability (ammonium and phosphate), salinity, and sulfide concentrations were assessed from pore water samples taken on a monthly basis in August, September, and October. Pore water samplers consisted of 20 mL acid-washed glass scintillation vials filled with deionized water, with a small section of 48 μm nylon mesh covering the top, and held in place by an open-top screw cap. Samplers were buried in the marsh horizontally at a depth of ~15 cm in the center of the rooting zone. Each plot contained one sampler, and subsequent samplers were put in the same location. Upon removal from the marsh, a subsample of unfiltered water was treated with zinc acetate for sulfide preservation. The remaining sample was filtered through a 0.45 μm nitrocellulose filter (Millipore Corporation, Billerica, Massachusetts, USA) and acidified with hydrochloric acid prior to the remaining analyses. Ammonium and phosphate were analyzed on an autoanalyzer. Chloride concentrations were determined by coulometric titration on a Haake Buchler chloridometer (Haake-Buchler Instruments, Saddle Brook, New Jersey, USA), and salinities (ppt) were calculated using a 1.80655 conversion factor from g Cl/kg. Finally, sulfide concentrations were determined on a spectrophotometer following the method described by Cline (1969).

Statistical analyses

All statistical analyses were conducted using SPSS, version 13.0 (SPSS 2004). Treatments entailed two fixed factors: warming (two levels) and precipitation (three levels), though it was not a fully factorial design since we lacked a warming × decreased precipitation treatment. We conducted two main sets of analyses to address this, while avoiding the problems associated with unbalanced designs. First, the three precipitation treatments (ambient, increased, and decreased) were analyzed by one-way ANOVA, including data from only the ambient temperature plots. Second, the four treatments that did comprise a fully factorial warming × precipitation experiment were analyzed by two-way ANOVA. We focused on the effects of warming in these analyses, and if any interactions between warming and precipitation were found, we present the full results. Analyses were conducted separately for the two plant communities; but for a few variables, we also combined the data to assess effects across the marsh (provided units of measurement were the same). In these cases, the one-way ANOVA became a two-way ANOVA (plant community × precipitation), and the two-way ANOVA became a

three-way ANOVA (plant community × warming × precipitation). For decomposition, we conducted the previous analyses for *S. alterniflora* litter, since it was located in both plant communities, as well as litter type × treatment ANOVAs for *S. patens–Distichlis* plots since they contained two litter types. Pore water chemistry results, which were obtained over three time points with no a priori reason to suspect that these time points would differ, were analyzed with repeated measures ANOVA (RM-ANOVA). Note that in the discussion of response variables, precipitation data are taken from the one-way ANOVAs that exclude the warming treatment, unless there are interactive effects of precipitation and warming, or if precipitation and plant community or litter type are being considered together in the analysis. Homogeneity of variance was tested with Levene's test and examination of box plots; sphericity was tested with Mauchly's test, and if violated, the Greenhouse–Geisser correction was reported. Percentages were arcsine square-root transformed for analyses; all other data are untransformed. Post-hoc multiple comparisons between group means were conducted with the Tukey's hsd test. Finally, control plots were compared with open plots using a standard t test, to assess whether the basic infrastructure affected measurements.

RESULTS

Temperature, precipitation, salinity, and light

Chambers increased air temperatures relative to control frames or rainout shelters, but this increase was temporally variable (Fig. 2). Temperature differences were assessed by comparing daily means of temperatures from 07:00 to 19:00 and from 19:00 to 07:00 hours for each infrastructure type, using dataloggers in the same infrastructure type as replicates. During daytime hours, chambers warmed air relative to control frames and rainout shelters, which did not differ from one another (Fig. 2a; Tukey's hsd between control and chamber, $P = 0.028$; between rainout and chamber, $P = 0.015$; between control and rainout, $P = 0.492$). At night, rainout shelters warmed air slightly relative to control frames and chambers, which did not differ from one another (Fig. 2b; Tukey's hsd between control and rainout, $P = 0.004$; between chamber and rainout, $P = 0.010$; between control and chamber, $P = 0.155$). Temperature differences were averaged for each month for all logged time points, for time points between 07:00 and 19:00 hours (within six hours of solar noon, approximately), and for time points between 10:00 and 16:00 hours (within three hours of solar noon, approximately). Overall warming in experimental warming chambers averaged 0.47–1.17°C. Since the amount of warming depends on solar input, warming from 07:00 to 19:00 hours averaged 0.89–2.27°C, and warming from 10:00 to 16:00 hours averaged 1.23–2.77°C. In June, chambers did not warm air until the end of the month, when partially open tops were added to the structures.

PLATE 1.   Experimental plots and infrastructure in the *Spartina patens–Distichlis spicata* salt marsh plant community. Photo credit: J. S. Dukes.

For this reason, the earlier time points were not included above. Air temperatures in framed controls did not differ from those in open controls (day, RM-ANOVA, $F_{1,2} = 0.365$, $P = 0.607$; night, RM-ANOVA, $F_{1,2} = 1.056$, $P = 0.412$). See Appendix A for further details on temperature differences.

Chemical properties of the well water used to supplement rainfall were compared with properties of rain sampled weekly (approximately) at the weather station from June 2000 to June 2001 (data *available online*).[3] Well water had a higher average pH than natural rainfall (6.86 vs. 4.55), higher ammonium concentration (94 μmol/L vs. 13.61 μmol/L, though rainfall ranged from 0.64 μmol/L to 86.33 μmol/L), and higher phosphate concentrations (15 μmol/L vs. 0.05 μmol/L, though rainfall ranged from 0 μmol/L to 0.83 μmol/L). The well water did not contain sulfides and had a very low salinity (1.6 ppt or 0.886 g Cl/kg). We expect these variables to be very low or negligible in rainwater, though they were not directly measured. Prior to watering, salinities of surface water ranged from 19–25 ppt (10.52–13.84 g Cl/kg) in all plots, as measured by refractometer. Immediately after watering, salinity dropped to 0–2.5 ppt (0–1.38 g Cl/kg), and returned slowly to previous salinities, showing a mean of 5 ppt (2.77 g Cl/kg) one to two hours after watering, and 10

ppt (5.54 g Cl/kg) four to five hours after watering (also see pore water salinity results).

