Tidal marsh plant responses to elevated CO_2, nitrogen fertilization, and sea level rise

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Abstract

Elevated CO_2 and nitrogen (N) addition directly affect plant productivity and the mechanisms that allow tidal marshes to maintain a constant elevation relative to sea level, but it remains unknown how these global change drivers modify marsh plant response to sea level rise. Here we manipulated factorial combinations of CO_2 concentration (two levels), N availability (two levels) and relative sea level (six levels) using *in situ* mesocosms containing a tidal marsh community composed of a sedge, *Schoenoplectus americanus*, and a grass, *Spartina patens*. Our objective is to determine, if elevated CO_2 and N alter the growth and persistence of these plants in coastal ecosystems facing rising sea levels. After two growing seasons, we found that N addition enhanced plant growth particularly at sea levels where plants were most stressed by flooding (114% stimulation in the + 10 cm treatment), and N effects were generally larger in combination with elevated CO_2 (288% stimulation). N fertilization shifted the optimal productivity of *S. patens* to a higher sea level, but did not confer *S. patens* an enhanced ability to tolerate sea level rise. *S. americanus* responded strongly to N only in the higher sea level treatments that excluded *S. patens*. Interestingly, addition of N, which has been suggested to accelerate marsh loss, may afford some marsh plants, such as the widespread sedge, *S. americanus*, the enhanced ability to tolerate inundation. However, if chronic N pollution reduces the availability of propagules of *S. americanus* or other flood-tolerant species on the landscape scale, this shift in species dominance could render tidal marshes more susceptible to marsh collapse.

Keywords: marsh organ, mesocosms, plant productivity, *Schoenoplectus americanus*, soil elevation, *Spartina patens*

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Introduction

Tidal wetlands build soil vertically by accumulating inorganic and organic material to maintain a constant elevation relative to rising seas (Redfield, 1965; Morris *et al.*, 2002). Both mechanisms of soil gain – inorganic and organic – are controlled largely by plant growth (Mudd *et al.*, 2009; Baustian *et al.*, 2012). The amount of mineral and allochthonous organic sediment deposited in a wetland depends strongly on the ability of aboveground plant biomass to trap sediment (Gleason *et al.*, 1979; Palmer *et al.*, 2004), while autochthonous organic matter that gives rise to soil organic carbon arises primarily from belowground productivity (Nyman *et al.*, 2006). Therefore, any perturbation that changes plant growth may alter the mechanisms of soil gain and maintenance, thereby altering the threshold rate of sea level rise that coastal wetlands can tolerate. Accurately forecasting tidal wetland responses to accelerated sea level rise requires understanding the mechanisms that contribute to soil elevation gain and how these mechanisms respond to plant resource perturbations.

A body of recent research has focused on determining how plant resource perturbations, such as elevated CO_2 and nutrient pollution, affect the soil-building mechanisms that sustain coastal wetlands. Elevated CO_2 increases the growth of C_3 wetland plants and promotes elevation gain (Cherry *et al.*, 2009; Langley *et al.*, 2009a). The effects of nitrogen (N) addition are less clear, with studies most commonly reporting decreases in marsh elevation or soil stability (Darby & Turner, 2008a; Langley *et al.*, 2009a; Wigand *et al.* 2009, Turner, 2011; Deegan *et al.*, 2012), but also finding increases in soil elevation gain (Morris *et al.*, 2002; Fox *et al.*, 2012), or no change (Anisfeld & Hill, 2012). Few studies have examined how such resource perturbations interact with perhaps the most critical perturbation of tidal wetland productivity, changes in inundation frequency and flooding stress associated with accelerated sea level rise. Although insights on how soil elevation dynamics will respond to accelerated sea level rise can be gleaned from observations of contemporary systems (Cahoon & Reed, 1995), experimental manipulations of inundation

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frequency are required to reveal what will happen under conditions of actual sea level rise.

