

Manuscript details:

Manuscript Number: NCLIM-18020326B

Title: Nitrogen status regulates morphological adaptation of marsh plants to elevated CO₂

11 words, 82 characters

Abstract: 195 words

Length of the text: 10 paragraphs, 1944 words

Methods: 960 words

Number of references: 38

Figures and Tables: 1 Table, 3 Figures

Size: Table 1: 16 kb, Figure 1: 50 kb, Figure 2: 80 kb, Figure3: 40 kb

Appendix: Appendix 1 and Appendix 2

Data Availability:

Morphometric and derived biomass data from the experiments are posted on the Global Change Research Wetland website (<http://serc.si.edu/gcrew/data>) and all data are available from the corresponding authors upon request.

1 **Nitrogen status regulates morphological adaptation of marsh plants to elevated CO₂**

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9 **Coastal wetlands provide valuable ecosystem services that are increasingly threatened by**
10 **anthropogenic activities¹. Atmospheric carbon dioxide (CO₂) concentration has increased**
11 **from 280 to 404 ppm since the industrial revolution, and is projected to exceed 900 ppm by**
12 **2100². In terrestrial ecosystems, elevated CO₂ typically stimulates C₃ plant photosynthesis**
13 **and primary productivity leading to an increase in plant size³. However, compared to woody**
14 **plants or crops⁴, the morphological responses of clonal non-woody plants to elevated CO₂**
15 **have been less well-studied. We show that 30 years of experimental CO₂ enrichment in a**
16 **brackish marsh increased primary productivity and stem density, but decreased the stem**
17 **diameter and height of the dominant clonal species *Schoenoplectus americanus*. Smaller,**
18 **denser stems were associated with the expansion of roots and rhizomes to alleviate nitrogen**
19 **(N) limitation as evidenced by high N immobilization in live tissue and litter, high tissue C:N,**
20 **and low available porewater N. Changes in morphology and tissue chemistry induced by**
21 **elevated CO₂ were reversed by N addition. We demonstrate that morphological responses to**
22 **CO₂ and N supply in a clonal plant species influences the capacity of marshes to gain elevation**
23 **at rates that keep pace with rising sea levels.**

24 Terrestrial plants are experiencing the highest atmospheric CO₂ concentration in the past
25 800,000 years⁵. The stimulation of carbon (C) fixation by elevated CO₂ -- the CO₂ fertilization
26 effect -- is well documented⁶. Increases in leaf-level C uptake rates are often accompanied by
27 changes in plant morphology or morphometric sizes, such as increased height, stem diameter,
28 leaf area index, leaf number, and root volume^{7, 8, 9, 10}. These morphometric changes are widely
29 observed to influence competitive dynamics^{11, 12}, with implications for ecosystem structure and
30 function.

31 Resource availability regulates the effect of elevated CO₂ on total biomass production but
32 can also influence changes in plant size and patterns of biomass allocation. Elevated CO₂-
33 induced changes in plant morphology are poorly understood compared to changes in total
34 biomass, and morphological changes are highly variable along environmental gradients and
35 between plant functional groups, reflecting species-specific strategies for resource acquisition^{7,}
36 ⁹. For instance, plant species can overcome N limitation caused by CO₂ fertilization in low-N
37 environments if they possess traits to mine and recycle N through shared underground
38 networks of ectomycorrhizae¹³, illustrating the importance of understanding how resource
39 acquisition influences plant responses to elevated CO₂. Similarly, clonal plants employ shared
40 underground networks of roots and rhizomes to exploit heterogeneous soil resources, affording
41 a competitive advantage in resource-poor environments¹⁴. Clonal plants are ubiquitous,
42 occurring in 10 out of 11 classes of vascular plants, and are an important component of many
43 ecosystems¹⁵; yet, their morphological responses to elevated CO₂ are understudied compared
44 to other functional groups such as non-clonal trees, shrubs, herbs, and crops. Clonal
45 architecture has important implications for biomass allocation and resource acquisition strategy

46 that can propagate into ecosystem level responses to global change. For example, growth
47 allocation to rhizomes and ramets may influence stem density and decrease interannual
48 variation in plant growth by storing resources when conditions are favorable and remobilizing
49 them when conditions are adverse¹⁴.

50 Our objective was to examine the morphological responses of a clonal marsh plant species
51 to elevated CO₂ and N addition using long-term data from two field experiments in a tidal
52 marsh on the Chesapeake Bay. The native plant community is dominated by the perennial C₃
53 sedge *Schoenoplectus americanus* and two co-dominant C₄ grasses, *Spartina patens* and
54 *Distichlis spicata*. *Experiment 1* began in 1987 and consists of open-top chambers ventilated
55 with either ambient air or CO₂ concentrations elevated to 700-800 ppm. *Experiment 2* began in
56 2006 to investigate interactions between elevated CO₂ and N addition with 4 treatments:
57 ambient CO₂, ambient CO₂ + N, elevated CO₂, and elevated CO₂ + N. In both experiments, we
58 made annual measurements of stem morphology (height, width, and density), stem biomass,
59 belowground productivity, tissue chemistry, porewater ammonium (NH₄⁺, started in 2002 in
60 *Experiment 1*), and soil surface elevation change. Morphometric data were collected only for *S.*
61 *americanus*; the morphometric responses of C₄ grasses were not examined because the growth
62 form of these species does not lend itself to such measurements¹⁶.