A comparison of the two greenhouse plastics (coated to retain infrared and not coated) revealed that under ideal conditions (sunny day, light directly overhead, plastic wrinkle free and clean, ceptometer close to plastic during measurements), both let through 91–92% of PAR, per their specifications. Light levels were also tested in the field and the three designs (Fig. 1a, b, c) were compared. In October, when plastic had been exposed to the elements for several months, the designs did not differ in PAR transmission (one-way ANOVA, $F_{2,27} = 2.151$, $P = 0.136$; means, open-topped chamber 82%, control frame 78%, rainout shelter 83%).

Plant production

Precipitation suppressed shoot growth in both plant communities, though effects were greater in the *S. alterniflora* community (Fig. 4), and warming enhanced shoot growth in the *S. alterniflora* community (Fig. 5). Across both plant communities, precipitation decreased total aboveground biomass (including live and dead biomass of all species present) in the October harvest (Fig. 4; two-way ANOVA, $F_{2,24} = 5.312$, $P = 0.012$). There was no interaction between plant community and precipitation treatment. However, there was a marginally significant interaction between plant community and warming treatment in September (three-way AN-OVA, $F_{1,32} = 4.067$, $P = 0.052$) as well as a significant interaction in October ($F_{1,32} = 8.092$, $P = 0.008$). In both cases, analyses suggest that warming increased above-

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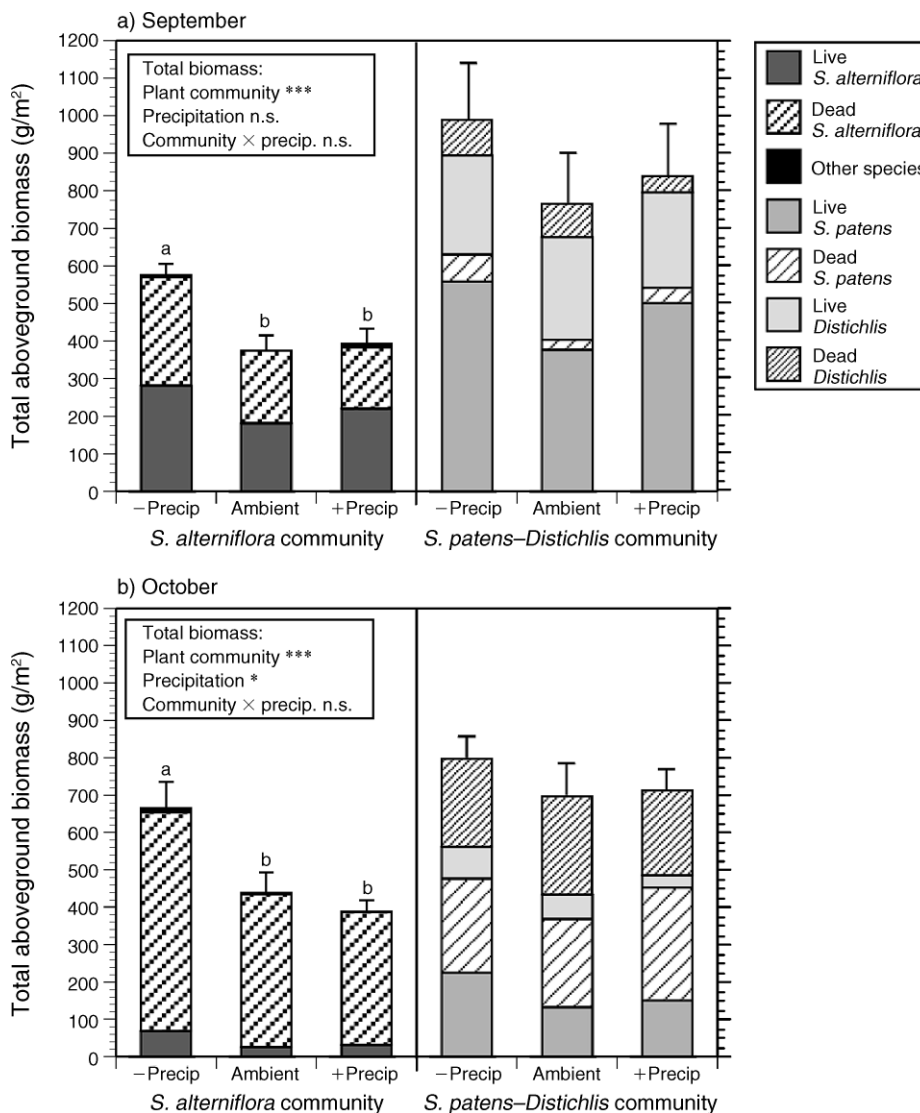[3] ⟨ecosystems.mbl.edu/pie/data/wat/WAT-VA-rainfall.htm⟩

FIG. 4.   Aboveground biomass for ambient and altered precipitation treatments in the *S. alterniflora* and *S. patens–Distichlis* communities harvested in (a) September and (b) October. Other species in the *S. alterniflora* community include *S. patens*, *Salicornia*, and *Atriplex*. Different letters above columns represent statistically significant ($P < 0.05$) differences between total biomass for different treatments. See *Results: Plant production* for additional information on live and standing dead results. Error bars represent standard error for total biomass (live + dead). Results are shown from two-way ANOVA of total biomass considering both plant communities together for the three precipitation treatments.
  * $P < 0.05$; *** $P < 0.001$; n.s. = not significant.

ground biomass production in the *S. alterniflora* community, and either did not change or decreased it in the *S. patens–Distichlis* community. Differences between treatments also tended to be enhanced over time in both communities, with more highly significant results in October.