In addition to influencing the long-term mechanisms by which marshes gain elevation, resource perturbation could alter the ability of plants to tolerate short-term flooding stress caused by anomalously high sea level. Rather than rising smoothly, sea level rises vary dramatically from year to year, such that a marsh experiences a sea level rise increment in any given year that is often much higher or lower than predicted by the longer term trends (Morris *et al.*, 2002). This pattern occurs on a global scale but is pronounced on the local scale relevant to individual marshes, and particularly those subject to variable estuarine forcings such as wind. For example, the linear sea level trend in Annapolis, Maryland, USA is 4.7 mm/yr, while the detrended annual standard deviation is 45.9 mm (NOAA 2012). Often these cycles reflect tidal forcings such as the lunar nodal cycle, or other climatic decadal-scale oscillations, such that an area will experience several years of rise followed by several years with no rise (Morris & Haskin, 1990). Therefore, multiyear events of anomalously high tides may compound plant stress imposed by long-term disparities between sea level rise and soil elevation gain. Altered resource availability could change the inundation tolerance of tidal marsh plants.

Here we manipulated atmospheric CO_2, soil N availability and relative sea level in field-based mesocosms over two growing seasons. Previous work has shown that despite hydrological artifacts that may affect some soil properties, these types of manipulations accurately represent plant response to sea level (Kirwan & Guntenspergen, 2012). Our multifactorial design allowed exploration of how resource manipulation may influence marsh plant survival in response to realistic annual and seasonal variations in sea level rise *in situ*. We hypothesized the resource amendment would support greater productivity, even at relatively high sea levels and associated inundation stress. Deploying experimental mesocosms for two consecutive growing seasons allowed us to estimate more effectively which treatments are likely to yield long-term marsh stability. Using mixed assemblages of native marsh plants, we were able to generate total ecosystem response curves for interacting species as a function of sea level and predicted global change factors.

Materials and methods

Study site

The field experiment was conducted at the Global Change Research Wetland of the Smithsonian Environmental Research Center in Edgewater, Maryland, USA (38°53′ N, 76°33′ W). It

was located in the primary tidal creek serving Kirkpatrick Marsh, on the Rhode River sub-estuary, where suspended sediment concentrations are 26 ± 13 mg L^{-1} (Jordan *et al.*, 1983). The plant community in the high marsh platform we were simulating is dominated by the C_3 sedge, *Schoenoplectus americanus* (75% of biomass) and the C_4 grasses, *Spartina patens* (18%) and *Distichlis spicata* (7%, Langley & Megonigal, 2010). The grasses are dominant at higher elevations within the marsh (Arp *et al.*, 1993). Soils at the site are peats composed of ~80% organic matter to a depth of 5 m (Langley *et al.*, 2009a). Mean tidal range is 44 cm, and the high marsh platform is 40–60 cm above daily mean low water level. Salinity ranges from 4 to 15 ppt, with an average near 10 ppt (Keller *et al.*, 2009).

Experimental design

Mesocosms were exposed to a combination of sea level and resource treatments (ambient CO_2 or elevated CO_2 crossed with ambient N levels or N fertilization). We manipulated sea level using marsh organs established within the main tidal creek of Kirkpatrick Marsh. Marsh organs, described by Morris (2007), allow for direct manipulation of sea level in the field. There were six marsh organs, each composed of 24 mesocosms arranged in six rows, where each row corresponds to a different sea level, ranging from a 35 cm drop to a 30 cm rise in sea level (Fig. 1). The target sea level treatments were 10, 20, and 30 cm lower in elevation, and 15 and 35 cm higher in elevation relative to the current marsh platform (nominally 0 cm). In the notation we adopted, negative values indicate that sea level relative to the marsh surface decreased (i.e., soils were less frequently inundated than normal) and *vice versa*. Because the mesocosms were placed in the field, the hydroperiod they actually experienced was subject to variable sea level. Mean sea level was anomalously high in both years, so that plants in the "0 cm" treatment actually experienced greater inundation both years than they would have in a normal year in the adjacent marsh platform (normal fractional inundation period for marsh platform = ~0.35, see Fig. 2).

The mesocosms were constructed from thin-walled PVC pipe 10 cm in diameter and 72 cm tall, capped at the bottom, and filled with reed-sedge peat (Baccto Peat, Houston, TX, USA). Each cap had five 1 cm holes to allow vertical water flow. The pots restricted lateral flow, mimicking the high marsh reference area where lateral flow of water is negligible (Jordan *et al.*, 1983). The six organs were surrounded by a screened perimeter in the tidal creek to reduce water velocity around the organs and to exclude large debris. Each mesocosm was initially planted with *Schoenoplectus americanus* on one half and *Spartina patens* on the other half, each at stem densities that simulated those in the high marsh. During spring 2010, *S. americanus* rhizomes were collected from several haphazardly chosen locations in Kirkpatrick Marsh and cultivated in a greenhouse at Villanova University. These sprouted rhizomes were planted two per pot. *Spartina patens* was obtained from a marsh located ~15 km from Kirkpatrick Marsh (propagated by Environmental Concern, St. Michaels, MD, USA), and planted in one $5 \times 5 \times 5$ cm plug averaging 10 viable stems. These initial plantings simulated natural stem densities for each