63 Elevated CO₂ increased sedge total biomass by an average of 20% over the control in
64 *Experiment 1*. The CO₂-driven increase in belowground biomass productivity (34% ± 7) was
65 larger than the increase in aboveground biomass (17% ± 4), resulting in a 16% ± 6 increase in
66 the below:above biomass ratio (Fig. 1a). Simultaneously, the density of stems increased 51% ± 6

67 (Fig. 2a, Appendix 1, Table S1) and the biomass of individual sedge stems decreased $16\% \pm 1$
68 (Fig. 2b), corresponding to a 5% decline in stem height and a 10% decline in diameter (Fig. 2c,
69 d). Moreover, stem density and rhizome biomass were positively correlated ($R^2=0.30$, $P <$
70 0.0001 , Fig. S1), suggesting that the CO_2 -induced increase in belowground allocation was
71 expressed through the clonal architecture of the sedge.

72 Plants shift biomass allocation between roots and shoots to optimize resource capture and
73 use, with allocation to photosynthetic aboveground biomass for CO_2 uptake, and to
74 belowground biomass for nutrient uptake¹⁷. Salt and brackish systems tend to be N limited
75 because the phosphorus that would be bound to iron in freshwater systems is liberated by the
76 sulfates in seawater¹⁸. N limitation is known to constrain the CO_2 fertilization effect^{13, 19, 20}, and
77 in our experiments elevated CO_2 induced the classic symptoms of progressive N limitation in
78 this coastal wetland ecosystem¹⁹. Elevated CO_2 plots in *Experiment 1* had more N sequestered
79 in plant biomass (i.e., 5% increase in shoot N and 12% increase in root N) and litter (21%
80 increment, Fig. 1a), and less plant-available inorganic soil N (i.e., 47% lower porewater $[\text{NH}_4^+]$;
81 $[\text{NO}_3^-]$ was below detection, Fig. 1a, Fig. S2a), implying soil N depletion in the rooting zone.
82 Elevated CO_2 increased the C:N ratio in sedge shoot, root, and rhizome biomass by 18%, 10%,
83 and 23%, respectively (Fig. 1a), consistent with a CO_2 -induced increase in N use efficiency²¹.
84 Preferential allocation of photosynthate to roots and the rhizome network helps alleviate N
85 depletion by expanding the surface area for N acquisition²². In this clonal species, rhizome
86 extension leads to increased tiller recruitment and ultimately higher stem density²³.

87 *Experiment 2* provides an experimental test of inferences about CO₂-induced N limitation
88 from *Experiment 1*. In *Experiment 2*, elevated CO₂ alone produced the same response in sedge
89 density and size observed *Experiment 1*, but the effect was absent when elevated CO₂ was
90 crossed with N addition, in which case individual *S. americanus* stem size increased (Fig. 1b). As
91 in *Experiment 1*, the CO₂-only treatment decreased inorganic N by 48% ± 4 (Fig. 1b, Fig. S2b),
92 while adding N to elevated CO₂ plots increased porewater inorganic N by 5% ± 9 higher than
93 that in ambient plots. Moreover, the N-only treatment resulted in a 15% decrease in
94 belowground productivity, indicating reduced plants biomass allocation to root systems for N
95 uptake under N enrichment.

96 In contrast to the common result that plant size increases under elevated CO₂, we
97 observed that elevated CO₂ caused a clonal plant to produce smaller individual stems at higher
98 density. While “shrinking stems” in response to elevated CO₂ have been observed in other C₃
99 grasses⁸, we clearly demonstrate that this is an indirect response to N deficiency in a clonal
100 plant species through manipulative experiments. We propose a conceptual framework for the
101 responses of clonal plant growth to CO₂ enrichment (Fig. 3). Elevated CO₂-stimulation of plant
102 productivity (clonal and non-clonal) leads to soil N deficiency because the increase in N demand
103 is not satisfied by a combination of increased N uptake and shifts in plant C:N ratio. In most
104 plant functional groups, this shift leads to an increase in growth allocation to belowground
105 structures and increased N uptake without necessarily changing plant density. However, in
106 clonal species, increasing belowground growth generates a more extensive rhizome system,
107 more tiller-recruitment of stems, and increased stem density. Because the increase in stem
108 density is not entirely compensated by higher ecosystem NPP, individual plant stems are

109 smaller. Because shrinking stems coincide with N depletion and can be reversed by N
110 enrichment (Fig. 1b), we conclude that the response of clonal plant morphology to elevated CO₂
111 is regulated by soil N limitation (Fig. 3, Fig. S3) and suggest that shrinking stem sizes can be used
112 as evidence of N limitation in clonal plant communities. Such responses to CO₂-induced N
113 limitation are observed in a variety of terrestrial ecosystems where clonal species occur, but the
114 consequences of allocation shifts for plant morphology, stand structure, and ecosystem
115 function have been largely overlooked.

116 The phenotypic plasticity of marsh plants in response to elevated CO₂ has an important
117 impact on the survival of coastal wetlands and their ecosystem services. The effectiveness of
118 wetland vegetation in dissipating storm energy is tied to the density and morphology of stems,
119 and their effect on frontal area (i.e., the total cross-sectional area of stems perpendicular to
120 flow velocity)^{24, 25}. We calculated changes in frontal area in response to elevated CO₂ in
121 *Experiment 1* and *2* and found significant increases in frontal area due to increased stem
122 density (Table 1). The analysis indicates that elevated CO₂ may enhance the value of marshes as
123 natural infrastructure for coastal protection through a mechanism tied to clonal traits²⁴. These
124 morphological changes in response to elevated CO₂ also have important implications for the
125 habitats of wetland birds, nekton and benthic invertebrates^{26, 27, 28}, and they influence key
126 ecosystem processes such as soil formation, C storage, and nutrient retention²⁹.

