Spatial response of coastal marshes to increased atmospheric CO_2

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The elevation and extent of coastal marshes are dictated by the interplay between the rate of relative sea-level rise (RRSLR), surface accretion by inorganic sediment deposition, and organic soil production by plants. These accretion processes respond to changes in local and global forcings, such as sediment delivery to the coast, nutrient concentrations, and atmospheric CO_2, but their relative importance for marsh resilience to increasing RRSLR remains unclear. In particular, marshes up-take atmospheric CO_2 at high rates, thereby playing a major role in the global carbon cycle, but the morphologic expression of increasing atmospheric CO_2 concentration, an imminent aspect of climate change, has not yet been isolated and quantified. Using the available observational literature and a spatially explicit ecomorphodynamic model, we explore marsh responses to increased atmospheric CO_2, relative to changes in inorganic sediment availability and elevated nitrogen levels. We find that marsh vegetation response to foreseen elevated atmospheric CO_2 is similar in magnitude to the response induced by a varying inorganic sediment concentration, and that it increases the threshold RRSLR initiating marsh submergence by up to 60% in the range of forcings explored. Furthermore, we find that marsh responses are inherently spatially dependent, and cannot be adequately captured through 0-dimensional representations of marsh dynamics. Our results imply that coastal marshes, and the major carbon sink they represent, are significantly more resilient to foreseen climatic changes than previously thought.

sea-level rise | coastal marshes | coastal dynamics | atmospheric CO_2 | CO_2 fertilization

Coastal marsh extent and morphology are directly controlled by rate of relative sea-level rise (RRSLR) and the soil accretion rate, the latter associated with inorganic sediment deposition and organic soil production by plants. Previous studies observed that CO_2 fertilization increases marsh plant biomass productivity through increased water use efficiency and photosynthesis (1), and hypothesized that, as a consequence, marsh resilience should increase via increased organic accretion (2, 3). However, this hypothesis has not yet been tested, and the observed increased plant productivity in response to the CO_2 fertilization effect has not been translated into its actual geomorphic effects. In fact, direct CO_2 effects on vegetation and marsh accretion (as opposed to its indirect effects, e.g., via the increase in temperature) have not yet been incorporated into marsh models, and their importance relative to other leading forcings of marsh dynamics (e.g., inorganic deposition, RRSLR, nutrient levels) remains unknown. Here we use existing data and a 1D ecomorphodynamic model to assess the direct impacts of elevated CO_2 on marsh morphology, relative to ongoing [e.g., RRSLR, and suspended sediment concentration (SSC)] and emerging [nutrient levels (4–6)] environmental change.

Vegetation Responses to Changing Environmental Conditions

We use published observations of aboveground and belowground biomass productivity in coastal marshes under ambient and elevated CO_2 conditions to derive a range of possible marsh plant biomass responses to changing atmospheric CO_2 (3, 7–10). Because the photosynthetic pathway of C3 plants is CO_2-limited for a wider range of atmospheric CO_2 concentrations than in C4 plants, CO_2 fertilization effects are expected to be more evident in C3 species; elevated CO_2 concentrations may also give C3 species a competitive advantage over C4 species, and hence possibly favor an expansion of the former at the expense of the latter (1, 11). However, enclosure field experiments specifically focusing on marsh vegetation (3, 7–10) find both C3 and C4 marsh species to be responsive to increases in atmospheric CO_2. A meta-analysis of this literature (7–10) (Table S1), when the responses of C3-only, C4-only, and mixed communities are collectively considered, gives a median 39% increase in aboveground biomass and a median 33% increase in belowground biomass as CO_2 is elevated by 400 ppm with respect to current conditions. For comparison, the very limited available data documenting C4-only belowground productivity (including rhizomes and roots, both contributing to organic soil production) report increases between 13% and 47% (7). Because of the positive belowground response of marsh C4 vegetation, the expected competitive advantage of C3s, and the largely positive response of the latter to increased CO_2, we consider all of the available data to parameterize biomass response to elevated CO_2 (i.e., not separating C3s and C4s). Our parameterization expresses the biomass in the changed scenario as a linear function of CO_2 change (ΔCO_2), according to the median responses observed in the compiled dataset for both the aboveground [$B_a(\Delta CO_2) = (1 + (0.39/400 \text{ ppm}) \cdot \Delta CO_2) \cdot B_a(0)$, $B_a(0)$ being the current aboveground biomass productivity] and the belowground compartment [$B_b(\Delta CO_2) = (1 + (0.33/400 \text{ ppm}) \cdot \Delta CO_2) \cdot B_b(0)$]. To explore the range of potential vegetation responses to CO_2

Significance

Coastal marshes provide numerous ecosystem services, are an important carbon sink, and are exposed to drowning as sea-level rise accelerates. Using a meta-analysis of the available observational data, we model the coupled marsh vegetation and morphological dynamics. We find that the fertilization effect of elevated atmospheric CO_2 significantly increases marsh resilience to drowning and decreases the spatial extent of marsh retreat under high rates of sea-level rise. While this direct CO_2 fertilization effect has so far been neglected in marsh modeling, we find it is central in determining marsh survival under the foreseeable range of climatic changes.