Fig. 1 Photograph of the marsh organs within open-top chambers (left) and overhead view of one marsh organ within an open-top chamber (right). Photographs by Thomas J. Mozdzer.
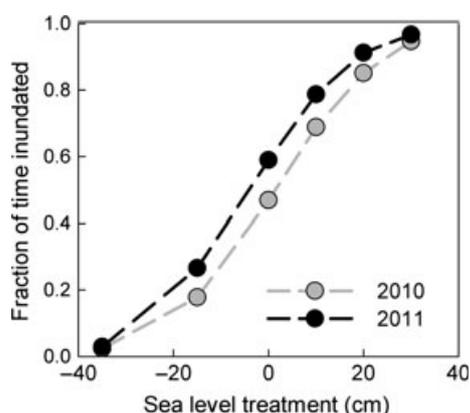

Fig. 2 The fraction of time flooded for each sea level treatment group over two growing seasons.

species (~500 stems m^{-2} for *S. americanus*, ~3000 stems m^{-2} for *S. patens*, White *et al.*, 2012; Shepard (2010)) based on half of the pot surface area (39.3 cm^{-2}). The mesocosms were maintained in a tank of mixed tap water and Rhode River water from May 15 to June 9, at which point they were flooded to the soil surface to allow the plants to acclimate to periodic flooding and salinity prior to transplantation. Salinity of the tank was slowly increased from 0 to 8 ppt by shifting from tap water to full strength Rhode River water during this interval.

Our design of the organ mesocosms differs from previous designs. Each mesocosm in this study had the same volume of soil confined within a PVC pipe, whereas in previous studies the length of the PVC pipes and confined soil volume varied with elevation. Moreover, in previous designs the variable confined volume sat atop unconfined tidal creek sediment, whereas the entire rooting volume was confined in our study. Thus, artifacts that may be caused by pot volume were held constant across elevations in the present design, but were confounded with elevation in previous studies. We used deep mesocosm pipes (~70 cm) to avoid the possibility that plant responses to elevated CO_2 would be limited by pot volume (Thomas & Strain, 1991).

Carbon dioxide

Each marsh organ was situated within an open-top chamber, inspired by that described by Drake *et al.* (1989), to control atmospheric CO_2 levels. The chambers were constructed from a PVC frame and clear, infrared-transmissive Aclar film walls (Honeywell, Morristown, NJ, USA), to allow natural light exposure (Langley *et al.*, 2009b). The tops and bottoms of the chambers were left open to allow air and water circulation. The chambers floated on the water surface, completely surrounding the marsh organ, rising and falling with the tide, and maintaining an air seal between the chamber bottom and the atmosphere. Three chambers received an elevated CO_2 treatment (Elev), while the other three received ambient air (Amb). In all the chambers, a remote blower delivered air at a rate that would exchange the chamber atmosphere twice per minute, but in the elevated CO_2 chambers, 100% CO_2 was injected into the air stream at the blower to increase chamber (CO_2) by ~300 ppm. Air from each chamber was sampled by an automated system and CO_2 concentration was measured using an infrared gas analyzer (Li-7000; Licor, Lincoln, NE, USA).

Nitrogen

Mesocosms were randomly assigned as N fertilized (+N) or N control, so that half of the mesocosms in each row received the equivalent of 25 g m^{-2} N through a biweekly injection of ammonium chloride solution in the center of the mesocosm at a depth of 10 cm throughout each growing season. That rate of N addition at an adjacent site increases the annual average background N concentration by about 40% (Langley & Megonigal, 2010). We used ammonium chloride because >99% of the inorganic N in the marsh pore-water occurs as ammonium.

Biomass assessment

On 28 September 2010, aboveground biomass was clipped at the soil surface and stored at 4°C until processing. This represented the point in time at which most productivity had ceased, but before a significant amount of dead plant matter

had been exported in tidal water. Two soil cores, 2 cm in diameter and 10 cm deep, were taken from each mesocosm for root biomass. Soil cores were stored at 4°C until sieved over a 2 mm screen to collect roots. To avoid the possibility that the mesocosm might freeze over winter, they were stored in a cold room at 4°C until redeployment the next spring on 15 May 2011. To avoid immediate flooding stress the following spring, the mesocosms were allowed to acclimate to conditions in the tidal creek at a single elevated height for 14 days before reapplying the original sea level treatments.