127 Perhaps most importantly, changes in root and shoot morphology directly influence the
128 capacity of coastal wetlands to build elevation in response to rising sea level^{30, 31}. At our high
129 marsh site in the Chesapeake Bay, 69% of the species are clonal, and clonal plants occupy 68%

130 of marsh area. Tradeoffs between shoot and root productivity under elevated CO₂ potentially
131 alter the balance between the contributions of surface mineral sedimentation and subsurface
132 root expansion to elevation gain¹. Long-term field measurements indicate that elevated CO₂-
133 enhanced belowground production increased elevation gain by 1.5 mm yr⁻¹ via subsurface
134 expansion³². As sea level rises and plants are flooded more frequently, aboveground biomass
135 and stem morphology also influence elevation gain by enhancing the settling of suspended
136 mineral sediments on the marsh surface^{33, 34, 35}. We explored the effects of changes in stem
137 structure on potential mineral deposition using a previously published model^{35, 36} to simulate
138 increased flooding 25 years in the future (~8 cm of increased flooding, Appendix 2). Modeled
139 surface sedimentation was enhanced an additional 0.7-1.5 mm yr⁻¹ by elevated CO₂ and the
140 combination of elevated CO₂ and N (Table 1), suggesting an aboveground mechanism for
141 increasing the resilience of C₃ marsh ecosystems to sea level rise. Feedbacks between
142 aboveground biomass and mineral sedimentation become stronger with increasing flooding
143 duration, and suspended sediment supply^{1, 35}, suggesting that the positive effects of elevated
144 CO₂ on elevation gain may amplify under these conditions. Such responses will vary with factors
145 such as suspended sediment supply, watershed N loading, plant traits, and other site-specific
146 characteristics. For example, plants responded to the combination of elevated CO₂ and N in
147 *Experiment 2* with an increase in stem size, density, aboveground biomass, and belowground
148 productivity compared to the ambient treatment, which translated into both higher modeled
149 surface accretion and subsurface expansion (Table 1). However, N can also cause root biomass
150 to decline³⁷, in which case elevation gains from increased surface accretion may be offset by
151 lower subsurface expansion. Process-based models informed by observations and experiments

152 are required to integrate the complex feedbacks that ultimately govern elevation gain. Plant
153 traits such as clonal architecture that govern density, height, root allocation, and other
154 morphological responses to global change have important ecosystem consequences that are
155 presently missing from forecast models.

156 We showed that elevated CO₂ and N addition elicit significant changes in the structure and
157 function of coastal marshes that arise from tractable plant traits such as clonal architecture.
158 The 30-year data set presented here raises additional questions that are outside the scope of
159 the present study. Firstly, Rasse et al. summarized the data from *Experiment 1* after 17 years
160 and found that *S. americanus* density in the C₃ community increased by 128% compared to 51%
161 in the present study³⁸ (Fig. 2a). Our results demonstrate that the direction of the density
162 responses remained the same after an additional 13 years CO₂ enrichment, but the amount of
163 stimulation has declined due to resource limitation, interactions with other variables such as
164 sea level rise, or other factors. Secondly, the stem biomass and density responses in the C₃
165 community changed over time (Table S1), perhaps with changes in salinity, NH₄⁺ discharges
166 from the Rhode River watershed, or other factors that require additional exploration (Table S2).
167 Thus, future studies must consider additional important factors such as warming temperatures,
168 changing precipitation and hydrologic extremes, changing salinity and inundation regimes, and
169 invasive species.

170

171 Supplementary Information

172 Appendix 1 and Appendix 2

173 Acknowledgements

174 We thank Bert Drake for conceiving the original study and leading it until 2010. We thank Gary
175 Peresta, James Duls, Andrew Peresta, Dennis Whigham, Thomas Jordan, Charles Gallegos, Jay
176 O'Neill, Chunwu Zhu, Hui Guo and the hundreds of volunteers who helped collect data during
177 annual censuses. This research was supported by the DOE-TES program (award DE-SC0008339),
178 the NSF-LTREB program (awards DEB-0950080 and DEB-1457100), the Maryland Sea Grant
179 program (award SA7528114-WW), and the Thousand Young Talents Program of Yunnan
180 Province.

181

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275

276 **Author Contributions** The analysis was conceived by M.L. and J.P.M. The ongoing operation of the
277 experiments were conducted by J.P.M. and J.A.L. The data were compiled and analyzed by M.L.
278 Accretion modelling was performed by E.H. All authors contributed to writing the paper.

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280 authors declare no competing financial interests. Correspondence and requests for materials should be
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282 Methods

283 The open top chamber (OTC) CO₂ enrichment experiment, initiated in 1986, is located at
284 Kirkpatrick marsh (38°53'N, 76°33'W), a 23-ha brackish salt marsh on the Rhode River estuary in
285 Chesapeake Bay, on the eastern coast of the United States. This common Chesapeake Bay high
286 marsh ecosystem is dominated by a perennial C₃ sedge *Schoenoplectus americanus*, and two
287 co-occurring C₄ grasses *Spartina patens* and *Distichlis spicata*. Mean annual temperature is 14.1
288 °C and mean annual precipitation is 948 mm. Mean tidal range is approximately 40 cm, and the
289 marsh platform is about 18 cm (in the C₃ plots) and 40 cm (in the C₄ plots) above daily mean low
290 water level. Water level is higher than mean marsh elevation about 25% of the time. The soils
291 contain approximately 80% organic matter (i.e. peat) to a depth of 5 m. The morphometric data
292 used in our analysis was available only for C₃ sedges; morphometric data are not collected on C₄
293 grasses in these long-term experiments because of their small stem diameter and high density
294 (Appendix 1).