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changes, we also consider the first quartile (13% increase in aboveground biomass and a 20% increase in belowground biomass) and the third quartile (101% increase in aboveground biomass and a 94% increase in belowground biomass) in the compiled dataset. This range in vegetation responses provides an estimate of the uncertainty in our evaluation of marsh responses to elevated CO_2.

Salinity, flooding, water stress, and eutrophication can all potentially influence the effects of CO_2 fertilization on marsh plants (3, 12–16). Overall, the available evidence is coherent in pointing to a significant CO_2 fertilization effect on organic accretion and plant production even in the presence of other simultaneous environmental changes (2, 3, 17, 18). However, we are here interested in isolating the effects of different forcings. Hence, to avoid the introduction of confounding factors, we do not use in our parameterization data that include the interactions between the above environmental conditions and CO_2 fertilization [e.g., Rasse et al. (18) and Cherry et al. (2)].

To quantify the geomorphic response of marshes to elevated CO_2 in the wider context of the main environmental changes expected over the next century, we compare it to the responses induced by changes in RRSLR, SSC, and nitrogen availability. Although the effects of the first two forcings are relatively well constrained, the effects of nitrogen are the subject of some controversy. In fact, an analysis of the extensive literature on elevated nitrogen levels in coastal marshes reveals large uncertainties in plant responses (Table S2). Fertilization experiments usually find that increased nitrogen promotes aboveground biomass productivity (3, 6), but a wide scatter characterizes the observations, even within the same study (Fig. S1). Nitrogen's effect on belowground biomass productivity is even less clear, such that even the sign of the change in productivity remains undetermined (4, 5) and may be dependent on the levels of nitrogen addition (6). Such scatter can be attributed to the fact that existing studies used different methods (e.g., the forms of nitrogen adopted for fertilization, such as ammonium sulfate, ammonium nitrate, etc.), and were conducted in different regions and under different environmental conditions. Species composition, baseline ambient nitrogen loading (19, 20), salinity, flooding frequency, and the concentration of other nutrients also vary widely across the existing literature, and can significantly affect the outcome of nitrogen addition experiments (4, 21–31). Hence, to isolate the potential impacts of increased nitrogen concentrations, we use the minimum ($55.2\ g\ N \cdot m^{-2} \cdot y^{-1}$) and maximum ($892.8\ g\ N \cdot m^{-2} \cdot y^{-1}$) nitrogen addition levels and the corresponding biomass responses from one study that explored a wide range of nitrogen addition levels at a single site (6). The minimum addition level corresponds to a 15% increase in both the aboveground and belowground biomass, whereas the maximum addition experiment caused a 134% increase in aboveground biomass and a 24% decrease in belowground biomass. Using these two cases to parameterize biomass response to nitrogen addition, we explore two end-member response scenarios with our experiments. The corresponding changes in aboveground and belowground productivity are representative of the range of responses observed in the dataset compiled (Fig. S1), yet avoid confounding factors from cross-study methodological heterogeneity, and preserve the observed belowground to aboveground biomass (root to shoot) ratios.

We use a spatially explicit 1D model of marsh ecomorphodynamic processes to evaluate the CO_2, nitrogen, and suspended sediment concentration impacts on marsh morphology (32). The model describes the evolution of a marsh transect perpendicular to a tidal channel, which delivers inorganic sediment, by focusing on accretion–submersion processes rather than on marsh lateral erosion or expansion (33, 34). Changes in the marsh surface elevation, z, at a position x along the marsh transect are dictated by the sum of the rate of inorganic soil deposition, $Q_s(x)$, the rate of sediment trapping by