Drought dramatically increased biomass of the *S. alterniflora* community in September and October (Fig. 4), with significant effects on live and standing dead *S. alterniflora*, and on total biomass (September *S. alterniflora* live, one-way ANOVA, $F_{2,12} = 4.766$, $P = 0.030$; *S. alterniflora* dead, $F_{2,12} = 16.737$, $P < 0.0001$; total

biomass, $F_{2,12} = 9.311$, $P = 0.004$; October *S. alterniflora* live, $F_{2,12} = 5.572$, $P = 0.019$; *S. alterniflora* dead, $F_{2,12} = 6.684$, $P = 0.011$; total biomass, $F_{2,12} = 7.397$, $P = 0.008$). In September, drought plots had 54% more biomass than ambient plots (Tukey's hsd, $P = 0.005$) and 46% more biomass than increased precipitation plots (Tukey's hsd, $P = 0.011$). In October, drought plots had 52% more biomass than ambient plots (Tukey's hsd, $P = 0.030$) and 71% more biomass than increased precipitation plots (Tukey's hsd, $P = 0.009$).

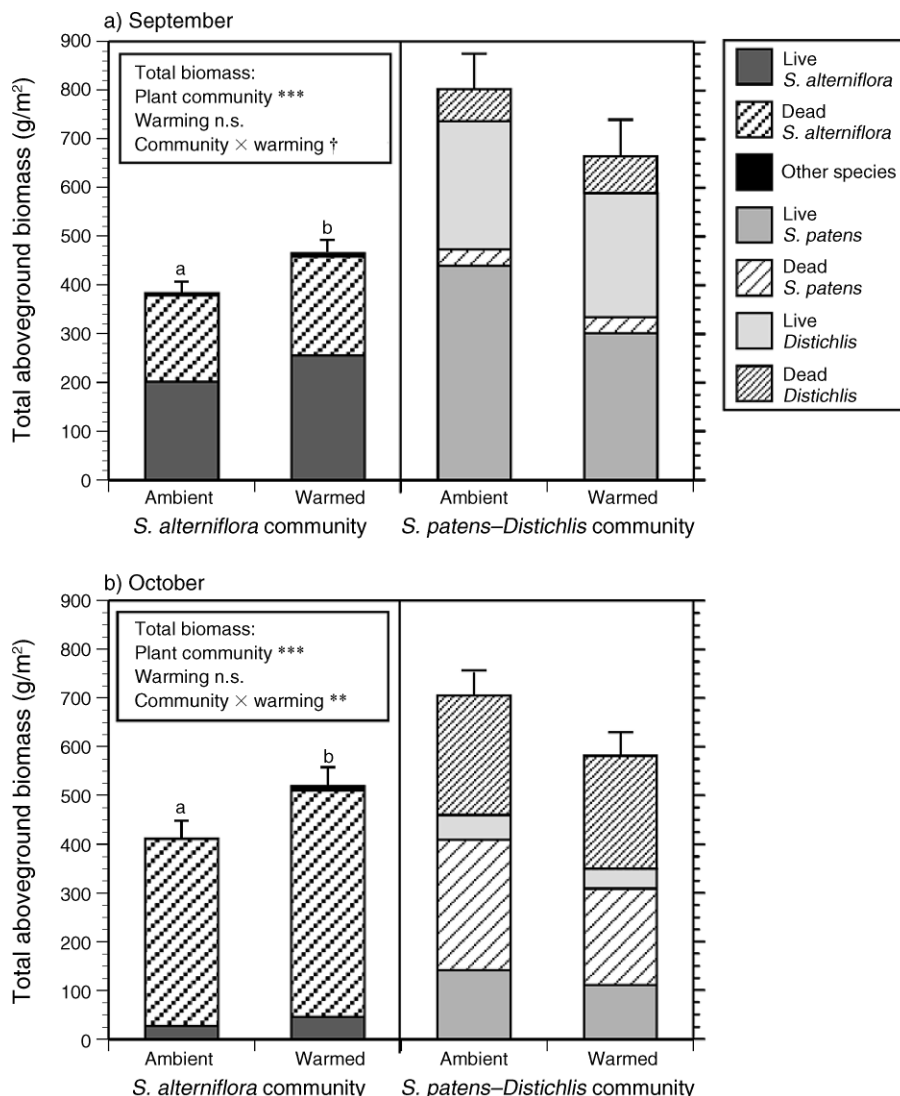Precipitation did not affect total biomass of the *S. patens–Distichlis* community in either month (Fig. 4),

FIG. 5. Aboveground biomass for ambient and warmed treatments in the *S. alterniflora* and *S. patens–Distichlis* communities harvested in (a) September and (b) October. Other species in the *S. alterniflora* community include *S. patens*, *Salicornia*, and *Atriplex*. Different letters above columns represent statistically significant ($P < 0.05$) differences between total biomass. See *Results: Plant production* for additional information on live and standing dead results. Error bars represent standard error for total biomass (live + dead). Results are shown from two-way ANOVA of total biomass considering both plant communities together for the ambient and warmed treatments.

† $P < 0.10$; ** $P < 0.01$; *** $P < 0.001$; n.s. = not significant.

although in October drought increased live *S. patens* biomass and total live biomass (by 69% for live *S. patens* compared to ambient plots; live *S. patens*, $F_{2,12} = 5.614$, $P = 0.019$; total live, $F_{2,12} = 3.977$, $P = 0.047$).