295 *Experiment 1:* Three plant communities were distinguished in the marsh, a C₃ community
296 dominated by *S. americanus*, a C₄ community consisting of *S. patens* and *D. spicata*, and a
297 mixed C₃/C₄ community. OTC was used to increase the CO₂ concentration around the plants in
298 each of the three communities. Ten circular chambers of 80 cm diameter and 100 cm height
299 were placed in each community. In five of the chambers, atmospheric [CO₂] was elevated to
300 340 μl CO₂ l⁻¹ above the ambient CO₂ concentration (about 340 μl CO₂ l⁻¹ at the beginning of the
301 study). The CO₂ concentration in the other five chambers was ventilated with ambient air as the
302 ambient treatment. To determine a possible OTC effect on plant growth, five outside chamber

303 control sites in each community were compared with the ambient CO₂ chambers. CO₂ exposure
304 began each year when the plants emerged in the spring and continued 24h a day through
305 autumn following total senescence. A survey of all plots was conducted in 1986 before initiation
306 of the treatments and showed no significant differences in plant biomass assigned to the three
307 treatments in each community.

308 *Experiment 2:* Twenty octagonal OTCs of 200 cm height and 150 cm diameter were established
309 adjacent to the site of *Experiment 1* in 2006. OTCs were randomly assigned to one of four
310 treatment groups (n=5): ambient CO₂, ambient CO₂ + N, elevated CO₂, and elevated CO₂ + N.
311 CO₂ treatment was consistent with *Experiment 1*. N was added by spraying NH₄Cl monthly from
312 May to September each year (total 25 g N m⁻² year⁻¹).

313 Total height, green height and half height diameter of each C₃ sedge stem were measured and
314 stem density was counted in the plots each year. The dry mass of individual stems was
315 determined using an allometric equation based on destructively harvested samples¹⁶, and the
316 resulting mean biomass was multiplied by the stem density to estimate aboveground biomass.
317 Belowground plant productivity was estimated each year by three root ingrowth cores in each
318 plot. Nine porewater wells were placed in each chamber with three depths: 15, 30 and 75 cm.
319 Porewater was sampled and NH₄⁺ concentration was analyzed approximately monthly during
320 the growing season. In these anaerobic marsh soils, porewater NO₃⁻ is typically below detection
321 limits and does not contribute substantially to soil available N.

322 In this study, we calculated the response ratio to reflect the response of plant and porewater N
323 to elevated CO₂. Response ratio is defined as the ratio of the mean value of a given variable in

324 the treatment group (elevated CO₂ or elevated CO₂ plus N addition) to that in the control
325 group. The ratio for each year was calculated from the means of replicate plots (generally n=5)
326 in each treatment. The annual ratios were then averaged to reflect the treatment effect across
327 the 30-year (*Experiment 1*) or 11 year (*Experiment 2*) record. Repeated measures using a mixed
328 effects model was used to test for significant differences in stem biomass, height, diameter,
329 and densities between the elevated CO₂ and ambient CO₂ chambers in SAS program (version
330 9.0). A discrete autoregressive correlation model was conducted to test time effects. The
331 environmental and climate impact was examined with correlations between C₃ sedge
332 aboveground biomass and annualized environmental factors using Pearson's r statistic. Figures
333 and linear regression results were conducted using SigmaPlot (version 10.0, SPSS Inc., Chicago,
334 IL, USA).

335 We modeled changes in potential mineral accretion using a previously published model of
336 marsh vertical accretion that takes into account the height, diameter, and density of marsh
337 vegetation^{35, 36}. We used treatment-specific relationships between aboveground biomass and
338 stem structure (density, diameter, and height) from *Experiments 1 and 2*. Because mineral
339 accretion rates at this high elevation marsh are presently limited by very infrequent surface
340 flooding, we modeled the effect of biomass and stem structure on mineral accretion rates for a
341 future marsh that is lower elevation and more frequently flooded due to accelerated sea level
342 rise. Specifically, model experiments used a lower elevation of Kirkpatrick Marsh (0.1 m above
343 MSL), which is approximately 0.08 m below the current elevation of *Experiments 1 and 2*, to
344 simulate an increase in inundation due to sea level rise (25 years at the current 3.4 mm yr⁻¹)
345 where surface accretion would be a significant contribution to vertical change. All other

346 parameters reflect current conditions (suspended sediment = 25 mg L⁻¹, 44 cm tidal amplitude)
347 or original model parameters used by Mudd et al. 2010. Finally, we calculated frontal area (λ)
348 as a proxy for the potential of vegetation to disperse storm energy:

349
$$\lambda = \frac{whn}{A}$$

350 where w and h are the plot-mean stem width and height, n is the number of stems per plot,
351 and A is the plot area.

Table 1. Treatment effects on mean frontal area per unit volume (m^{-1}), belowground organic accretion (mm yr^{-1} , from Pastore et al. 2017), total belowground productivity ($\text{g m}^{-2} \text{yr}^{-1}$), stem density (shoot m^{-2}), aboveground biomass (g m^{-2}), and modeled aboveground mineral accretion (mm yr^{-1}) for *Experiments 1* and 2. Means \pm s.e.m. with the same letter in the same column and experiment are not significantly different from one another (A, B for *Experiments 1* and a, b, c for *Experiments 2*).