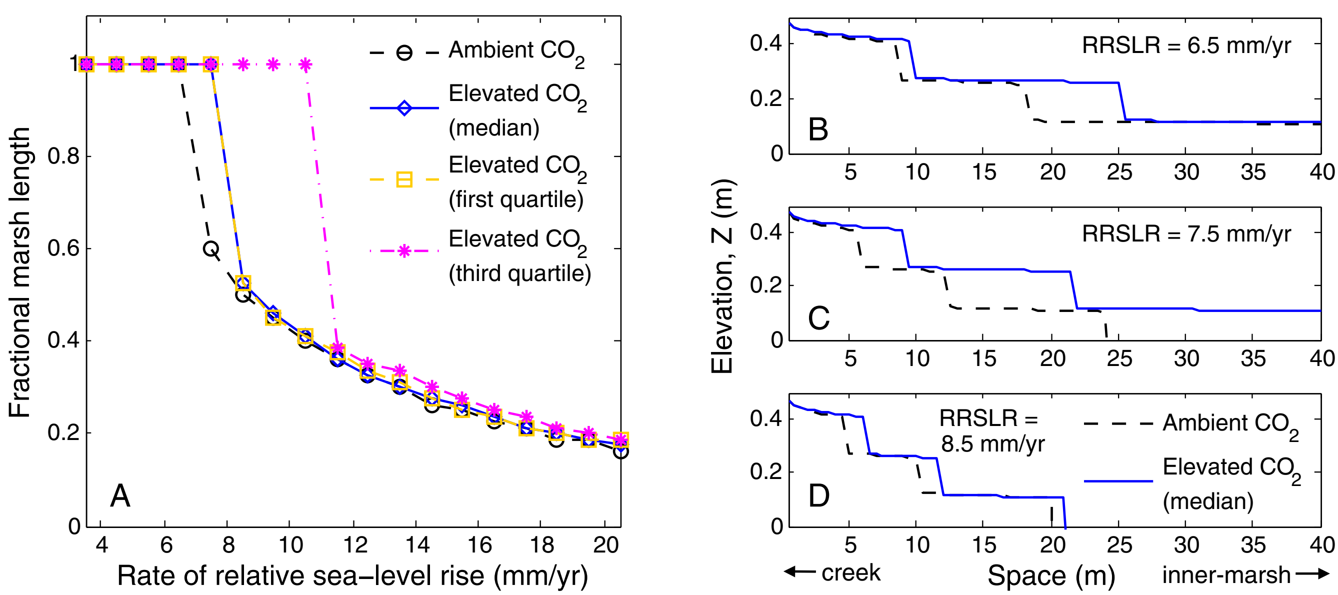

Fig. 1. Marsh model equilibrium profile lengths in response to current and elevated atmospheric CO_2 for a range of rates of RRSLR. (*A*) Fractional marsh length (equilibrium profile length divided by initial length, where a value of 1 represents no partial marsh drowning and 0 is completely submerged) for a range of RRSLR. Marsh partial drowning is initiated at RRSLR = 7.5 mm/y in the current CO_2 scenario, versus RRSLR = 8.5 mm/y in the median and first quartile elevated CO_2 cases, and 11.5 mm/y in the third quartile response case, where the CO_2 fertilization effect increases marsh resilience to higher RRSLR. Marsh equilibrium profiles [where space (m) represents distance from a tidal creek that delivers sediment from the left side of the figures] for both current and median biomass response to elevated CO_2 are shown for (*B*) RRSLR = 6.5 mm/y, before the drowning threshold has been crossed in either case; (*C*) RRSLR = 7.5 mm/y, where the current CO_2 scenario shows drowning initiation, but not the elevated CO_2 profile; and (*D*) RRSLR = 8.5 mm/y, where both marsh profiles are partially drowned.

Table 1. Predicted marsh loss under IPCC Fifth Assessment Report (41) RCP mean scenarios

	RCP2.6	RCP4.5	RCP6	RCP8.5
Atmospheric CO_2, ppm	421	538	667	930
Rate of sea-level rise, mm/y	4.4	6.2	7.5	12
Marsh loss no CO_2 effect, %	0	0	40	66
Marsh loss first quartile CO_2 effect, %	0	0	0	65
Marsh loss median CO_2 effect, %	0	0	0	63
Marsh loss third quartile CO_2 effect, %	0	0	0	0

marsh plants, $Q_t(x)$, the rate of organic soil production by vegetation, $Q_o(x)$, and the RRSLR,

$$\frac{\partial z}{\partial t}(x,t) = Q_s(x,t) + Q_t(B_a(x),t) + Q_o(B_b(x),t) - R \qquad [1]$$

where $B_a(x)$ and $B_b(x)$ are aboveground and belowground biomass (linear functions of ΔCO_2), and R is the RRSLR (Table S3). Surface erosion is set to zero in our experiments, as it is negligible in vegetated marshes (35). Settling of suspended sediment, which is transported from the channel across the marsh over a tidal cycle with period T through advection–dispersion, determines inorganic soil deposition. This sedimentation rate is calculated as $Q_s(z,B_a(x)) = w_s/(T\rho_b)\int_T C(z,B_a(x),t)dt$, where w_s is the settling velocity (here 2×10^{-4} m/s), ρ_b is the bulk density (1,325 kg/m^3), and C is the instantaneous SSC. The amount of belowground biomass $B_b(x)$, modulated by a factor γ (2.5×10^{-3} m^3/kg) that accounts for compaction and decomposition processes, governs the rate of organic soil production by $Q_o(x) = \gamma B_b(x) f_i(z)$. The fitness function $f_i(z)$ ($0 \le f_i(z) \le 1$) describes how biomass productivity and the competitive abilities of species i vary as a function of elevation z (32, 36). We note that, although decomposition is accounted for in a simplified manner through a refractory fraction coefficient (embedded in γ), the value of this parameter is defined on the basis of observations (35). Deposition by sediment trapping is calculated as a power-law function of aboveground plant biomass $B_a(x)$ (37, 38). We assume here that three marsh species (representative of low-, middle-, and high-marsh vegetation) compete for space, each adapted to a particular elevation range relative to mean sea level. Marani et al. (32) have shown that the biogeomorphic evolution of a marsh under these assumptions leads to geomorphic and ecological patterns along the marsh transect that are consistent with observed ones (39, 40).