Warming increased total biomass of the *S. alterniflora* community by 21% in September (two-way ANOVA, $F_{1,16} = 6.275$, $P = 0.023$), and by 26% in October ($F_{1,16} = 4.867$, $P = 0.042$; Fig. 5). Interestingly, total biomass showed the opposite trend in the *S. patens–Distichlis* community, although these results were only marginally significant (Fig. 5; September, $F_{1,16} = 1.769$, $P = 0.202$; October, $F_{1,16} = 3.641$, $P = 0.074$). Warming increased live *S. alterniflora* biomass in both months (September,

$F_{1,16} = 6.626$, $P = 0.02$; October, $F_{1,16} = 8.269$, $P = 0.011$), as did increased precipitation (September, $F_{1,16} = 3.543$, $P = 0.078$; October, $F_{1,16} = 11.787$, $P = 0.003$).

Total aboveground biomass did not vary between the open treatment (with no infrastructure) and the framed control treatment, regardless of community or harvest date (*S. alterniflora* community *t* test, $P = 0.195$ and $P = 0.471$ for September and October, respectively; *S. patens–Distichlis* community *t* test, $P = 0.316$ and $P = 0.892$ for September and October, respectively). Stem densities of the dominant species increased during the growing season, but stem counts did not vary with precipitation or warming treatments in any month.

Stem heights

Warming increased stem heights for all three of the main species in the plots, and at most of the measurement time points (Fig. 6). *Spartina alterniflora* stem height increased by 8% in July (two-way ANOVA, $F_{1,16} = 5.122$, $P = 0.038$), by 7% in August (though this was only marginally significant; $F_{1,16} = 3.625$, $P = 0.075$), and by 10% in September ($F_{1,16} = 6.982$, $P = 0.018$). Warming increased *S. patens* stem heights in August (11% increase, $F_{1,16} = 5.706$, $P = 0.030$); similar trends were not significant in July and September (July, 5% increase, $F_{1,16} = 2.372$, $P = 0.143$; September, 9% increase, $F_{1,16} = 1.376$, $P = 0.258$). Warming consistently increased *Distichlis* stem heights, by 16% in July ($F_{1,16} = 13.313$, $P = 0.002$), by 16% in August ($F_{1,16} = 13.927$, $P = 0.002$), and by 14% in September ($F_{1,16} = 4.800$, $P = 0.044$). Precipitation did not affect stem heights, though there was a trend towards increased stem heights with drought in most months (Appendix B). There were no interactions between warming and precipitation.

Stem height was one of the few variables where the chamber walls may have affected the measurements, though we would expect any effect to be the same across treatments due to the similarity of the infrastructure. Stem heights in open plots (no infrastructure) were compared to those in control plots to check for effects. The infrastructure did not affect *Spartina alterniflora* stem heights, but *S. patens* stems were taller in control plots in July (15%, *t* test, $P = 0.046$) and August (18%, *t* test, $P = 0.034$), as were *Distichlis* stems in August (17%, *t* test, $P = 0.034$). While these two species grew slightly taller in response to some feature of the infrastructure (perhaps diffusion of incident light), the observed responses to warming remain robust.

Flowering phenology

The proportion of flowering *S. alterniflora* stems was not affected by either precipitation (August, one-way ANOVA, $F_{2,12} = 0.182$, $P = 0.836$; September, $F_{2,12} = 0.090$, $P = 0.914$) or warming (August, two-way ANOVA, $F_{1,16} = 0.135$, $P = 0.718$; September, $F_{1,16} = 0.062$, $P = 0.807$). There were no *S. alterniflora* flowers at the first measurement time point in July. *Spartina patens* and *Distichlis* flowers were present at all of the time points, but there was no effect of precipitation on the proportion of flowering stems of either species (one-way ANOVA, all *P* values >0.07).

There were also no warming or interactive effects on *S. patens* in any month (two-way ANOVA, all *P* values >0.08); however in September there was an interaction between warming and precipitation that affected the proportion of *Distichlis* stems flowering (two-way ANOVA, $F_{1,16} = 5.034$, $P = 0.039$). Warming increased the percentage of flowering *Distichlis* stems if precipitation was increased (from 2% ± 1% to 5% ± 1% [mean ± SE]), but decreased the percentage of flowering stems in ambient precipitation. Earlier measurements show a similar trend, but these results were only marginally
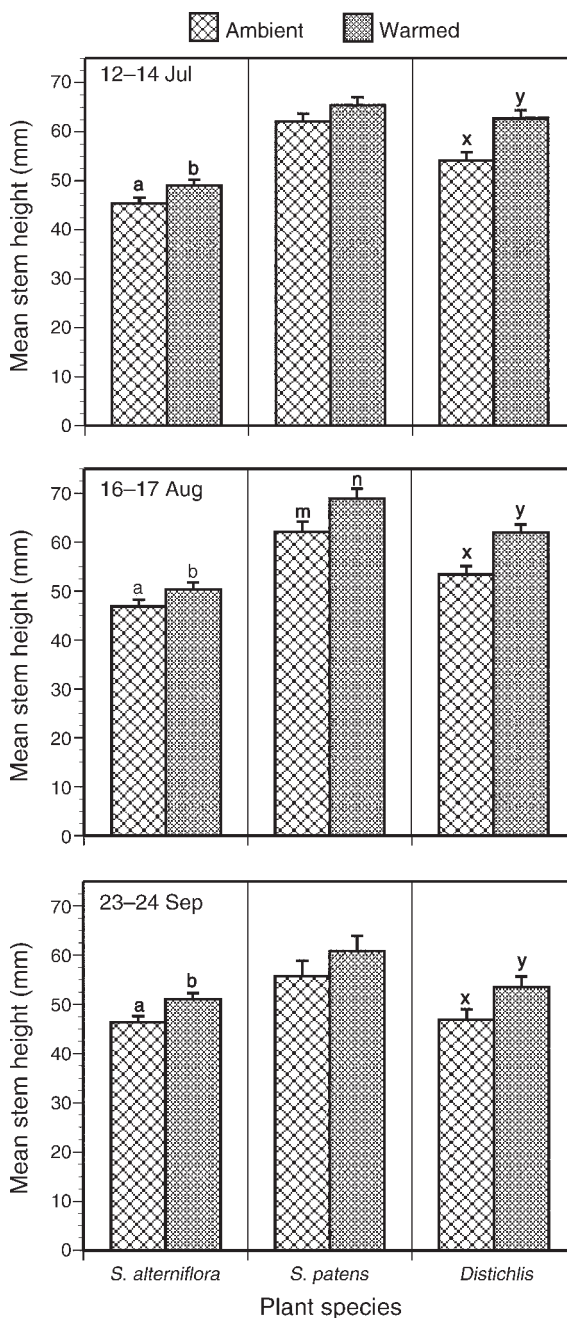