On 29 September 2011, aboveground biomass was again clipped at the soil surface and stored at 4°C until processing. Aboveground mass from 2010 to 2011 was processed in the same manner. Biomass was washed over a 2 mm sieve to remove sediment, separated by species, dried for 72 h at 60°C, and weighed. The belowground portion of the mesocosms was stored in a cold room at 4°C until processing for root biomass. Roots and rhizomes were washed over a screen to remove adhering peat and stored at 4°C until further processing. A second wash was necessary to carefully separate fine roots from peat. Root biomass from both years (from the core subsamples in 2010 and from the whole mesocosms in 2011) was sorted in the same manner. Belowground biomass was separated into the following categories: stem, rhizomes, or fine roots. Stems and coarse roots were separated by species based on visual physical characteristics (Saunders *et al.*, 2006). Fine roots could not be visually distinguished by species but were subsampled to determine live fraction (following Saunders *et al.*, 2006). Intact monoliths of soils were removed from a subset of mesocosms and sectioned for rooting depth profile analysis (data not presented). The roots therein were handled in the same manner; the sums of these segments were included in analyses presented here. Belowground-to-aboveground ratio was calculated as the sum of belowground masses divided by the shoot mass.

Statistical analyses

We performed three-way, split-plot ANOVAs to test for effects of N, CO_2, sea level, and factorial interactions thereof on response variables ($\alpha = 0.05$). The mean of each pair of replicates within each chamber was considered the experimental unit so that $n = 3$ per treatment. For the split-plot analysis, chamber was deemed a random effect nested within CO_2 treatment, the whole-plot factor (Quinn & Keough, 2002). Owing to the dominance of the sea level treatment on our results, data were analyzed by individual two-way split-plot ANOVAs ($CO_2 \times N$, $n = 3$, again with chamber as the whole-plot random effect) within each sea level treatment to better understand how resource amendments affect plant growth at each sea level.

Results

Sea level was the dominant factor affecting plant growth of both species aboveground and belowground over both growing seasons (Fig. 3). There were several significant interactions among resource treatments and sea level (Table 1). To explore these interactions more

carefully, we analyzed CO_2 and N treatment effects within individual sea level treatments using two-way ANOVAs. Both species responded most strongly to N, but that response depended on sea level, differed between species (Fig. 3), and was at times amplified by elevated CO_2. Over both years, *S. patens* tended to respond positively to N at lower sea levels, while *S. americanus* responded to N at higher sea levels. Importantly, N promoted greater plant growth at the threshold of flooding tolerance in both years (Fig. 3c and g), primarily ascribable to effects on *S. americanus*. N and CO_2 interacted positively to enhance belowground growth in 2011 (Fig. 3h).

No plants survived for 2 years in the +30 cm sea level treatment and only one pot had live plants in the +20 cm treatment, so those groups were excluded from statistical analyses. The resource treatment effect sizes (Fig. 4b) were generally positive over the other four sea levels. N addition increased biomass by 5–15 g per pot, and from 18 to 25 g per pot when applied in combination with elevated CO_2 (Fig. 4b), representing up to a 28% stimulation of biomass over the control in the +10 cm sea level treatment in the second year. Both BG : AG production ratio and% dominance by *Spartina patens* declined sharply with higher sea level and were unaffected by resource addition (Figs 4c, d).

Hump-shaped curves were found for most aboveground growth responses to sea level but were altered by resource treatments. *S. americanus* showed optimal aboveground productivity at the 0 cm sea level treatment in 2011 under all resource treatments (Fig 3e). N fertilization raised the optimum sea level for aboveground productivity of *S. patens* (Fig. 3f) from −35 to −15 cm. Total aboveground biomass was greatest at −15 cm for all resource amendment groups (Fig 3g). For belowground biomass, the responses were more linear and the optima commonly appeared to occur at sea levels lower than those simulated herein, but that pattern varied among treatment groups (Fig 3h).