| | Frontal Area | Measured Belowground Organic Accretion* | Belowground productivity | Stem density | Aboveground Biomass | Modeled Aboveground Mineral Accretion |
|---------------------|--------------------------|--|-----------------------------|-----------------|------------------------|--|
| <i>Experiment 1</i> | | | | | | |
| Ambient | 2.2 (0.2) ^A | N/A | 269 (21) | 538 (25) | 497 (33) | 4.5 (0.1) ^A |
| CO ₂ | 2.4 (0.2) ^B | N/A | 349 (28) | 784 (30) | 564 (33) | 5.7 (0.1) ^B |
| <i>Experiment 2</i> | | | | | | |
| Ambient | 2.4 (0.2) ^a | 0.46 (0.3) | 143 (23) | 527 (23) | 587 (52) | 4.2 (0.1) ^a |
| CO ₂ | 2.6 (0.2) ^{a,b} | 1.84 (0.4) | 228 (25) | 598 (30) | 645 (66) | 4.9 (0.1) ^b |
| CO ₂ xN | 3.2 (0.3) ^b | 1.70 (0.6) | 187 (35) | 633 (31) | 803 (83) | 5.7 (0.1) ^c |
| N | 2.3 (0.2) ^a | 1.81 (0.5) | 110 (15) | 503 (28) | 555 (60) | 4.4 (0.1) ^a |

*Pastore et al. 2017

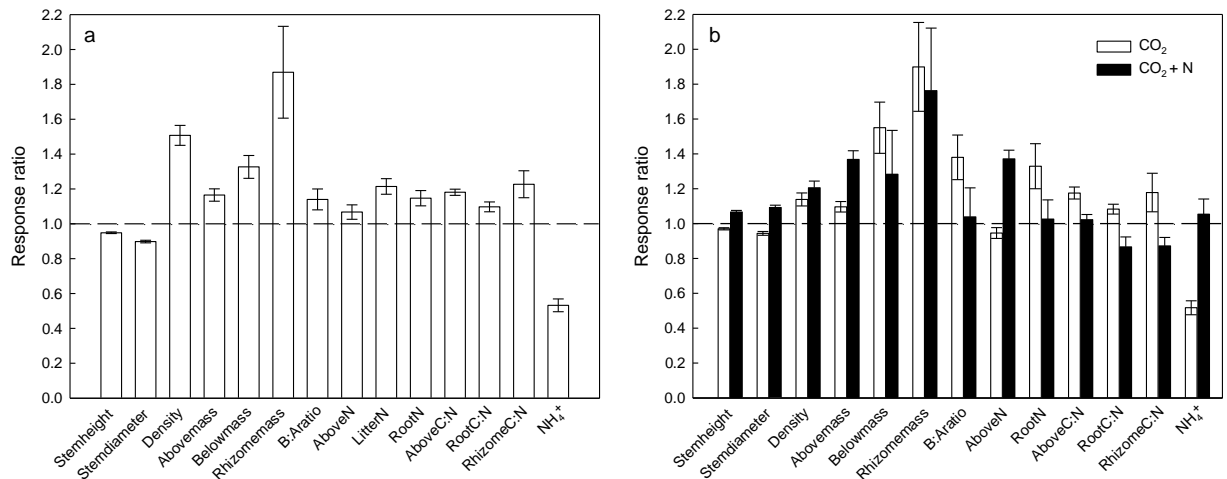


Figure 1. Plant and porewater N response ratios to elevated CO₂ (open bars) and elevated CO₂ plus N addition (filled bars) in *Experiment 1* (a) and *Experiment 2* (b). Each bar is the mean (\pm s.e.m.) response ratio (Elevated/Ambient) across all years in the record. The ratio for each year was calculated from the means of replicate plots (generally n=5) in each treatment. Horizontal dash lines are drawn at response ratio=1 (i.e. no response). Bar labels and units: Stemheight=individual stem height (cm), Stemdiameter=individual stem diameter (mm), Density=stem density (stems m⁻²), Abovemass=aboveground biomass (g m⁻²), Belowmass=total belowground productivity (g m⁻² yr⁻¹), Rhizomemass=rhizome productivity (g m⁻² yr⁻¹), B:Aratio=belowground:above ground mass ratio, AboveN=above ground N content (g N m⁻²), LitterN=litter N content (g m⁻²), RootN= root N content (g m⁻²), AboveC:N=aboveground C:N ratio, RootC:N=root C:N ratio, RhizomeC:N=rhizome C:N ratio, NH₄⁺=pore water NH₄⁺ concentration (μ mol L⁻¹).