FIG. 6. Mean stem height per plot for *S. alterniflora*, *S. patens*, and *Distichlis* under ambient and warmed treatments for three time periods: 12–14 July, 16–17 August, and 23–24 September. Different letters above columns represent statistically significant (or marginally significant) differences. Bold letters signify $P < 0.05$; standard letters, $P = 0.075$. Error bars represent standard error.

significant (two-way ANOVAS, $P \leq 0.068$–0.081 for all analyses).

Decomposition and litter nitrogen dynamics

Overall, *S. alterniflora* litter decomposed slightly faster in the *S. patens*–*Distichlis* community than in

Table 1. Decomposition rates and decay values (mean $\pm$ SE) for litter in different plant communities and with different precipitation treatments.

Plant community and precipitation treatment	Litter remaining at 3 months (%)	Decay constant (k) at 0–3 months	Litter remaining at 5 months (%)	Decay constant (k) at 3–5 months
S. alterniflora plots–*S. alterniflora* litter				
Decreased precipitation	59.2 $\pm$ 1.4	2.100 $\pm$ 0.094	51.8 $\pm$ 2.2	0.817 $\pm$ 0.244
Ambient precipitation	57.6 $\pm$ 2.1	2.216 $\pm$ 0.148	51.6 $\pm$ 1.5	0.657 $\pm$ 0.270
Increased precipitation	58.1 $\pm$ 1.4	2.176 $\pm$ 0.094	45.0 $\pm$ 3.1	1.590 $\pm$ 0.497
S. patens–*Distichlis* plots–*S. alterniflora* litter				
Decreased precipitation	58.6[a] $\pm$ 2.2	2.150[a] $\pm$ 0.154	49.2[a] $\pm$ 1.3	1.040 $\pm$ 0.320
Ambient precipitation	53.7[a,b] $\pm$ 2.2	2.503[a,b] $\pm$ 0.163	46.4[a,b] $\pm$ 2.3	0.884 $\pm$ 0.091
Increased precipitation	49.3[b] $\pm$ 2.9	2.854[b] $\pm$ 0.241	40.9[b] $\pm$ 2.9	1.170 $\pm$ 0.572
S. patens–*Distichlis* plots–*S. patens* litter				
Decreased precipitation	64.3 $\pm$ 1.9	1.775 $\pm$ 0.116	55.9 $\pm$ 1.9	0.839 $\pm$ 0.152
Ambient precipitation	59.7 $\pm$ 3.1	2.089 $\pm$ 0.215	50.2 $\pm$ 2.6	1.031 $\pm$ 0.431
Increased precipitation	56.0 $\pm$ 3.1	2.346 $\pm$ 0.218	48.3 $\pm$ 5.0	1.113 $\pm$ 0.317

Notes: Different lowercase letters represent marginally significant ($0.059 < P < 0.064$) differences. Warmed plots were not included since they were not significantly different. See *Results: Decomposition and litter nitrogen dynamics* for further information.

the *S. alterniflora* community, after both three months (two-way ANOVA, $F_{1,23} = 5.951$, $P = 0.023$) and five months ($F_{1,23} = 4.526$, $P = 0.044$). Analyses from the *S. patens–Distichlis* community showed that *S. alterniflora* litter decomposes faster than *S. patens* litter in general (percentage mass remaining at three months, $F_{1,22} = 8.576$, $P = 0.008$; percentage mass remaining at five months, $F_{1,22} = 7.281$, $P = 0.013$).

The rate of shoot litter decomposition was slightly accelerated by increased precipitation and slowed by the drought treatment, but the significance of this pattern depended on the plant community and litter type (Table 1). When considering data from both plant communities together, litter of *S. alterniflora* decomposed slightly faster under increased precipitation and slightly slower with decreased precipitation (marginally significant at three months: two-way ANOVA, $F_{2,23} = 2.730$, $P = 0.086$; highly significant at five months: $F_{2,23} = 5.974$, $P = 0.008$). The *S. patens–Distichlis* community had both *S. alterniflora* and *S. patens* litter bags. Combining data for both of these litter types showed a significant acceleration of decomposition with increasing precipitation in the *S. patens–Distichlis* community after both three months and five months (two-way ANOVA, $F_{2,28} = 4.122$, $P = 0.030$; $F_{2,28} = 4.200$, $P = 0.029$, respectively).

The effect of precipitation on decomposition was only marginally significant, but strongest for *S. alterniflora* litter in the *S. patens–Distichlis* community vs. other litter–plant community combinations (Table 1). Precipitation affected decomposition of *S. alterniflora* litter in the *S. patens–Distichlis* community after both three months (one-way ANOVA, $F_{2,12} = 3.604$, $P = 0.059$; Tukey's hsd between decreased and increased precipitation, $P = 0.049$) and five months ($F_{2,12} = 3.575$, $P = 0.064$; Tukey's hsd, $P = 0.055$).