Discussion

Plant responses to sea level manipulations in mesocosms corresponded well to the elevation range reported for these species in the marsh we were simulating (Arp *et al.*, 1993), and their responses to natural variation in sea level at our long-term study site (Erickson *et al.*, 2007) and elsewhere (Kirwan & Guntenspergen, 2012). The optimum elevation for *S. americanus* after 2 years was lower in the tidal frame than for *S. patens*, which is consistent with the known flooding tolerances and elevation-based zonation of the two species. The difference in flooding tolerance was reflected in the minimum elevation of survival in 2011, which was
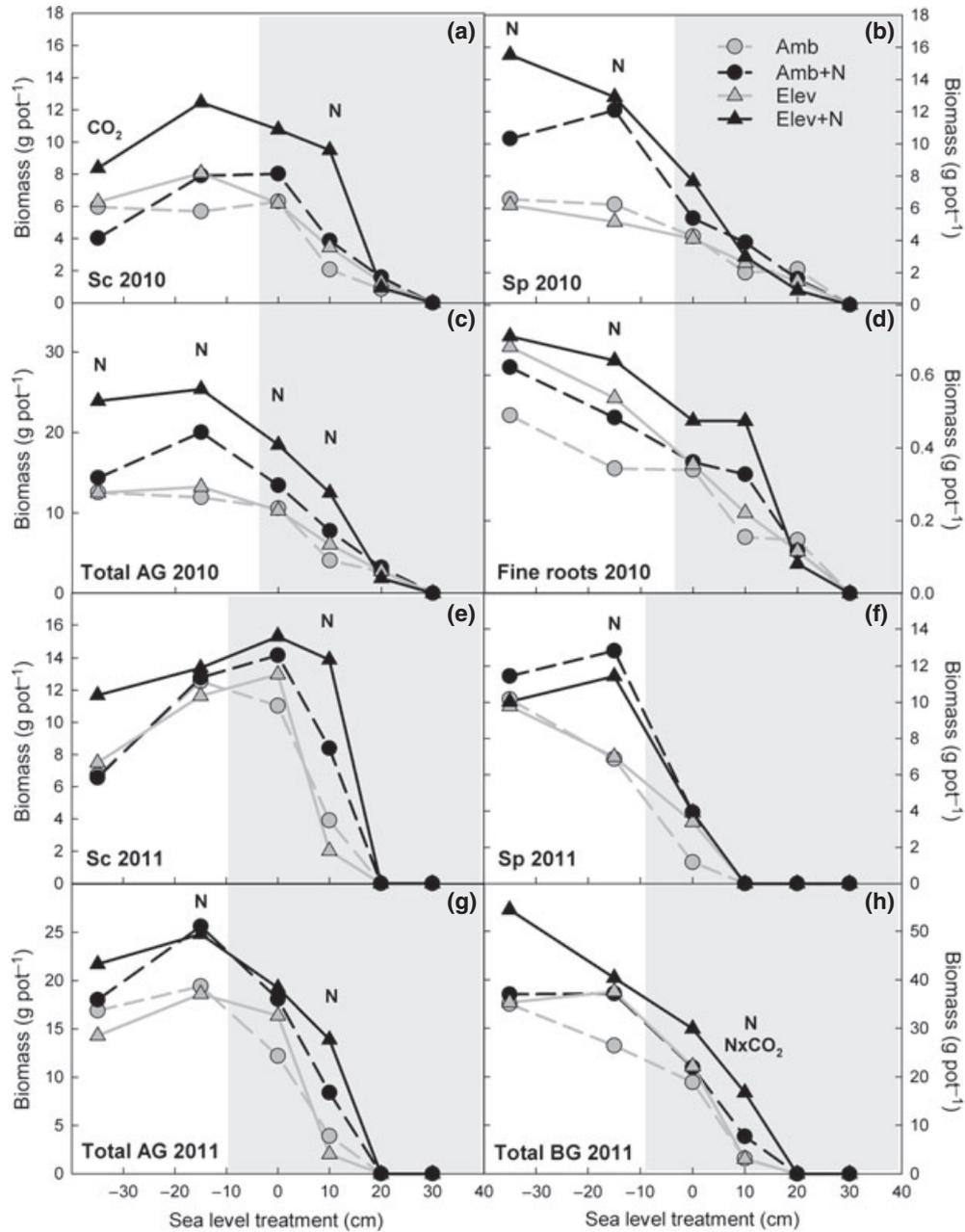
Fig. 3 Biomass by resource treatment group across sea level treatments. Significant effects within each sea level treatment (two-way ANOVA, $CO_2 \times N$, $P < 0.05$) are indicated in each panel. Shaded area represents the range of treatments that experienced more flooding than the mean marsh would in a growing season (May–September) with average sea level. Because, sea level was anomalously high in 2010 and 2011 growing seasons (+4.82 cm and +9.62 cm, respectively), the "0" sea level treatment, which was meant to simulate the average inundation of the current marsh platform, actually simulated higher than normal exposure to inundation. Sc: *Schoenoplectus americanus*; Sp: *Spartina patens*; AG: aboveground biomass; BG: belowground biomass; FR: fine root biomass.