Results and Discussion

An elevated atmospheric CO_2 concentration increases aboveground and belowground biomass productivity, which, in turn, increases marsh accretion rates and resilience to RRSLR. Increased belowground productivity enhances soil organic production, whereas increased aboveground productivity boosts suspended sediment trapping by standing biomass. For a marsh adjacent to a tidal creek with SSC = 20 mg/L and a tidal amplitude of 0.5 m, the threshold beyond which partial marsh drowning is initiated increases from an RRSLR of 6.5 mm/y in current conditions to 7.5 mm/y for both the first quartile and median response to elevated atmospheric CO_2 (Fig. 1*A*). The third quartile of plant responses, which nearly doubles vegetation biomass, extends the threshold for partial drowning to 10.5 mm/y. The values of these drowning thresholds will vary in marshes across the globe, depending on local environmental factors (e.g., SSC, tidal amplitude), but the significant increase in marsh resilience resulting from CO_2 fertilization observed here has broad global implications.

Even before the onset of marsh submergence, the marsh transects from the current and elevated CO_2 (median response) scenarios under the same RRSLR exhibit different morphologies (e.g., see RRSLR = 6.5 mm/y, Fig. 1*B*); the average elevation of the marsh is lower for the current CO_2 concentration than in the elevated CO_2 case, and the plant species distribution is shifted toward low-lying and more flooding-tolerant species. The two transect morphologies are most different beyond the threshold RRSLR for drowning in the current CO_2 scenario but before partial drowning of the elevated CO_2 case (Fig. 1*C*). For RRSLR

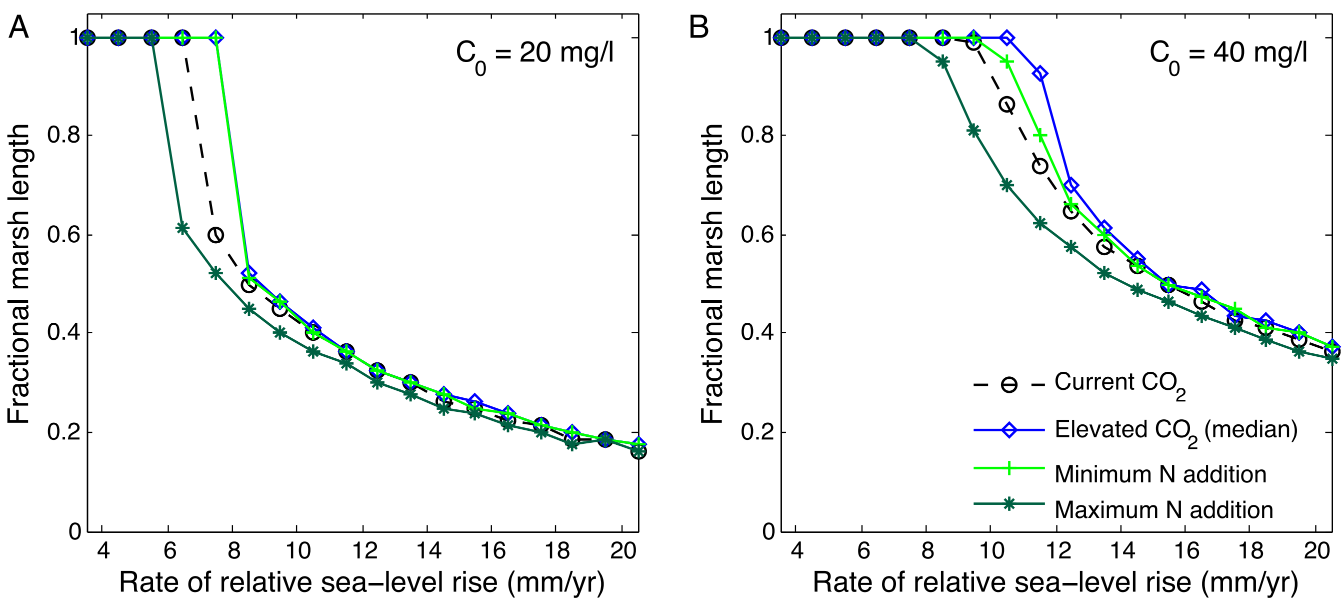

Fig. 2. Modeled marsh equilibrium profile lengths for changing forcings: varying CO_2, nitrogen addition, sediment delivery, and the rate of RRSLR. Fractional marsh lengths (equilibrium profile length divided by initial length, where a value of 1 represents no partial marsh drowning and 0 is completely submerged) as a function of RRSLR for two different CO_2 scenarios (current and median biomass response to elevated CO_2), two different nitrogen addition scenarios (minimum = 55.2 g N·m^{-2}·y^{-1} and maximum = 892.8 g N·m^{-2}·y^{-1}), and two different sediment delivery scenarios: (*A*) C_0 = 20 mg/L and (*B*) C_0 = 40 mg/L. Increased sediment supply increases the threshold for partial marsh profile drowning in all forcing scenarios.

