Seventeen years of elevated CO$_2$ exposure in a Chesapeake Bay Wetland: sustained but contrasting responses of plant growth and CO$_2$ uptake

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Abstract

Increased atmospheric CO$_2$ concentration (*Ca*) produces a short-term stimulation of photosynthesis and plant growth across terrestrial ecosystems. However, the long-term response remains uncertain and is thought to depend on environmental constraints. In the longest experiment on natural ecosystem response to elevated *Ca*, we measured the shoot-density, biomass and net CO$_2$ exchange (NEE) responses to elevated *Ca* from 1987 to 2003 in a *Scirpus olneyi* wetland sedge community of the Chesapeake Bay, MD, USA. Measurements were conducted in five replicated open-top chambers per CO$_2$ treatment (ambient and elevated). In addition, unchambered control plots were monitored for shoot density. Responses of daytime NEE, *Scirpus* plant biomass and shoot density to elevated *Ca* were positive for any single year of the 17-year period of study. Daytime NEE stimulation by elevated *Ca* rapidly dropped from 80% at the onset of the experiment to a long-term stimulation average of about 35%. Shoot-density stimulation by elevated *Ca* increased linearly with duration of exposure ($r^2 = 0.89$), exceeding 120% after 17 years. Although of lesser magnitude, the shoot biomass response to elevated *Ca* was similar to that of the shoot density. Daytime NEE response to elevated *Ca* was not explained by the duration of exposure, but negatively correlated with salinity of the marsh, indicating that this elevated-*Ca* response was decreased by water-related stress. By contrast, circumstantial evidence suggested that salinity stress increased the stimulation of shoot density by elevated *Ca*, which highlights the complexity of the interaction between water-related stresses and plant community responses to elevated *Ca*. Notwithstanding the effects of salinity stress, we believe that the most important finding of the present research is that a species response to elevated *Ca* can continually increase when this species is under stress and declining in its natural environment. This is particularly important because climate changes associated with elevated *Ca* are likely to increase environmental stresses on numerous species and modify their present distribution. Our results point to an increased resilience to change under elevated *Ca* when plants are exposed to adverse environmental conditions.

Keywords: acclimation, CO$_2$ response, NEE, OTC, wetlands

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Introduction

Elevated atmospheric CO$_2$ concentration (*Ca*) induces an initial stimulation of plant growth, as demonstrated by hundreds of studies (see reviews of Drake *et al.*,

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1997; Lee *et al.*, 1998; Norby *et al.*, 1999; Drake & Rasse, 2003). Nevertheless, there is much less confidence that the response will be sustained in native ecosystems over decades to centuries, largely owing to uncertainty of the effects of interactions between the responses to rising *Ca* and other environmental factors. Through acclimation mechanisms, native species might progressively lose their ability to benefit from elevated-*Ca*

conditions (Oren *et al.*, 2001; Marissink *et al.*, 2002). Other recent results from long-term studies suggest that the stimulation of plant photosynthesis and growth is sustained with time, especially in nutrient-rich systems (Idso & Kimball, 2001; Ainsworth *et al.*, 2003a,b; Temperton *et al.*, 2003) but also in other native ecosystems (Ainsworth *et al.*, 2002).

A central goal of such long-term studies is to help predict the evolution of net CO_2 exchange (NEE) of terrestrial ecosystems in the course of the 21st century. Nevertheless, this ecosystem-level response to elevated *Ca* might differ from that of individual species, especially given that species composition might shift in response to elevated *Ca* (Smith *et al.*, 2000; Niklaus *et al.*, 2001). In addition, environmental changes concomitant with the rise of atmospheric CO_2 levels might substantially modify plant and ecosystem-level responses. For example, some studies suggest that plants subjected to water stress respond more favorably to elevated *Ca* (Ottman *et al.*, 2001; Marissink *et al.*, 2002; Wullschleger *et al.*, 2002), while others reported the opposite (Gunderson *et al.*, 2002; Hymus *et al.*, 2003).

North Atlantic salt marshes are among the few ecosystems that, up to now, have proven to be negatively impacted by incipient global climate change (Donnelly & Bertness, 2001; Scavia *et al.*, 2002). As such, they represent an outstanding model for ecosystem response to 21st-century environmental conditions. In May 1987, we began an *in situ* elevated-*Ca* experiment in a North Atlantic wetland located at the Smithsonian Environmental Research Center on the Chesapeake Bay. This ongoing study is now, after 17 years, the longest running *Ca*-enrichment experiment ever undertaken. Here, our objective was to determine the long-term effects of elevated *Ca* both on the NEE and on the shoot density and biomass of the dominant species *Scirpus olneyi*, and to analyze the interannual variation in these responses to the interaction between elevated *Ca* and salinity, one of the main environmental stressors in these wetlands.

