

Elevated CO₂ stimulates marsh elevation gain, counterbalancing sea-level rise

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Tidal wetlands experiencing increased rates of sea-level rise (SLR) must increase rates of soil elevation gain to avoid permanent conversion to open water. The maximal rate of SLR that these ecosystems can tolerate depends partly on mineral sediment deposition, but the accumulation of organic matter is equally important for many wetlands. Plant productivity drives organic matter dynamics and is sensitive to global change factors, such as rising atmospheric CO₂ concentration. It remains unknown how global change will influence organic mechanisms that determine future tidal wetland viability. Here, we present experimental evidence that plant response to elevated atmospheric [CO₂] stimulates biogenic mechanisms of elevation gain in a brackish marsh. Elevated CO₂ (ambient + 340 ppm) accelerated soil elevation gain by 3.9 mm yr⁻¹ in this 2-year field study, an effect mediated by stimulation of below-ground plant productivity. Further, a companion greenhouse experiment revealed that the CO₂ effect was enhanced under salinity and flooding conditions likely to accompany future SLR. Our results indicate that by stimulating biogenic contributions to marsh elevation, increases in the greenhouse gas, CO₂, may paradoxically aid some coastal wetlands in counterbalancing rising seas.

coastal wetlands | nitrogen pollution | tidal marsh loss | root productivity | salinity

The world currently loses thousands of hectares of low-lying coastal wetlands to shallow open water each year (1–3), attributable, in part, to a recent acceleration of sea-level rise (SLR) (4–6). Loss of coastal wetlands threatens critical services these ecosystems provide, such as supporting commercially important fisheries, providing a wildlife habitat, improving water quality, and buffering human populations from oceanic forces (3). Recent catastrophes, such as Hurricane Katrina and the Asian Tsunami, have underscored the importance of understanding factors that govern sustainability of coastal wetlands in the face of climate change and accelerating SLR. Marshes must build vertically through accumulation of mineral and organic matter to maintain a constant elevation relative to sea level (7). To explain the dynamics of coastal wetland elevation, researchers have traditionally focused on abiotic factors, such as reductions of mineral sediment loads from hydrologic modifications (8). However, organic matter dynamics have a clear importance in peaty soils, which are composed mostly of live and dead plant tissues (9, 10) and may also play an important role in stabilizing mineral soils (11). Organic mechanisms may be especially sensitive to other global change factors and may determine the fate of tidal wetlands.

Rising atmospheric CO₂ is largely responsible for recent global warming and will continue to contribute to accelerating SLR through thermal expansion and ice melt (12). Elevated CO₂, in addition to accelerating SLR, may have important biologically mediated effects on coastal wetland ecosystems, such as stimulating plant productivity (13). The effects of elevated CO₂ must be considered along with other regionally or locally important

factors that are changing simultaneously, such as nitrogen enrichment (14), flooding (15), and salinity (13).

We manipulated atmospheric CO₂ and soil nitrogen availability in a tidal marsh with low mineral sediment inputs, allowing us to isolate organic controls on marsh elevation in Chesapeake Bay. This experiment was designed to track sensitively how changes in plant productivity influenced soil elevation. Determining soil surface elevation change is important for 2 reasons. First, the loss in soil elevation relative to local sea level may provide an early indication of the syndrome of tidal wetland collapse (16). Second, tracking elevation changes in discrete strata through time, along with measurements of plant productivity and other environmental variables, allows identification of specific mechanisms critical to the persistence of tidal wetlands under accelerating SLR. To examine how CO₂ may interact with other factors that will accompany SLR, we manipulated CO₂, salinity, and flooding in a companion greenhouse study (17).