beyond the elevated CO_2 drowning threshold (i.e., both marshes are becoming shorter due to the progressive submergence of their interior zones), the marsh morphologies under the current and elevated CO_2 concentrations converge toward similar profiles (Fig. 1*D*). In both cases, the lowered marsh elevation increases the duration of submergence, thus increasing the amount of inorganic sediment deposition (which only occurs during flooding periods). Hence, at high RRSLR, the profile is mostly maintained by inorganic sedimentation, which is almost independent of the atmospheric CO_2 concentration (except indirectly, through the effect of enhanced sediment trapping by increased standing plant biomass). This explains the observed weak dependence of marsh resilience on atmospheric CO_2 concentration at high RRSLR, and the similarity of the submerging marsh profiles for both CO_2 scenarios.

We also tested the possible effects of the end-of-century concurrent atmospheric CO_2 concentration and RRSLR values projected in the Representative Concentration Pathways (RCP) adopted in the latest Intergovernmental Panel on Climate Change (IPCC) report (41). We note that we are here assuming the local subsidence rate and mean sea-level changes to be negligible, and take RRSLR to be equal to global eustatic SLR. Under the environmental conditions examined here, our analyses show that, without the CO_2 fertilization effect, about 40% of the marsh will be lost under the mean RCP6 in 2100 (end-of-century RRSLR = 7.5 mm/y), whereas the marsh loss becomes 66% under the mean RCP8.5 (end-of-century RRSLR = 12 mm/y). No marsh loss occurs under the remaining RCPs (Table 1). First quartile, median, and third quartile plant biomass responses to increased atmospheric CO_2 show no marsh loss under the RCP2.6, RCP4.5, and RCP6 scenarios. The median and first quartile biomass responses in the RCP8.5 scenario result in 65% and 63% marsh loss, respectively. The third quartile CO_2 fertilization effect completely negates marsh loss in all RCP scenarios.

The absolute values of marsh loss in the RCP scenarios will vary depending on other forcings that differ across tidal environments. For example, in marshes with high sediment supply and inorganic sedimentation rates, the effects of CO_2 fertilization on marsh elevation and extent may be reduced (42). However, our results show that the CO_2 fertilization effect plays a central role in determining marsh resilience globally and that it can significantly offset marsh drowning induced by an accelerated RRSLR. Previous models of marsh dynamics under environmental change have neglected this effect (or heuristically assumed it is implicitly represented in temperature responses), and, although additional observational work is urgently needed to further improve our understanding and modeling representations, this mechanism is established as an important marsh response.

Suspended sediments play a fundamental role in marsh survival (43), and marsh responses to changing SSC serve to evaluate the relative importance of and the interplay with the CO_2 fertilization impacts. Doubling the available SSC (C_0) from 20 mg/L to 40 mg/L increases inorganic sedimentation rates and therefore the threshold RRSLR for partial drowning in all cases. The increase is about 1 mm/y (Fig. 2), which is of the same order as the increase in the threshold RRSLR caused by a doubling of CO_2 concentration (for the median fertilization response). In the "sediment-poor" case (C_0 = 20 mg/L), just beyond the threshold RRSLR for drowning, marsh loss is between 39% and 61% (Fig. 2*A*). Marsh loss occurs more gradually in the higher-SSC scenarios, where marsh extent is only reduced by 1–8% just beyond the initiation of partial drowning (Fig. 2*B*). Damming, the construction of levees, and other anthropogenic manipulations of upstream catchments have largely decreased sediment delivery to coastal environments (44). Our results confirm that this trend, likely to continue at the global scale, will significantly diminish marsh resilience to increasing RRSLR. In model experiments with nitrogen addition, elevated levels of nitrogen showed competing effects on marsh resilience (Fig. 2). A minimum nitrogen addition (55.2 g $N \cdot m^{-2} \cdot y^{-1}$) slightly increased the drowning initiation threshold RRSLR by 1 mm/y in both SSC cases, and the maximum addition scenario (892.8 g $N \cdot m^{-2} \cdot y^{-1}$) slightly decreased the drowning threshold (also by 1 mm/y for both SSC scenarios). Our results suggest that the impacts of increased nitrogen concentrations on marsh stability could be significant, but that they remain uncertain, due to the wide range of observed plant responses to nitrogen fertilization.