Material and methods

The open-top chambers (OTCs) considered in this study were installed in May 1987 on stands of *S. olneyi* growing in Kirkpatrick Marsh (38°53'N, 76°33'W), a brackish ecosystem on the Rhode River Estuary, Chesapeake Bay, MD, USA. Chambers were 1 m tall and covered 0.47 m^2 of the surface area (Drake *et al.*, 1989). Five chambers were ventilated with ambient air (from approximately 340 ppm CO_2 in 1987 to 365 ppm in 2002), while five other chambers were ventilated with ambient air +340 ppm CO_2, which represents a doubling of *Ca* as compared with 1987 levels. This

research paper compares shoot growth, biomass and net ecosystem CO_2 exchange (NEE) data between the five ambient-*Ca* chambers and the five elevated-*Ca* chambers, which are identical in design and field conditions, except for the CO_2 concentration (Leadly & Drake, 1993). In addition to the chambered plots, five unchambered control plots have been monitored for shoot growth since the beginning of the experiment. The unchambered plots were used to check for overall chamber effects on the *Scirpus* growth. The elevated-*Ca* effects on shoot density, biomass and NEE, hereafter called stimulation (*Stim*, %), were expressed as the relative difference between the ambient (*A*) and the elevated (*E*) treatments ($Stim = [(E-A)/A] \times 100$).

Each year, from 1987 to 2003, the total number of *S. olneyi* shoots was manually counted at the peak of the growing season in early August in each of the 10 chambers and in the five unchambered control plots. Shoot biomass was estimated from shoot census through allometric relationships computed each year and for each *Ca* treatment on randomly selected shoots, as explained in Curtis *et al.* (1989). The NEE per ground area was measured in the OTCs by fitting a lid equipped with an exit chimney to help prevent back flow of ambient air (Leadly & Drake, 1993). The net CO_2 flux was computed as the product of the air flow through the chambers by the difference in CO_2 concentration between sampling ports located at the inlet blower and above the canopy. The NEE has rarely been measured in ecosystems subjected to artificial increases in *Ca*, although in a recent study Dore *et al.* (2003) have demonstrated that NEE estimates in ambient-*Ca* OTCs were consistent with eddy covariance measurements conducted above unchambered canopies. In addition, recent studies have shown that NEE measurements conducted in OTCs were well described by mechanistic models (Rasse *et al.*, 2003) and that *Ca* fluctuations within OTCs closely mimicked measurements conducted within unchambered canopies (Rasse *et al.*, 2002).

Because the present study focuses on plant responses, we used NEE data collected when photosynthesis largely dominates respiratory fluxes: from 10:00 to 16:00 hours during the summer season. We will therefore refer to it as daytime NEE. Fitting a chimney-equipped lid to the OTCs restricts the period of measurement to a few days per month, so that environmental conditions in the chambers are not substantially altered. The complexity of maintaining NEE measurements in field-installed OTCs for 17 years in a flooding-prone ecosystem further limited the amount of available data. In an effort to standardize our annual daytime NEE estimates, we selected the 1 day of measurement closest to the time of biomass

measurement (between mid-July and mid-August) with apparently nonlimiting insolation during all or most of the 10:00–16:00-hour period. To verify that these 1-day estimates were representative of season-long processes, we compared these data with spring–summer NEE averages obtained over an 11-year period that had been thoroughly quality checked and contained an average of 13 days of reliable data per season. Correlation coefficients between 1-day and season-long daytime NEE measurements were: 0.90 ($P \leq 0.001$) for both ambient- and elevated-Ca NEE measurements and 0.82 ($P \leq 0.01$) for stimulation of NEE by elevated Ca (data not shown). This analysis confirmed that our 1-day estimates were highly representative of growing-season-long processes.

Salinity of the marsh was measured by refractometry every 2 weeks from 1987 to 2003 at the closest point from the chambers where open water was available (about 200 m). We had no *a priori* information as to the period of time when salinity of the marsh influences the *Scirpus* community, so we used the March–July period of each year. March was chosen as a starting point because, for most years, data had not been collected in January and February. July was chosen as an end period because shoot densities were measured in early August of each year. Influence of the salinity of the previous year was ruled out by a multiple correlation study. Monthly precipitation data were obtained from the National Weather Service Forecast Office (http://www.erh.noaa.gov/er/lwx/climate.htm) and averaged for Baltimore Washington International Airport, about 30 km to the North-East, and Reagan National Airport, about 50 km to the South-East.

Statistical analyses

Repeated measure analyses were conducted to test for significant differences in shoot densities between the elevated-Ca, ambient-Ca and unchambered control plots, using the mixed model procedure of the SAS system (Littell *et al.*, 1996; Schabenberger & Pierce, 2002). A discrete autoregressive correlation model was used for the equally spaced observations in time. A similar repeated measure analysis was conducted to test for significant differences in NEE and shoot biomass between ambient- and elevated-Ca chambers. Linear regressions presented in this article were conducted using SigmaPlot version 8.02 (SPSS Inc., Chicago, IL, USA).