Results and Discussion

Elevated CO₂ stimulated above-ground productivity in the marsh by 30% in 2006 (Table 1; two-way ANOVA, CO₂ effect: $P < 0.05$) but not in 2007 ($P > 0.70$) during a severe drought. These responses were consistent with a 20-year record of elevated CO₂ treatment in a previous CO₂ study on the same marsh (13). Strikingly, elevated CO₂ accelerated the rate of soil elevation gain over 2 years of treatment. Least-squares linear trends revealed a slight loss of elevation in ambient CO₂ (–0.9 mm yr⁻¹) compared with an elevation gain (3.0 mm yr⁻¹) in the elevated CO₂ treatment (Fig. 1A; two-way ANOVA comparing linear trends, $n = 5$, CO₂ effect: $P < 0.05$). Nitrogen addition tended to affect elevation negatively, although the overall nitrogen effect was not significant. Deposition of mineral sediment on the marsh surface is negligible at this site. Root zone expansion by accumulation of plant material is essential to maintaining a constant surface elevation relative to rising sea level. Indeed, changes in marsh surface elevation mirrored changes in root zone thickness (Fig. 1B). Elevated CO₂ caused an increase in thickness of 4.9 mm yr⁻¹ compared with 0.7 mm yr⁻¹ in the ambient CO₂ treatment, an effect that could increase marsh tolerance for SLR.

Increases in soil elevation were driven by a stimulation of subsurface plant productivity. Changes in soil elevation over each growing season closely followed the pattern of treatment

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Table 1. Above-ground plant biomass and fine root production over 2 growing seasons of the field study

Treatments	Aboveground		Fine roots	Aboveground		Fine roots
	Jul-06	Oct-06	2006	July-07	Oct-07	2007
Ambient CO ₂	387 (27) ^a	677 (68) ^a	56 (11) ^{ab}	524 (53) ^a	449 (25) ^a	108 (17) ^{ab}
Ambient CO ₂ +Nitrogen	603 (127) ^b	952 (144) ^a	40 (11) ^a	842 (149) ^b	697 (167) ^b	63 (9) ^a
Elevated CO ₂	387 (26) ^a	883 (111) ^a	98 (39) ^{ab}	530 (39) ^a	399 (34) ^a	146 (14) ^b
Elevated CO ₂ +Nitrogen	560 (44) ^{ab}	1393 (82) ^b	110 (13) ^b	902 (65) ^b	702 (55) ^b	104 (16) ^{ab}

Values represent means (SE) in g m⁻². Treatment means without common superscript symbols were different ($P \leq 0.05$) according to a Student's *t* test multiple comparison.

effects on fine root productivity (Fig. 2; $r^2 = 0.86$, $P < 0.05$). By the end of the second year, above-ground litter also may have entered the soil and contributed to a CO₂ effect on elevation. Rhizome and subsurface stem productivity were likely also important but could not be quantified nondestructively in the field. Although the presence or absence of an elevated CO₂ effect on above-ground production each year depended on climatic conditions, elevated CO₂ strongly stimulated fine root productivity both years, by 48% in 2006 (two-way ANOVA, $n = 5$, $P < 0.05$) and by 26% in 2007 ($P < 0.05$). This finding concurs with previous work at this site and many other CO₂ studies that report an inordinately large stimulation of root growth (18).

The timing of the below-ground response further supports the important role of plant growth in driving soil elevation gain. The CO₂ effects on root zone elevation arose during the first growing season (Fig. 1), concurrent with the production of live plant biomass. CO₂ effects on elevation during the growing season were not reversed by plant senescence and decomposition. Because anaerobic conditions in saturated soils substantially slow soil organic matter decay (11), the effects of productivity on elevation during the growing season persist through the non-growing season. Consequently, elevated CO₂ forced the soil surface upward by stimulating the accumulation of both live and dead organic matter.

Other perturbations, particularly those that may accompany SLR, could modify the influence of elevated CO₂ on marsh elevation gain. To understand better how the CO₂ response under current sea-level conditions might differ with accelerating SLR, we examined the effect of CO₂ in combination with flooding and salinity in a mesocosm study. This experimental approach allowed isolation of root-zone controls on soil elevation dynamics and manipulation of factors known to influence root growth. The objective of our treatments was to vary the depth and duration of flooding in combination with a range of salinities anticipated under different SLR scenarios (17).