Warming marginally accelerated decomposition of *S. alterniflora* litter in the *S. alterniflora* community during the first three months (53.6% vs. 57.9% mass remaining,

two-way ANOVA, $F_{1,16} = 4.295$, $P = 0.055$). Afterwards, this trend disappeared, perhaps due to the overall slowing of decomposition, or due to a significant interaction between warming and precipitation at this point (percentage mass remaining, two-way ANOVA, $F_{1,16} = 8.406$, $P = 0.010$). Warming did not affect the rate of decomposition of either *S. alterniflora* or *S. patens–Distichlis* litter in the *S. patens–Distichlis* community.

Precipitation also affected the nitrogen concentration of *S. alterniflora* litter in the *S. alterniflora* community after three months (one-way ANOVA, $F_{2,12} = 6.791$, $P = 0.011$). From an initial concentration of 0.52%, nitrogen concentrations increased to 0.69% in decreased precipitation plots, 0.83% in control plots, and 0.92% in increased precipitation plots (Tukey's hsd between decreased and increased precipitation, $P = 0.009$; Tukey's hsd between control and decreased precipitation, $P = 0.081$). At five months, the trend was similar, but no longer significant ($F_{2,12} = 2.210$, $P = 0.152$). Likewise, the total amount of nitrogen in the litter was significantly affected after three months ($F_{2,12} = 11.082$, $P = 0.002$). Nitrogen mineralization was greatest under drought conditions, whereas nitrogen content stayed roughly the same with doubled rainfall. Initial nitrogen content of *S. alterniflora* litter was 5.19 mg per gram of litter. After decomposition, the total nitrogen content per gram of initial litter ranged from 4.07 $\pm$ 0.20 mg (mean $\pm$ SE) for drought plots, to 4.78 $\pm$ 0.21 mg for control plots, to 5.30 $\pm$ 0.15 mg for increased precipitation plots (Tukey's hsd between decreased and increased precipitation, $P = 0.001$; Tukey's hsd between control and decreased precipitation, $P = 0.045$). The *S. patens–Distichlis* community showed similar trends for nitrogen content of both litter types, but the differences were not significant ($P > 0.2$ for all analyses). Warming did not significantly alter nitrogen dynamics in either plant community or litter type.

Pore water chemistry

Pore water salinity and ammonium and phosphate concentrations were analyzed for both plant communities; sulfide concentrations were analyzed for the *S. alterniflora* community, but not for the *S. patens–Distichlis* community as measurements were below the detection limit of 0.134 μmol/L (Appendix C). Precipitation did not affect any of the pore water variables considered in either the *S. alterniflora* community (RM-ANOVA, $F_{8,20} = 0.484$, $P = 0.853$) or the *S. patens–Distichlis* community (RM-ANOVA, $F_{6,22} = 0.790$, $P = 0.587$). Likewise, warming did not significantly affect pore water chemistry in either community (*S. alterniflora* community, RM-ANOVA, $F_{4,13} = 0.861$, $P = 0.512$; *S. patens–Distichlis* community, RM-ANOVA, $F_{3,14} = 0.708$, $P = 0.563$). The clearest pore water result was an effect of the month of sampling in all analyses (Appendix C; RM-ANOVA, all P values <0.01). These results suggest that nutrient concentrations, salinity, and sulfide all varied temporally in the marsh, mostly independently of any experimental treatments. In addition, and as expected, pore water chemistry varied substantially between plant communities in the marsh.

DISCUSSION

Climate change clearly poses a major risk to salt marsh habitats through its effects on sea level. The ability of marshes to keep pace with sea-level rise and to provide shoreline protection will depend on their ability to accrete both vertically and horizontally. Although inorganic sedimentation is more important in some marshes, organic inputs from the marshes themselves also contribute to accretion (Chmura and Hung 2004, Nyman et al. 2006), particularly in marshes where sediment inputs tend to be less important (e.g., marshes along the northern Atlantic coast of the United States vs. the southern Atlantic coast; Bertness 1999). A more productive marsh, as we observed with drought and warming, could trap more inorganic sediments during tidal flushing (Leonard and Croft 2006) and directly contribute more organic inputs to the sediment. Although we did not observe differences in stem density among our treatments, such differences have been shown to reduce wave energy and contribute to sedimentation (Lightbody and Nepf 2006). We speculate that increased allocation to leaves or increased stem widths may have occurred, both of which could also contribute to sedimentation to a lesser degree. In the case of *Spartina patens* and *Distichlis spicata*, biomass did not increase, but stems were longer. Long, thin stems such as these often bend and lay flat or at an angle on the marsh surface, which could also enhance sedimentation. Aboveground biomass is also complemented by the larger pool of belowground biomass, which is considered by Turner et al. (2004) to be even more important in determining marsh elevation. This would be a useful variable to assess in future experiments.

We expected to see increases in shoot biomass and decomposition rates with warming, but only observed these responses in the *Spartina alterniflora* community. While our measurements were unable to identify a conclusive mechanism for the responses, increased allocation to leaves, which are more prominent in *S. alterniflora* than in the other perennials, could have increased photosynthesis at the whole-plant level, leading to higher aboveground biomass. We expected that warming would increase leaf-level photosynthetic rates and soil microbial activity (with associated increases in nutrient availability), stimulating biomass production. Unfortunately, our measurements of these factors were inconclusive. In the case of photosynthesis, data from a single measurement date suggested the opposite pattern (Charles 2007), but we did not have a rich enough data set to draw robust conclusions. In the case of soil microbial activity, our pore water samplers did not detect increases in nutrient availability. This could have been an artifact of sampler placement; because our pore water samplers were located in the middle of the rooting zone, they may have missed changes in chemical composition and nutrient concentrations occurring at shallower depths. The chambers may have only warmed the top few centimeters of sediment. We also speculate that differences in the phenotypic plasticity of species contributed to the difference in warming response among communities. *Spartina alterniflora* has been shown to be very plastic in terms of height, as demonstrated by its high tolerance of, and strong response to, salinity (Nestler 1977).