0 cm for *S. patens* and +10 cm for *S. americanus*. Increased inundation frequency favored increased dominance by the more flood-tolerant species (Fig. 4d), as observed *in situ*. Likewise, the biomass responses of each plant species to elevated CO_2 and N addition (pooled across the sea level treatments that best represent marsh platform) generally agreed with the

magnitude of treatment effects that we have measured in the target marsh (Langley & Megonigal, 2010; White *et al.*, 2012). Although the mesocosms may have produced some artifacts (e.g., soil biogeochemical parameters), the agreement of our present results with previous field studies of plant elevation ranges (Arp *et al.*, 1993) and root distribution (Saunders *et al.*, 2006)

Table 1 Resulting *P*-values from three-way split-plot ANOVAs (CO_2 × Nitrogen × Sea level with chamber as nested within the whole-plot factor, CO_2) on plant growth responses from 2010 to 2011

	2010				2011				Cumulative		
	Sc. AG	Sp. AG	AG	FR	Sc. AG	Sp. AG	AG	BG	AG + BG	BG : AG	%Sp.
CO_2	0.0093	0.5576	0.0259	0.2802	0.3738	0.9096	0.6149	0.1237	0.0346	0.2895	0.9494
N	0.0002	<0.0001	<0.0001	0.0056	0.0112	0.1009	0.0006	0.0225	0.0002	0.7973	0.8583
CO_2 × N	0.0249	0.1159	0.0109	0.9147	0.2399	0.6014	0.3899	0.3916	0.0518	0.7797	0.3305
SL	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
SL × CO_2	0.1679	0.3487	0.2437	0.2712	0.8663	0.9630	0.9030	0.8576	0.8067	0.9915	0.8812
SL × N	0.0610	0.0001	0.0032	0.1792	0.1354	0.3493	0.3177	0.7396	0.3098	0.9117	0.2507
SL × CO_2 × N	0.5074	0.2873	0.2547	0.8279	0.7196	0.9936	0.6156	0.6739	0.6824	0.8964	0.9689

Sc: *Schoenoplectus americanus*.
Sp: *Spartina patens*.
AG: aboveground biomass.
BG: belowground biomass.
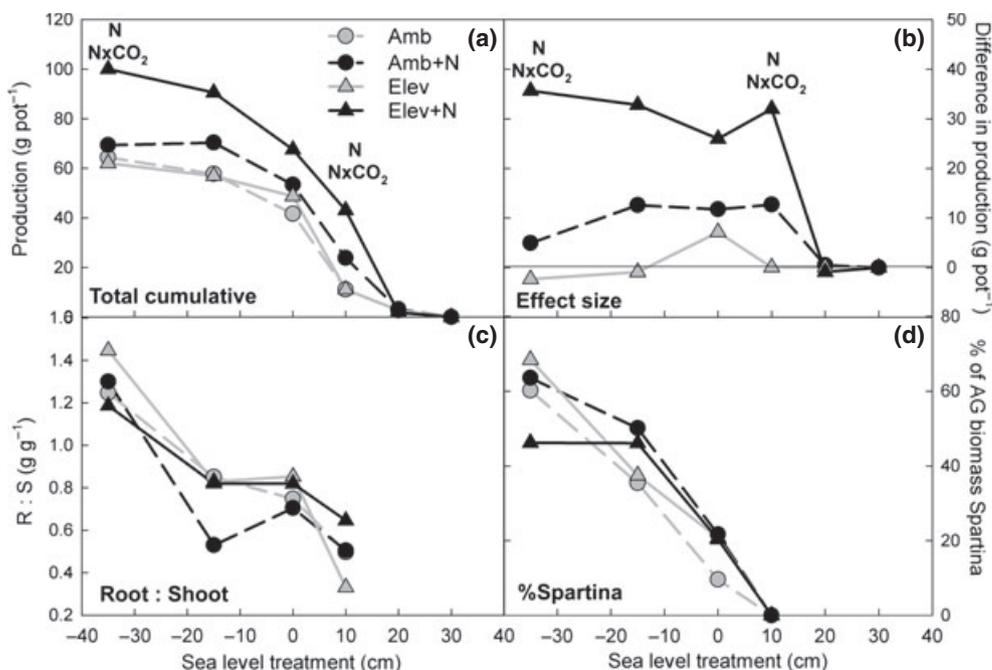FR: fine root biomass.
SL: Sea level.
N: nitrogen.