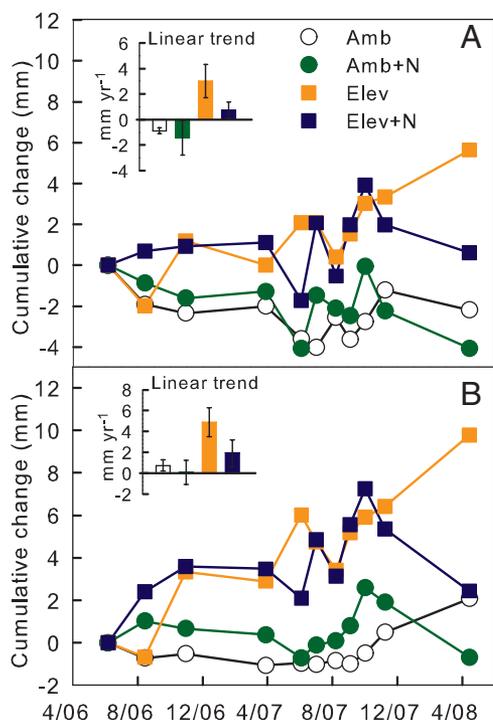


Fig. 1. Relative surface elevation (A) and root zone thickness (B) over 2 growing seasons in a brackish marsh (Chesapeake Bay) exposed to ambient (Amb) or elevated (Elev) atmospheric [CO₂] in open-top chambers and to factorial soil nitrogen (+N) enrichment. The slopes of the linear trends in elevation are inset in each panel (mean \pm 1 SE). Elevated CO₂ increased elevation (two-way ANOVA, CO₂ effect: $P < 0.05$), an effect that mirrored CO₂ stimulation of root zone thickness ($P < 0.05$). Nitrogen addition had a non-significant tendency to reduce total elevation gain ($P = 0.18$) and root zone expansion ($P = 0.13$), despite stimulating above-ground plant productivity.

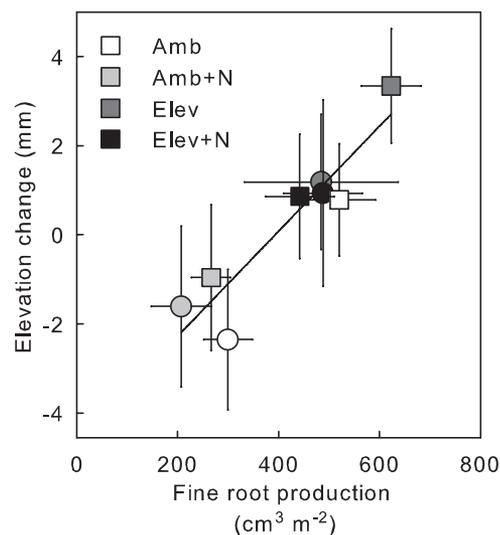


Fig. 2. Relation of subsurface biovolume production to vertical change in the field. Values represent treatment means (\pm 1 SE) of relative elevation change and fine root productivity over each field season, 2006 (circles) and 2007 (squares). Amb, ambient; Elev, elevated; N, nitrogen.

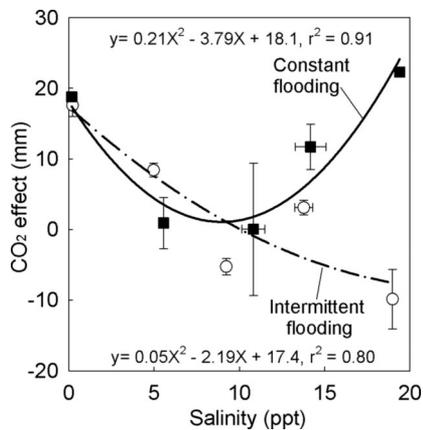


Fig. 3. Elevated CO_2 effects on marsh elevation in greenhouse mesocosms subjected to different salinity and flooding treatments. Values are the difference in elevation (mm) between mesocosms under elevated CO_2 (720 ppm) and ambient CO_2 (380 ppm). The y axis values represent mean differences in CO_2 response (± 1 SE) under intermittent (circles) and constant (squares) flooding in relation to mean interstitial salinity (± 1 SE) measured biweekly in mesocosms (x axis). Second-order polynomial curves were fitted to the data; t tests of quadratic coefficients indicated a significant change over salinity for both flooding treatments ($P < 0.05$). Patterns of response for the 2 flooding treatments were significantly different ($F = 3.03$, $P = 0.10$; analysis of covariance).