We anticipated that additional precipitation would decrease soil salinity and alleviate salt stress, leading to increased plant growth. Although surface water showed decreased salinity for several hours or longer after watering, watered plots did not have significantly different pore water salinities, which may explain the lack of a biomass response to increased precipitation. Freshwater may have decreased salinity in the rooting zone, but with only brief effects, as has been seen with natural heavy rainfall events (Alexander and Dunton 2002), or increased waterlogging may have offset any positive effects of transient decreases in salinity (Morris and Haskin 1990). Likewise, the drought treatment could have slightly alleviated waterlogging, particularly during an unusually wet late spring and early summer. However, we have no data with which to assess the importance of this mechanism. Increased aeration and oxidation of the rhizosphere in the drought treatment may have enhanced production by leading to higher nutrient and lower sulfide concentrations (Portnoy and Giblin 1997). Pore water chemical analyses also showed no difference with the drought treatment, but short-term effects may have been missed by our monthly sampling schedule, since Noe and Zedler (2001) have observed strikingly different salinity and soil moisture patterns when measuring pore water daily after rainfall vs. weekly or monthly. In addition, our pore water samplers

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may have been buried too deeply to detect important salinity differences at shallow depths. Finally, side effects of the infrastructure could partially explain the observed biomass differences. In particular, the chambers could have altered nighttime air temperatures (Fig. 2b), relative or absolute humidity (a common side effect of open-topped chambers and partial enclosures [Marion et al. 1997], though this may be partially ameliorated by the wet marsh environment), or had undetected effects on light reaching the plants. Although infrastructure shading could in theory increase stem heights, the lack of a difference in biomass between open and control plots suggests this mechanism is unlikely. Regardless of the mechanisms underlying the precipitation-induced shifts in production, our results suggest that marsh communities that are flooded infrequently (e.g., by spring tides only) are sensitive to altered precipitation.

It is critical to consider our plot-scale results in the context of larger, regional-scale effects of precipitation change. Regional projections for precipitation are less certain than those for warming (Hayhoe et al. 2007). Nevertheless, many model projections for the northeastern United States include increased runoff, an advancement in the timing of spring peak stream flows, and a shift in the timing of precipitation to include more periods of both heavy rainfall and drought (Hayhoe et al. 2007). Such changes would likely affect estuarine salinities, as has been shown for Chesapeake Bay (Saenger 2006). Decreased estuarine salinities would decrease plant stress, and could lead to increased productivity and shifts in species composition toward more freshwater-tolerant species. Increased estuarine salinities would have the opposite effect, but our plot-scale results suggest that plant stress could be partly offset by decreased waterlogging or some other aspect of drought conditions.

Likewise, regional and global predictions for sea-level rise are highly variable (IPCC 2007). However, even a relatively small rise would have a variety of dramatic impacts on marshes, beyond the major threats from inundation discussed earlier. Sea level itself (specifically duration and frequency of tidal flooding) is a major determinant of marsh productivity, particularly during the summer months when growth rate is maximal. The impact of sea level may depend on the amount of rainfall in a given year, becoming more important in a year with low rainfall for example (Morris and Haskin 1990). The increased productivity that we witnessed under drought conditions may slightly decrease the significance of shifting tidal regimes to these plants. As marshes become inundated, peat saturation, salinity, and sulfide concentrations increase, and redox potential decreases, leading to a predictable shift in plant community composition. For example, in New England marshes, salt tolerant *S. alterniflora* and annual forbs often replace *S. patens*, *Distichlis*, and *Juncus gerardi* in areas of increased inundation (Warren and Niering 1993, Donnelly and Bertness 2001). In marshes where landward migration is

impeded by human development, marshes may not only become smaller, but large areas may shift to these early successional species, and in the case of *S. alterniflora* in our study, may be more susceptible to the effects of warming and precipitation. Other studies indicate that recruitment of seed bank species, such as *Salicornia* and *Atriplex* in this marsh, may decrease with increasing tidal inundation (Baldwin 1996), and losing these pioneer species could lead to less plant growth in salt pannes on the marsh platform.

We did not focus on recruitment effects within the plant communities. In the fall, as well as the following early spring, when most recruitment occurs, an increase in the number of heavy rainfall events is likely to accelerate germination, with consequences for species composition and productivity of the marsh (Noe and Zedler 2001, Alexander and Dunton 2002). Our different results from the two plant communities suggest that shifts in species composition could modify some of the biomass responses we observed. Similarly, responses could be modified by changes in community structure due to sea-level rise or warmer temperatures, as described in the previous paragraph. Marshes at lower latitudes tend to have relatively more stressful environments due to warmer temperatures for a longer portion of the year, leading to increased evaporation and salt accumulation. Under these conditions, facilitative plant interactions (e.g., shading by neighboring plants leading to decreased salt stress) are more common and become very important (Bertness and Ewanchuk 2002). In the relatively less stressful northern marshes, including our study site, warmer conditions could cause plant interactions to become more facilitative, reducing the strength of interspecific competition.