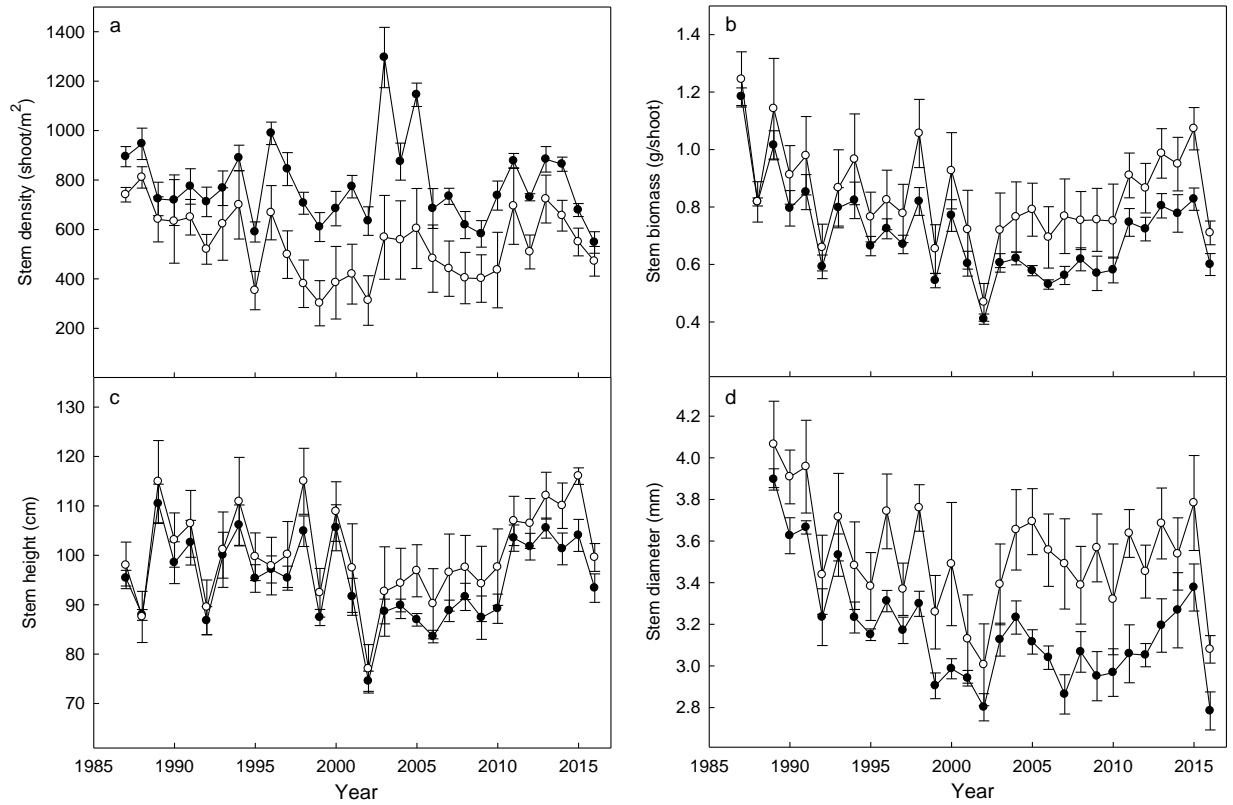


Figure 2. Elevated CO₂ responses of individual stem of *S. americanus* in the C₃ community of *Experiment 1* from 1987 to 2016. The mean \pm s.e.m. (n=5 replicate plots) of stem density (a), stem biomass (b), stem height (c), and stem diameter (d) are shown separately for ambient CO₂ (open circles) and elevated CO₂ chambers (filled circles).

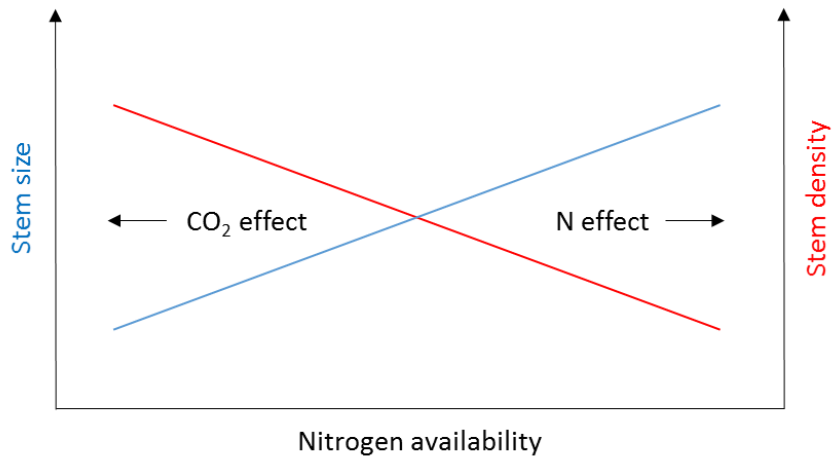


Figure 3. A conceptual framework for the responses of clonal plant aboveground growth pattern to CO₂ enrichment and nitrogen availability. The “←” symbol indicates that CO₂ enrichment of C₃ species causes plant N demand to increase and soil N availability to decline. Clonal species respond to increased N limitation by producing smaller individual stems (blue line) at a higher density (red line). N enrichment (→) relieves N limitation with the opposite response.

1 **Supplementary Methods**

2 Following previous models of saltmarsh vertical accretion (e.g. Fagherazzi et al., 2012),
3 sedimentation is a product of mineral sediment deposited on the marsh surface via sediment
4 capture (q_c) and settling (q_s), divided by the density of the marsh soil formed (ρ_m):

$$5 \quad dz/dt = -R + \frac{[q_s(z, L) + q_t(z, L)]}{\rho_m}$$

6 where ρ_m is calculated from an empirical relationship between organic content and density in
7 marsh soils (Morris et al. 2016). L is the aboveground biomass (g m^{-2}) which is modulated by
8 approximating monthly biomass using a sinusoidal curve that varies between 0 in the winter
9 and maximum L in the summer. Following Morris et al. (2002), L is also a quadratic function
10 of D (D is instantaneous water depth below high tide). Settling (q_s) is the product of the
11 sediment effective settling velocity (w_e) and the suspended sediment concentration $C(z, L, t)$,
12 integrated over the tidal cycle. Settling velocity was parameterized following Mudd et al. (2010)
13 as a balance between increases in w_e driven by vegetative drag, and reductions in w_e due to
14 the generation of turbulent kinetic energy and upward velocity by vegetation structure. The
15 relationship between L and q_s is parameterized using empirical data from each experiment
16 and treatment group to calculate projected plant area per unit volume, a_c (m^{-1}) (Nepf 2004),
17 as $a_c = d_c * n_c$ where d_c is the diameter (m) of stems and n_s is the number of stems per
18 unit ground area (m^{-2}). Alpha and β are the coefficient and exponent, respectively, of the
19 power law describing the relationship between a_c and L . Mu and ϕ are the coefficient and
20 exponent, respectively, of the power law describing the relationship between d_c and biomass.

$$21 \quad a_c = \alpha L^\beta$$

22
$$d_c = \mu L^\gamma$$

23 Trapping (q_t) is proportional to C , d_s , density (n_c), and height (h_c) of stems on the marsh
24 surface (D'Alpaos et al. 2007). We use the formulation of Palmer et al. (2004) to calculate
25 trapping as:

26
$$q_t = C U \epsilon d_c n_c \min[h_c, D]$$

27 where D is instantaneous water depth below high tide and d_c , n_c , and h_c stem height. Stem
28 density and h_c are related to L via empirically derived power-law functions for each
29 experiment and treatment.