As found in the field study, CO_2 had a significant effect on marsh elevations in mesocosms (17). However, the patterns of soil expansion, driven by below-ground production, varied in a complex manner because of interactions of CO_2 , flooding, and salinity (Fig. 3). Under intermittent flooding, CO_2 enhanced elevation at lower salinities but had no effect or a negative effect at higher salinities (Fig. 3). Under constant flooding, however, the pattern of CO_2 response was different, with expansion greatest both above and below the current salinity range for this marsh type (Fig. 3). In particular, CO_2 treatment increased elevation in flooded mesocosms at high salinities (i.e., conditions that simulated future SLR). Although the precise CO_2 response in nature will depend on many other factors in addition to salinity and flooding, our findings indicate that future CO_2 effects on elevation in Kirkpatrick Marsh will likely be modified by conditions that accompany SLR.

Agricultural and municipal runoff increases nitrogen (N) loading in estuaries, particularly those that drain densely populated watersheds. In the field study, nitrogen addition, simulating coastal eutrophication, tended to negate elevation gains caused by elevated CO_2 alone (Fig. 1A, *Inset*). Although nitrogen addition stimulated above-ground biomass, it decreased root productivity (Fig. 2 and Table 1). N addition commonly decreases carbon allocation to root productivity (19). Furthermore, N addition has been shown to stimulate decomposition in other nitrogen-limited peat-based wetlands (20). Nitrogen pollution may contribute to marsh loss (5), although the mechanisms have not been described. In our study, N addition tended to reduce elevation gain, partially by reducing root productivity, but also may have stimulated organic matter decomposition.

Plant community composition will modify ecosystem responses to elevated CO_2 . Plants with the C_3 photosynthetic pathway typically exhibit a stronger CO_2 response than C_4 plants (13). The CO_2 effect may be particularly important for C_3 -dominated marshes experiencing SLR, which includes many brackish marshes and mangrove swamps. In this marsh community, the responsive C_3 species is more flood-tolerant and less salt-tolerant than the C_4 species (21, 22). The mesocosm experiment also provided insight into C_3 vs. C_4 contributions to soil

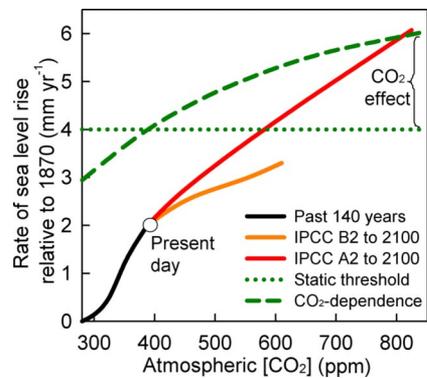


Fig. 4. Conceptual comparison of SLR and atmospheric $[\text{CO}_2]$ scenarios from the Inter-governmental Panel on Climate Change (IPCC) to hypothetical thresholds of marsh tolerance for increasing SLR. The black line approximates a simplified SLR \times CO_2 relation for the past 140 years (4, 12, 29, 30). Red and orange lines represent most probable increases in atmospheric $[\text{CO}_2]$ and SLR rates for the years 2090–2100 according to model projections for 2 moderate IPCC socioeconomic scenarios, A2 and B2 (31). The difference between the 2 lines depends on socioeconomic uncertainties. Each model output has its own error based on physical uncertainties that are not shown here. The relation between SLR and CO_2 appears approximately linear in the 100-year projections, but other relations are possible. The dotted green line represents a threshold SLR rate fixed at 4 mm yr^{-1} , a rate that would threaten many marshes (6). The dashed green line represents a hypothetical threshold rate that depends on atmospheric $[\text{CO}_2]$ and is based on our finding of increased marsh elevation gain with elevated CO_2 . The CO_2 effect (difference between the 2 green lines) portrayed here ($\approx 2 \text{ mm yr}^{-1}$ at 720 ppm) is conservative compared with that measured in the field experiment (3.9 mm yr^{-1}) because of uncertainties in extrapolating from short-term CO_2 effects on elevation to actual marsh thresholds. Marshes collapse when the rate of SLR (red or orange lines) exceeds the threshold of marsh tolerance for SLR (green lines). Thresholds may have been lower in the past when $[\text{CO}_2]$ was at preindustrial levels ($\approx 280 \text{ ppm}$), because many plants likely exhibited reduced below-ground growth compared with today, and thus made smaller contributions to marsh elevation gain.