Fig. 4 Total cumulative production (above + belowground) in 2010 and 2011 (a), treatment effects (treatment–control) in total production (b), total root-to-shoot production ratio (c), and % dominance by *S. patens* (*S. patens*/total) in aboveground biomass in 2011 (d). Significant effects within each sea level treatment (two-way ANOVA, CO_2 × N, $P < 0.05$) are indicated in each panel.

indicate that our mesocosms captured realistic interactions between inundation frequency and plant dynamics under ambient resource availability. Thus, the design served our primary goal of understanding how changes in resources availability associated with global change will affect the productivity, optimum elevation, and minimum elevation of these species.

We observed stimulations of both aboveground and belowground plant mass in response to N and CO_2 that varied by year and sea level. Stimulation of plant growth by N fertilization was the most common and consistent. The magnitude of the N stimulation increased in combination with elevated CO_2 for belowground production in 2012 and cumulative production over both years (Fig. 4). We interpret the results of the second growing season to be more indicative of minimum elevations (i.e., sea levels above which plant growth will not be sustained in the long term) because

it encompassed 2 years of cumulative stress. For instance, though *S. patens* persisted in the "0 cm" sea level treatment in 2010, those pots had very little regrowth in 2011 (Fig 3). For *S. americanus*, several plants survived in the lowest two elevations for 1 year, but none was able to survive for 2 years.

The stimulation by resource enhancement was significant in the +10 cm sea level treatment, the steepest portion of the sea level response curve (Fig. 4a), indicating that resource enhancement can partially offset the negative effects of sea level rise on plant growth. Here, unamended mesocosms yielded high mortality and low growth where plants survived. By contrast, the Elev + N mesocosms all produced viable plants with as much *S. americanus* biomass as in the more benign sea level treatments. Both N and CO_2 qualitatively tended to broaden the range of optimal productivity into higher sea levels for *S. americanus* (Fig. 3e). N addition likewise broadened the range of optimal productivity for *S. patens* (Fig. 3).

Implications for elevation gain

Patterns of biomass production in response to sea level manipulation can be used to extrapolate how plants will affect marsh elevation in response to sea level change in the actual marsh (Morris *et al.*, 2002; Kirwan & Guntenspergen, 2012). For instance, *Spartina alterniflora* has been shown to increase biomass in response to flooding, thereby trapping more sediment and gaining elevation, which ultimately maintains a constant soil surface elevation relative to sea level (Morris, 2006). Under conditions of no resource addition in 2011 (Fig. 3, gray circles), *S. patens* had a production optimum at a relative sea level (−35 cm) that is lower than that of the current marsh in a year of average sea level, whereas *S. americanus* had an optimum (−15 cm) that was equivalent to average sea level. This finding indicates that the present marsh elevation (simulated by the 0 cm treatment) is currently suboptimal for the productivity of either species during periods of relatively high local sea level. Thus, if resource levels remain constant, we can forecast that further increases in sea level will elicit approximately linear declines in production. The resulting decline in organic accumulation will lead to eventual marsh collapse unless it is compensated by an increase in mineral accumulation or a decrease in soil organic matter decomposition rates, factors that we do not address herein. Such stabilizing ecogeomorphic feedbacks to sea level rise under the current ambient conditions may not occur in Chesapeake Bay marshes and in other microtidal environments because of low sediment supply (~20 mg L^{-1}, Wilson & Morris, 2012), and the apparent insensitivity of decomposition to sea level (Kirwan *et al.*, 2012).

However, the observation that increased resource availability led to a broadening of the optimum elevation range of these species, suggests that potential decline in organic matter inputs may be partly mitigated by an increase in plant resources such as CO_2 and nitrogen.