Decomposition, like production, has implications for accretion and marsh elevation, in addition to nutrient cycling, soil formation, carbon sequestration, and waste treatment. Decomposition is particularly important for accretion in the high marsh where plants tend to decay more slowly due to less frequent tidal flushing, lower sediment input, and lower litter quality, in the case of *S. patens* and *Distichlis* (Valiela et al. 1985). If, as we observed, marsh productivity remains steady or increases, then reductions in decomposition would accelerate accretion (Foote and Reynolds 1997). However, our results also suggest that wetter conditions could speed decomposition and offset changes in productivity, primarily because microbes decompose wet substrates faster (Foote and Reynolds 1997). Similarly, microbial activity increases in response to warming, likely leading to the increased rate of decay observed in the *S. alterniflora* community. This result supports the observations of Montagna and Ruber (1980) that decomposition of *S. alterniflora* litter responds to seasonal temperature differences. Decomposition in the *S. patens–Distichlis* community may have been less responsive to warming due to differences in litter quality or microclimate. At a regional scale, warmer water can also

increase decomposition, either via warming of oceans, rivers, and estuaries, or of standing water on the marsh surface (Valiela et al. 1985). Taken together, these results suggest that decomposition rates are likely to increase in the future, although periodic decreases during periods of drought may offset increases to some extent.

The litter nitrogen retention associated with increasing precipitation in the *S. alterniflora* community suggests that any additional nitrogen lost through leaching or other processes was compensated for by accumulation of microbial biomass or exudates, or by greater incorporation of nitrogen via nitrogen fixation or uptake of dissolved nitrogen (White 1994). White (1994) found that external nitrogen incorporation was associated with warmer temperatures and higher moisture content, and may be beneficial to the marsh as a mechanism of nitrogen gain and retention, even leading to increased availability the following year. Interestingly, Parton et al. (2007) have shown that nitrogen immobilization and release from litter are predictably dependent on initial tissue nitrogen, regardless of climate, across a broad range of ecosystems. The precipitation-induced changes we observed in litter nitrogen dynamics did not translate into changes in pore water nutrient concentrations. However, it is possible that any increase in remineralization of nutrients was offset by increased plant growth and uptake, leading to no net change in pore water.

Salt marshes sequester carbon due to their high productivity and slow decomposition under anaerobic conditions. Hussein et al. (2004) calculated that a Maryland marsh had stored 83.5 ± 23 g $C \cdot m^{-2} \cdot yr^{-1}$ over the most recent 150-yr period. Their model of the marsh predicted higher future carbon sequestration, which could be a negative feedback to global warming if marsh elevation keeps pace with sea-level rise. Redfield (1972), studying the development of a New England marsh, discovered layers of high marsh peat more than 20 feet thick, and estimated them to be 3600 years old. Whether salt marshes continue to sequester carbon at current rates or begin to lose carbon depends in part on the balance between production and decomposition described previously. Sea-level rise may also lead to carbon loss from marshes by altering the balance between production and respiration (Miller et al. 2001).

Salt marshes export biomass and nutrients, to the direct benefit of marine food webs, and the indirect benefit of humans. Teal (1962) estimated outwelling of organic particulate matter and detritus to an estuary as being equivalent to 40% of marsh productivity. More recently, Duarte and Cebrián (1996) reported a mean export of 18.6% for marsh plants, after evaluating all the available studies that reported the fate of net primary productivity in marine ecosystems, and dividing the pathways of organic carbon transfer into decomposition, herbivory, exportation, and storage. Export percentages vary widely across marshes, but even

marshes with low export may make a significant contribution to local marsh creeks and estuaries, if not to the regional coastal waters. We did not directly examine export in our study. However, since marshes concurrently store and export biomass, and we have shown stable or increasing productivity, our results suggest that export is likely to continue. This conclusion could be strengthened by modeling efforts that include a more comprehensive assessment of inputs to the marsh (from sedimentation, aboveground and belowground biomass). Such efforts could produce an organic matter budget that would give further insight into the ability of New England marshes to accrete in the face of sea-level rise. Such efforts could also include countervailing effects of climate change, such as the possibility that increased rainfall would erode the marsh surface and enhance the movement of particulate and dissolved organic carbon into tidal creeks (Chalmers et al. 1985).

Little is known about the controls on phenology of flowering in salt marsh plants. We expected that warming would advance the timing of flowering, but did not find clear evidence for this. Blits and Gallagher (1991) found that increasing salinity can both delay and decrease inflorescence production for the marsh ecotype of *Sporobolus virginicus*, leading to greater allocation of resources to belowground growth. Although such changes in phenology have important implications for future plant growth, organic matter accumulation, and carbon sequestration, little research has been conducted in this area.

Many questions regarding the effects of warming and altered precipitation on both salt marshes and other ecosystems remain unanswered, particularly whether there will be interactions between these variables and other components of climate change. In a long-term study (now >20 years), researchers have shown that sedge-dominated wetland communities respond to supplemental CO_2 by increasing plant growth, shoot density, and net ecosystem exchange (NEE), with drought-induced salinity stress reducing these responses (Rasse et al. 2005). Taken together, data from this and other studies suggest that there could be important interactive effects of different climate change drivers. The combined effects of climate change and other global changes such as eutrophication, increasing waterborne pollution, the spread of invasive species, and land use change may strongly affect marsh composition and function during this century. Our short-term study suggests that marshes may be fairly resilient to large changes in precipitation and modest levels of warming. Nonetheless, the changes we observed indicate that production and nutrient cycling in marshes will respond to both warming and precipitation, with implications for marsh ecosystem services. Further study, as well as incorporation of these types of data into modeling efforts, is warranted to assess whether these impacts will be amplified over a longer time period, whether the measured variables will respond in a linear fashion to

more extreme climate predictions, how regional-scale precipitation changes will work in conjunction with local impacts, and whether marshes in other regions will respond similarly.

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APPENDIX A

Additional temperature data for controls and open-topped chambers (*Ecological Archives* A019-071-A1).

APPENDIX B

Stem heights under different precipitation treatments (*Ecological Archives* A019-071-A2).

APPENDIX C

Pore water chemistry results (*Ecological Archives* A019-071-A3).