expansion (17). Separation of roots by species was not possible, but species contributions to soil volume in the mesocosms could be assessed by measuring the final volume of shoot bases (i.e., the below-ground portion of the shoot that serves as a storage organ in graminoids). Vertical change in soil elevation was positively correlated with subsurface shoot volume of the C_3 but not the C_4 species (17). Consequently, the potential for CO_2 stimulation under an accelerating SLR scenario may depend on the inherent tolerance of component species to salinity, flooding, and other factors as well as their potential to respond to CO_2 (17).

Our findings bear particular importance given the threat of accelerating SLR to coastal wetlands worldwide. A recent report suggests that a 2-mm increase in the rate of SLR will threaten or eliminate a large portion of mid-Atlantic marshes (6). The threshold rate of SLR (i.e., the SLR rate at which the marsh converts to open water) depends on the rate of marsh elevation gain by accumulating sediment or endogenous organic material (7). For instance, models predict that increasing mineral sediment load should increase this threshold rate (7, 23). Nevertheless, many marshes, like Kirkpatrick Marsh, naturally receive very little exogenous sediment. Therefore, the critical SLR threshold depends almost entirely on biological mechanisms that have been more difficult to describe and predict. We suggest that elevated CO_2 , by stimulating below-ground plant productivity and biogenic elevation gain, may also increase the capacity of coastal wetlands to tolerate SLR (Fig. 4).

Atmospheric CO_2 has risen 40% from preindustrial levels ($\approx 280 \text{ ppm}$) to the current concentration ($\approx 388 \text{ ppm}$) over the past 200 years and has enhanced plant productivity globally. A CO_2 effect on coastal wetland elevation may have already

mitigated a significant amount of marsh loss acting through the biological mechanisms demonstrated in our study (Fig. 4). However, the stimulatory effects of CO₂ on leaf-level photosynthesis are known to diminish with each marginal increase in CO₂ concentration (24), and a similar attenuation of the stimulatory effect of elevated CO₂ on soil elevation gain should follow. Consequently, further increases in atmospheric CO₂ beyond 720 ppm may yield diminishing benefits for plant productivity and marsh elevation, while further accelerating SLR through greenhouse warming (12). A simultaneous increase in plant stressors, such as salinity and flooding, however, may sustain or enhance the CO₂ effect, as found in the mesocosm study.

Our findings show that elevated CO₂ stimulates plant productivity, particularly below ground, thereby boosting marsh surface elevation. In addition to providing evidence for organic control of wetland topography on the landscape scale, we show how elevated CO₂ may strengthen the organic mechanisms that sustain marsh elevation relative to SLR in the future. These effects likely extend beyond biogenic marshes, because organic processes can exert control over elevation dynamics in mineral-soil wetlands as well (11). For instance, marshes in the Mississippi River delta have high rates of subsidence that were naturally countered by mineral sediment deposition (25). However, hydrological modifications by humans have diminished sediment deposition in this system. Such sediment-deficient deltas, which once would have been buffered against increasing SLR, have been rendered more vulnerable, and hence more dependent on organic contributions to sustain a constant elevation relative to SLR. To manage or restore such ecosystems to a self-sustaining state, we must explore further how global change interactions will influence key biological mechanisms that maintain soil elevations in coastal wetland ecosystems.