Our results emphasize that marsh responses to environmental change are spatially variable. Many empirical studies and field experiments (4, 12) have focused on measuring the effects of elevated CO_2 and nitrogen addition in single plots or chambers. Similarly, numerous modeling studies have used a point model framework to explore marsh dynamics (35, 45–48). These approaches made it possible to identify marsh response mechanisms and feedbacks but do not capture actual marsh responses as they unfold in time and space (32, 49, 50). In particular, point models cannot reproduce the observed marsh drowning dynamics, moving from the inner part of a marsh toward the creeks that feed it (51, 52), or the persistence of the marsh portion adjacent to the tidal creek (maintained by inorganic sedimentation) even at very high RRSLR, after a majority of the marsh has drowned. The CO_2 fertilization effect increases the lateral extent of marshes (as well as their average elevation), resulting in marshes that are more resilient to increasing RRSLR. In turn, more-expansive marshes provide a greater area for sequestering more carbon (45, 53) than those that are retreating and drowning. Consequently, the fertilization effect may also contribute to a stabilizing feedback within the climate system, where increasing biomass production and organic deposition consequently sequester greater amounts of CO_2. The marsh resilience evidenced by our results suggests that this feedback will be robust with respect to foreseeable values of the RRSLR.

Although higher levels of atmospheric CO_2 are inevitable (41), sediment delivery to the coast continues to decline globally (44). Elevated CO_2 may possibly partially balance the negative effects of land use change and damming, but reduced sediment supply is likely to remain the most serious threat to marsh survival.

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1. McKee K, Rogers K, Saintilan N (2012) Response of salt marsh and mangrove wetlands to changes in atmospheric CO_2, climate, and sea level. *Global Change and the Function and Distribution of Wetlands* (Springer, Dordrecht, The Netherlands), pp 63–96.
2. Cherry JA, McKee KL, Grace JB (2009) Elevated CO_2 enhances biological contributions to elevation change in coastal wetlands by offsetting stressors associated with sea-level rise. *J Ecol* 97(1):67–77.
3. Langley JA, McKee KL, Cahoon DR, Cherry JA, Megonigal JP (2009) Elevated CO_2 stimulates marsh elevation gain, counterbalancing sea-level rise. *Proc Natl Acad Sci USA* 106(15):6182–6186.
4. Morris J, Shaffer G, Nyman J (2013) Brinson review: Perspectives on the influence of nutrients on the sustainability of coastal wetlands. *Wetlands* 33(6):975–988.
5. Turner RE, et al. (2009) Salt marshes and eutrophication: An unsustainable outcome. *Limnol Oceanogr* 54(5):1634–1642.
6. Darby FA, Turner RE (2008) Below-and aboveground biomass of *Spartina alterniflora*: Response to nutrient addition in a Louisiana salt marsh. *Estuaries Coasts* 31(2): 326–334.
7. Curtis PS, Balduman LM, Drake BG, Whigham DF (1990) Elevated atmospheric CO_2 effects on belowground processes in C_3 and C_4 estuarine marsh communities. *Ecology* 71(5):2001–2006.
8. Curtis PS, Drake BG, Leadley PW, Arp WJ, Whigham DF (1989) Growth and senescence in plant communities exposed to elevated CO_2 concentrations on an estuarine marsh. *Oecologia* 78(1):20–26.
9. Drake BG (1992) A field-study of the effects of elevated CO_2 on ecosystem processes in a Chesapeake Bay wetland. *Aust J Bot* 40(5):579–595.