30
$$h_c = \delta L^\phi$$

31
$$d_c = \varphi L^\sigma$$

32 Particle capture efficiency ϵ , is calculated as:

33
$$\epsilon = \alpha_\epsilon \left(\frac{U d_c}{\nu} \right)^{\beta_\epsilon} \left(\frac{d_p}{d_c} \right)^{\gamma_\epsilon}$$

34 where α_ϵ , β_ϵ & γ_ϵ are empirical coefficients (0.224, 0.718 & 2.08; Palmer et al. 2004), ν is
35 the kinematic viscosity of water ($10^{-6} \text{ m}^2 \text{ s}^{-1}$) and d_p is particle diameter (2×10^{-4} ; Mudd et al.
36 2010).

37 It should be noted that the Kirkpatrick marsh site is currently dominated by belowground
38 productivity because it is infrequently flooded. However, the importance of mineral sediment
39 deposition should increase in the future because deposition rates typically increase with
40 flooding duration and the rate of sea level rise (Friedrichs and Perry, 2001; Kirwan et al., 2010).
41 For instance, the relative mean sea level measured at Annapolis, Maryland (less than 10 miles

42 from our site) increased about 15 cm during our 30 years experimental duration
43 (tidesandcurrents.noaa.gov). The model experiments recognize that the current elevation of
44 the Kirkpatrick marsh is too high for significant mineral sediment deposition, and therefore we
45 simulated a lower elevation marsh to represent conditions at Kirkpatrick marsh or elsewhere
46 under accelerated sea level rise.

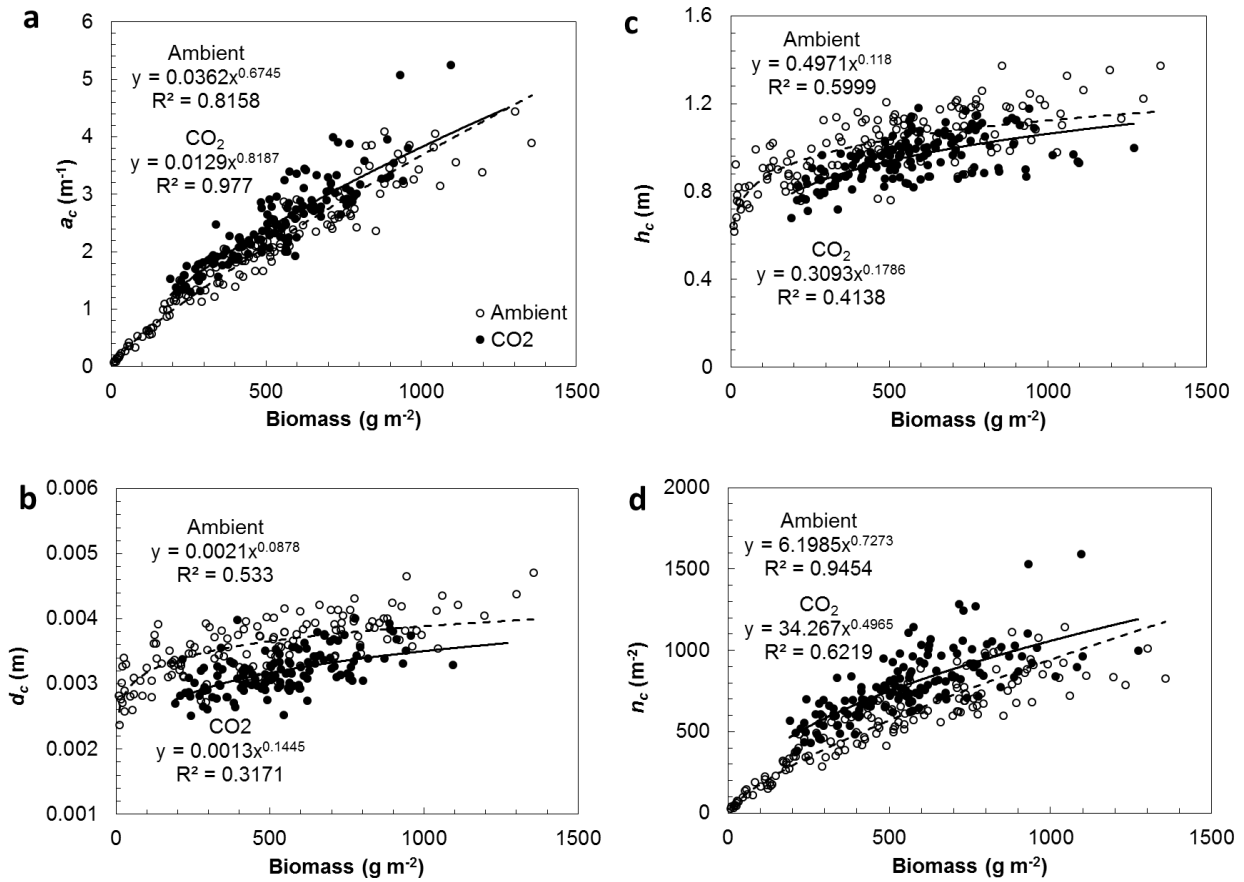
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48 **Table S3.** Coefficients used in power law functions relating aboveground biomass (L) to plant
 49 area per unit volume (a_c), stem diameter (d_c), stem density (n_c), and stem height (h_c).