Materials and Methods

The field study was conducted in Kirkpatrick Marsh (38°53' North, 76°33' West), located on a microtidal subestuary of Chesapeake Bay. The site is dominated by a perennial C₃ sedge, *Schoenoplectus americanus*, and the C₄ perennial grasses *Spartina patens* and *Distichlis spicata* and is representative of brackish high marshes of mid-Atlantic North America (26). The soils at the site are organic (>80% organic matter) to a depth of ≈5 m. Mean tidal range is 44 cm. The high marsh zone is 40–60 cm (26) above daily mean low water level and is inundated by 28% of high tides. Salinity averages 10 parts per thousand (ppt) and ranges seasonally from 4 to 15 ppt. The average daily air temperature reaches a low of –4 °C in January and a high of 31 °C in July. The 80-year trend of SLR is ≈3.4 mm yr⁻¹ (tidesandcurrents.noaa.gov, Annapolis), which outpaces the long-term local eustatic trend attributable to glacial isostatic adjustment (27).

Beginning in May 2006, we exposed 20 3.3-m² marsh plots to 2 atmospheric CO₂ concentrations (ambient and ambient + 340 ppm) to simulate a likely atmospheric CO₂ concentration projected for the year 2100. The 2 CO₂ levels were crossed with 2 levels of N addition (0 and 25 g of nitrogen m⁻² yr⁻¹). Ammonium chloride was dissolved in 5 L of water from the Rhode River, the subestuary adjacent to the site. On 5 dates (approximately monthly, avoiding high tides) throughout the growing season, we used backpack sprayers to deliver a fertilizer solution to 10 plots. The fertilizer solution was then rinsed

from standing vegetation with another 5 L of unamended river water applied with backpack sprayers. Each fertilizer application simulated 5 g of nitrogen m⁻² in the equivalent of 0.5 cm of river water. The 10 unfertilized chambers received 10 L of unamended river water applied in the same manner (see [SI Text](#)).

We outfitted each plot with a surface elevation table (SET) to measure soil elevation change sensitively (Figs. S1 and S2). Deep-rod SETs, used in conjunction with shallow benchmarks, enabled elevation changes to be partitioned between the root zone (0–0.3 m in depth) and the deep zone (0.3–4.5 m in depth). We used elevation measurements in adjacent unchambered reference plots to account for chamber effects and to minimize the confounding effects of spatial variability.

Greenhouse Methods

To examine how CO₂ might affect elevation response under simulated SLR scenarios, data from a greenhouse mesocosm experiment (17) were used. This experiment used the same marsh type as the field study at the mid-Atlantic location but was conducted using soil and plant material from the Mississippi River delta and carried out at the Wetland Elevated CO₂ Experimental Facility (National Wetlands Research Center, Lafayette, LA). A detailed description of the facility and the experimental design is given elsewhere (17, 28) but is briefly repeated here to provide context for this study.

Blocks of peat with intact vegetation (sods) were collected from a brackish marsh community (ca. 50:50 mixture of *S. americanus* and *S. patens*) in coastal Louisiana and established in mesocosms (0.1-m² area × 0.4 m in depth, 25-L volume). In March 2005, 60 replicate mesocosms were randomly assigned to 1 of 4 greenhouses with atmospheric concentrations of 380 (ambient) or 720 (elevated) ppm of CO₂, 3 flooding levels (constantly flooded, intermittently flooded, drained), and 5 salinity levels (0, 5, 10, 15, 20 ppt of sea salts). All above-ground material was removed on senescence so that the only inputs were from below-ground production. Expansion or contraction of the marsh sods was measured for 1 year with mini-SETs [modeled after SETs used in the field study (17)]. CO₂ response was calculated as the difference between elevated and ambient CO₂ treatments and plotted vs. interstitial salinity (averaged over experimental period).

The drained treatment was not included in the analysis, because our objective in this study was to understand better how CO₂ response to current SLR (observed in the field) might change under a future SLR scenario of increased flooding. Second-order polynomial curves were fitted to the data, and overall differences were tested with analysis of covariance (using salinity as a continuous effect and flooding as a categorical effect in the model); *t* tests of quadratic and linear coefficients (for each fitted curve) also were used to assess differences.

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