ENVIRONMENTAL SCIENCES

10. Erickson JE, Megonigal JP, Peresta G, Drake BG (2007) Salinity and sea level mediate elevated CO_2 effects on C_3–C_4 plant interactions and tissue nitrogen in a Chesapeake Bay tidal wetland. *Glob Change Biol* 13(1):202–215.
11. Henderson S, Hattersley P, Von Caemmerer S, Osmond C (1995) Are C_4 pathway plants threatened by global climatic change? *Ecophysiology of Photosynthesis* (Springer, Berlin), pp 529–549.
12. Adam Langley J, Mozdzer TJ, Shepard KA, Hagerty SB, Patrick Megonigal J (2013) Tidal marsh plant responses to elevated CO_2, nitrogen fertilization, and sea level rise. *Glob Change Biol* 19(5):1495–1503.
13. Lenssen G, Lamers J, Stroetenga M, Rozema J (1993) Interactive effects of atmospheric CO_2 enrichment, salinity and flooding on growth of C_3 (*Elymus athericus*) and C_4 (*Spartina anglica*) salt marsh species. *Vegetatio* 104(1):379–388.
14. Owensby CE, Ham J, Knapp A, Auen L (1999) Biomass production and species composition change in a tallgrass prairie ecosystem after long-term exposure to elevated atmospheric CO_2. *Glob Change Biol* 5(5):497–506.
15. Rozema J, et al. (1991) Effect of elevated atmospheric CO_2 on growth, photosynthesis and water relations of salt marsh grass species. *Aquat Bot* 39(1):45–55.
16. Ward J, Tissue DT, Thomas RB, Strain B (1999) Comparative responses of model C3 and C4 plants to drought in low and elevated CO_2. *Glob Change Biol* 5(8):857–867.
17. Langley JA, Megonigal JP (2010) Ecosystem response to elevated CO_2 levels limited by nitrogen-induced plant species shift. *Nature* 466(7302):96–99.
18. Rasse DP, Peresta G, Drake BG (2005) Seventeen years of elevated CO_2 exposure in a Chesapeake Bay Wetland: Sustained but contrasting responses of plant growth and CO_2 uptake. *Glob Change Biol* 11(3):369–377.
19. Wigand C, McKinney RA, Charpentier MA, Chintala MM, Thursby GB (2003) Relationships of nitrogen loadings, residential development, and physical characteristics with plant structure in New England salt marshes. *Estuaries* 26(6):1494–1504.
20. Graham SA, Mendelssohn IA (2010) Multiple levels of nitrogen applied to an oligohaline marsh identify a plant community response sequence to eutrophication. *Mar Ecol Prog Ser* 417:73–82.
21. Boyer KE, Fong P, Vance RR, Ambrose RF (2001) *Salicornia virginica* in a southern California salt marsh: Seasonal patterns and a nutrient-enrichment experiment. *Wetlands* 21(3):315–326.
22. Boyer KE, Zedler JB (1998) Effects of nitrogen additions on the vertical structure of a constructed cordgrass marsh. *Ecol Appl* 8(3):692–705.
23. Crain CM (2007) Shifting nutrient limitation and eutrophication effects in marsh vegetation across estuarine salinity gradients. *Estuaries Coasts* 30(1):26–34.
24. Deegan LA, et al. (2007) Susceptibility of salt marshes to nutrient enrichment and predator removal. *Ecol Appl* 17(sp5):S42–S63.
25. Gough L, Grace JB (1999) Effects of environmental change on plant species density: Comparing predictions with experiments. *Ecology* 80(3):882–890.
26. Loomis MJ, Craft CB (2010) Carbon sequestration and nutrient (nitrogen, phosphorus) accumulation in river-dominated tidal marshes, Georgia, USA. *Soil Sci Soc Am J* 74(3): 1028–1036.
27. McFarlin CR, Brewer JS, Buck TL, Pennings SC (2008) Impact of fertilization on a salt marsh food web in Georgia. *Estuaries Coasts* 31(2):313–325.
28. Pennings SC, Stanton LE, Brewer JS (2002) Nutrient effects on the composition of salt marsh plant communities along the southern Atlantic and Gulf coasts of the United States. *Estuaries* 25(6):1164–1173.
29. Ryan AB, Boyer KE (2012) Nitrogen further promotes a dominant salt marsh plant in an increasingly saline environment. *J Plant Ecol* 5(4):429–441.
30. Vivanco L, Irvine IC, Martiny JB (2015) Nonlinear responses in salt marsh functioning to increased nitrogen addition. *Ecology* 96(4):936–947.
31. Wigand C, Thursby GB, McKinney RA, Santos AF (2004) Response of *Spartina patens* to dissolved inorganic nutrient additions in the field. *J Coast Res* 45:134–149.
32. Marani M, Da Lio C, D'Alpaos A (2013) Vegetation engineers marsh morphology through multiple competing stable states. *Proc Natl Acad Sci USA* 110(9):3259–3263.
33. Donnelly JP, Bertness MD (2001) Rapid shoreward encroachment of salt marsh cordgrass in response to accelerated sea-level rise. *Proc Natl Acad Sci USA* 98(25): 14218–14223.
34. Mariotti G, Fagherazzi S (2010) A numerical model for the coupled long-term evolution of salt marshes and tidal flats. *J Geophys Res* 115(F1):F01004.
35. Marani M, D'Alpaos A, Lanzoni S, Carniello L, Rinaldo A (2007) Biologically-controlled multiple equilibria of tidal landforms and the fate of the Venice lagoon. *Geophys Res Lett* 34(11):L11402.