| | | Plant area (a_c) | | Stem diameter (d_c) | | Stem density (n_c) | | Stem height (h_c) | |
|---------------------|-------------------|----------------------|---------|----------------------------|----------|------------------------|----------|-----------------------|--------|
| | | α | β | μ | γ | φ | σ | δ | ϕ |
| Experiment 1 | Ambient | 0.0362 | 0.6745 | 0.0021 | 0.0878 | 6.1985 | 0.7273 | 0.4971 | 0.118 |
| | CO ₂ | 0.0129 | 0.8187 | 0.0013 | 0.1445 | 34.267 | 0.4965 | 0.3093 | 0.1786 |
| Experiment 2 | Ambient | 0.0263 | 0.6841 | 0.002 | 0.1052 | 13.39 | 0.5789 | 0.3046 | 0.2124 |
| | CO ₂ | 0.0913 | 0.4914 | 0.0022 | 0.0782 | 41.998 | 0.4132 | 0.1615 | 0.3086 |
| | N | 0.0206 | 0.7212 | 0.0018 | 0.1236 | 11.704 | 0.5976 | 0.3686 | 0.1835 |
| | CO ₂ N | 0.0641 | 0.5501 | 0.0018 | 0.1161 | 35.238 | 0.434 | 0.1696 | 0.3001 |

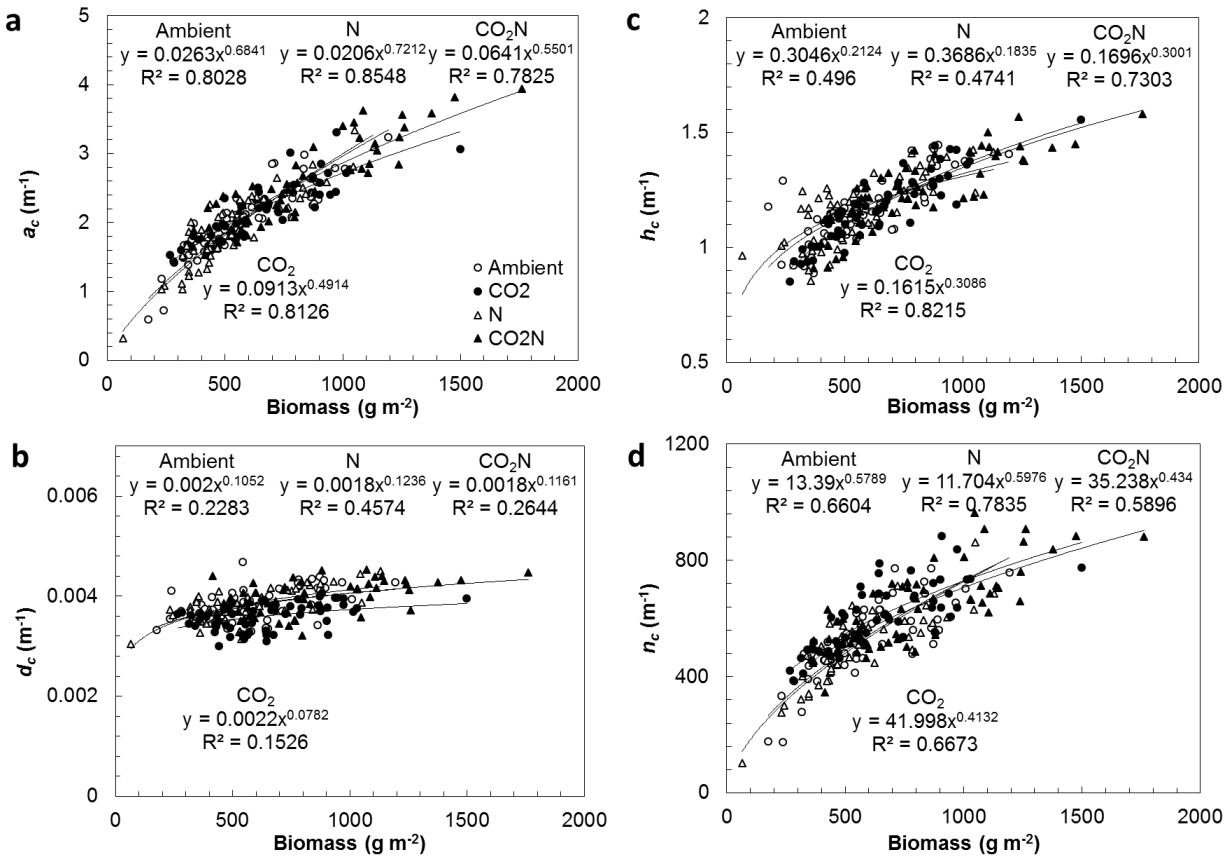
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51



52

53 **Figure S6.** Empirical relationships between aboveground biomass and (a) projected plant area
 54 per unit volume (a_c), (b) stem diameter (d_c), (c) stem height (h_c), and (d) stem density (n_c) for
 55 *Experiment 1*.



56

57 **Figure S7.** Empirical relationships between aboveground biomass and (a) projected plant area
 58 per unit volume (a_c), (b) stem diameter (d_c), (c) stem height (h_c), and (d) stem density (n_c) for
 59 *Experiment 2*.

60

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