Our data suggest that in the case of severe flooding stress, fertilization can increase plant survivorship in part by stimulating root growth compared with controls. In this sediment-poor marsh, belowground production of organic matter is the primary mechanism by which the marsh accrues soil to maintain a constant elevation relative to rising seas. We expected that N addition would reduce root production as has been observed previously in this marsh (Langley *et al.*, 2009a; White *et al.*, 2012) as well as others (Darby & Turner, 2008b). Surprisingly, N addition, especially in combination with elevated CO_2, increased root production, particularly in the sea level treatment (+10 cm) that most closely represented the threshold of plant survival (Fig. 3h). Under the relatively modest flooding stress environment of our previous studies, adding N diminished root production (White *et al.*, 2012) owing to reduced need for nutrient foraging (Darby & Turner, 2008b). Perhaps, nutrient limitation remained so severe, even with fertilization, in our more flooded mesocosms that plants did not down-regulate root foraging.

Implications for plant tolerance of high sea level

The effect of resource enhancement on plant tolerance of sea level rise may differ from the effect on plant contribution to elevation gain. A variety of stressors confront marsh vegetation exposed to prolonged inundation, including oxidative stress induced by reduced soil conditions, salinity stress, and accumulation of phytotoxic byproducts. Here, fertilization with N partially ameliorated the effects of flooding on plant growth. Low redox potential associated with flooding in brackish marshes can generate high hydrogen sulfide concentrations that interfere with root NH_4^+ uptake (King *et al.*, 1982; Delaune *et al.*, 1983; Bradley & Morris, 1990; Koch *et al.*, 1990). Our results indicate that added NH_4^+ can offset some of the nutrient stress associated with flooding. A similar response was discovered in freshwater wetland plants (Xie *et al.*, 2009) that should experience little exposure to hydrogen sulfide, so other, unidentified mechanisms may be at work.

Species shifts

This experiment exposed realistic plant assemblages, rather than single species, to sea level manipulation so that we could evaluate how global change treatments

interacted to influence species abundance. N fertilization has been shown to strongly favor grasses, *S. patens* and *D. spicata* (Langley & Megonigal, 2010), which are more sensitive to inundation than the sedge, *S. americanus*, they tend to displace (Broome *et al.*, 1995). Therefore, N pollution could elicit a species shift that renders the entire ecosystem more susceptible to sea level rise (White *et al.*, 2012). Here, the sea level manipulation was the dominant factor that changed species composition, yielding a linear decline in *S. patens* abundance with increased sea level (Table 1, Fig 4d). Although this result indicates that abiotic stressors such as sea level trump resource availability in determining plant species composition where both plants occur, there are scenarios where the interaction of these stressors can lead to alternate stable states. For example, if chronic N pollution favored less flood tolerant species (e.g., *S. patens*) to the exclusion and local extirpation of more flood tolerant species (e.g., *S. americanus*), then a rapid and sustained high sea level event could trigger a conversion to open water before recolonization by a flood tolerant plant community, jeopardizing the sustainability of tidal ecosystems.

This experimental design allowed for unique insight into how nutrient competition can interact with abiotic stresses. Previous work from the high marsh platform of the Smithsonian Global Change Research Wetland showed that *S. americanus* responded positively to N addition in the first growing season of application, but the N effect diminished thereafter (Langley & Megonigal, 2010). Most likely, *S. americanus* was outcompeted by grasses that were dramatically in dominance in response to N addition by the second year. Similarly, by 2011 in this study, *S. americanus* aboveground biomass only responded positively to N addition where *S. patens* was excluded by higher sea level (Fig. 3e). Only *S. patens* responded positively to N in the lower sea level treatments (Fig. 3f), demonstrating that resource competition is modified by abiotic factors (Emery *et al.*, 2001).

In addition to affecting the processes that allow marshes to accumulate soil, global change factors such as elevated CO_2 and N may affect marsh viability by modifying plant tolerance for sea level rise. Interestingly, while increased N loads have been suggested to play a role in degrading coastal wetlands in marsh ecosystems (e.g., Hartig *et al.*, 2002; Turner, 2011; Deegan *et al.*, 2012), we found that, when applied in combination with experimentally imposed sea level stress, added N may afford plants enhanced ability to tolerate flooding. This result suggests that at least some portion of the stress associated with flooding may be alleviated by increasing N availability in the short term. However, the effects of N pollution on elevation gain are complex, and it may still interrupt the mechanisms that allow marshes to keep up with sea level rise, causing long-term deficits in elevation that increase flooding and overwhelm the stimulating effects of N identified herein.

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