36. Morris JT (2006) Competition among marsh macrophytes by means of geomorphological displacement in the intertidal zone. *Estuar Coast Shelf Sci* 69(3):395–402.
37. D'Alpaos A, Lanzoni S, Marani M, Rinaldo A (2007) Landscape evolution in tidal embayments: Modeling the interplay of erosion, sedimentation, and vegetation dynamics. *J Geophys Res* 112(F1):F01008.
38. Mudd SM, D'Alpaos A, Morris JT (2010) How does vegetation affect sedimentation on tidal marshes? Investigating particle capture and hydrodynamic controls on biologically mediated sedimentation. *J Geophys Res* 115(F3):F03029.
39. Marani M, Zillio T, Belluco E, Silvestri S, Maritan A (2006) Non-neutral vegetation dynamics. *PLoS One* 1(1):e78.
40. Silvestri S, Defina A, Marani M (2005) Tidal regime, salinity and salt marsh plant zonation. *Estuar Coast Shelf Sci* 62(1):119–130.
41. IPCC (2013) *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (Cambridge Univ Press, CambridgeUK).
42. Mudd SM, Howell SM, Morris JT (2009) Impact of dynamic feedbacks between sedimentation, sea-level rise, and biomass production on near-surface marsh stratigraphy and carbon accumulation. *Estuar Coast Shelf Sci* 82(3):377–389.
43. Kirwan ML, Murray AB, Donnelly JP, Corbett DR (2011) Rapid wetland expansion during European settlement and its implication for marsh survival under modern sediment delivery rates. *Geology* 39(5):507–510.
44. Syvitski JP, Vörösmarty CJ, Kettner AJ, Green P (2005) Impact of humans on the flux of terrestrial sediment to the global coastal ocean. *Science* 308(5720):376–380.
45. Kirwan ML, Mudd SM (2012) Response of salt-marsh carbon accumulation to climate change. *Nature* 489(7417):550–553.
46. Morris JT, Sundareshwar P, Nietch CT, Kjerfve B, Cahoon DR (2002) Responses of coastal wetlands to rising sea level. *Ecology* 83(10):2869–2877.
47. D'Alpaos A, Mudd S, Carniello L (2011) Dynamic response of marshes to perturbations in suspended sediment concentrations and rates of relative sea level rise. *J Geophys Res* 116(F4):F04020.
48. Fagherazzi S, et al. (2012) Numerical models of salt marsh evolution: Ecological, geomorphic, and climatic factors. *Rev Geophys* 50(1):RG1002.
49. Da Lio C, D'Alpaos A, Marani M (2013) The secret gardener: Vegetation and the emergence of biogeomorphic patterns in tidal environments. *Philos Trans R Soc London A* 371(2004):20120367.
50. D'Alpaos A, Marani M (2015) Reading the signatures of biologic-geomorphic feedbacks in salt-marsh landscapes. *Adv Water Resour*, 10.1016/j.advwatres.2015.09.004.
51. DeLaune R, Nyman J, Patrick W, Jr (1994) Peat collapse, ponding and wetland loss in a rapidly submerging coastal marsh. *J Coast Res* 10(4):1021–1030.
52. Erwin RM, Sanders GM, Prosser DJ (2004) Changes in lagoonal marsh morphology at selected northeastern Atlantic coast sites of significance to migratory waterbirds. *Wetlands* 24(4):891–903.
53. Mcleod E, et al. (2011) A blueprint for blue carbon: Toward an improved understanding of the role of vegetated coastal habitats in sequestering CO_2. *Front Ecol Environ* 9(10):552–560.
54. Buresh RJ, DeLaune RD, Patrick WH (1980) Nitrogen and phosphorus distribution and utilization by *Spartina alterniflora* in a Louisiana Gulf Coast marsh. *Estuaries* 3(2): 111–121.
55. Patrick W, DeLaune R (1976) Nitrogen and phosphorus utilization by *Spartina alterniflora* in a salt marsh in Barataria Bay, Louisiana. *Estuar Coast Mar Sci* 4(1):59–64.
56. Sullivan MJ, Daiber FC (1974) Response in production of cord grass, *Spartina alterniflora*, to inorganic nitrogen and phosphorus fertilizer. *Chesap Sci* 15(2):121–123.
57. Gallagher JL (1975) Effect of an ammonium nitrate pulse on the growth and elemental composition of natural stands of *Spartina alterniflora* and *Juncus roemerianus*. *Am J Bot* 62(6):644–648.
58. Covin JD, Zedler JB (1988) Nitrogen effects on *Spartina foliosa* and *Salicornia virginica* in the salt marsh at Tijuana Estuary, California. *Wetlands* 8(1):51–65.
59. Van Wijnen H, Bakker J (1999) Nitrogen and phosphorus limitation in a coastal barrier salt marsh: The implications for vegetation succession. *J Ecol* 87(2):265–272.
60. Tyler AC, Lambrinos JG, Grosholz ED (2007) Nitrogen inputs promote the spread of an invasive marsh grass. *Ecol Appl* 17(7):1886–1898.
61. Valiela I, Teal JM, Persson NY (1976) Production and dynamics of experimentally enriched salt marsh vegetation: Belowground biomass. *Limnol Oceanogr* 21(2): 245–252.
62. Gratton C, Denno RF (2003) Inter-year carryover effects of a nutrient pulse on *Spartina* plants, herbivores, and natural enemies. *Ecology* 84(10):2692–2707.
63. Traut BH (2005) Effects of nitrogen addition and salt grass (*Distichlis spicata*) upon high salt marsh vegetation in northern California, USA. *Estuaries* 28(2):286–295.