Results

Responses of daytime NEE, *Scirpus* plant biomass and shoot density to elevated Ca were positive for any

single year of the 17-year period of study (Fig. 1). Repeated measure analyses conducted throughout the duration of the experiment confirmed that the effect of elevated Ca was highly significant for daytime NEE, *Scirpus* plant biomass and shoot density (Table 1). Plant biomass and density responses to elevated Ca changed over time, as indicated by the significant interactions between the treatment and time effects (Table 1). Throughout the course of the experiment, there was a
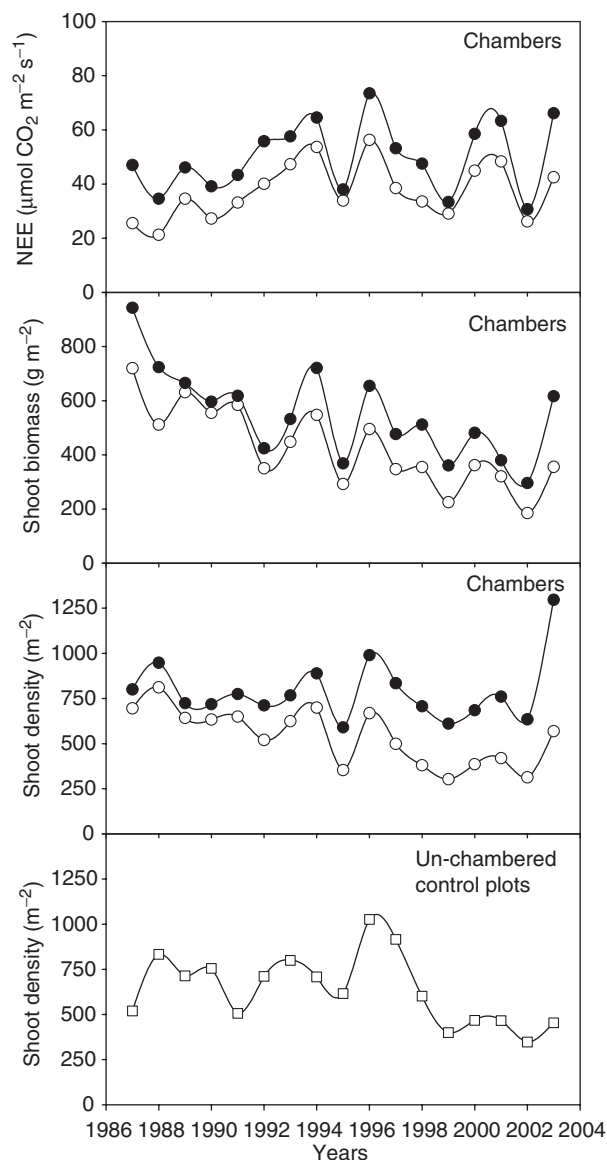

Fig. 1 Daytime net CO_2 exchange (NEE) measured 1 day per growing season, shoot biomass and shoot density of *Scirpus olneyi* in ambient (open symbols) and elevated CO_2 (close symbols) treatments in open-top chambers, and shoot density in the unchambered control plots. Each data point is the average of $n = 5$. Significant differences between treatments are presented in Table 1.

Table 1 Repeated measure analyses of daytime NEE, shoot biomass and density in ambient, elevated and control chambers

Test	Effect	Daytime NEE	Shoot biomass	Shoot density
			P-values	
Ambient vs. elevated	Treatment	0.002	0.030	0.006
	Treatment × time	0.457	0.002	0.010
Ambient vs. control	Treatment	–	0.221	0.778
	Treatment × time	–	0.214	0.261

NEE, net CO_2 exchange.

general decline in *Scirpus* shoot biomass and density in the ambient-*Ca* treatment (Fig. 1). This decline was not observed for shoot density in the elevated-*Ca* treatment, suggesting that elevated *Ca* increasingly stimulated the initiation of new shoots throughout the course of the experiment. It is notable that the effect of the chamber on microclimate was not the main factor explaining the decrease in shoot density under ambient *Ca* as a similar decline in shoot density was also observed in the control plots (Fig. 1). In addition, repeated measure analyses indicated that shoot densities in ambient-*Ca* chambers and unchambered plots were each significantly different from those in the elevated-*Ca* chambers, while they did not significantly differ from each other (Table 1). There were no significant treatment effect and no significant treatment × time interaction between the shoot densities measured in the ambient and control plots (Table 1). This decrease in shoot density and biomass under ambient *Ca*, especially dramatic between 1995 and 1998 (Fig. 1), was not specific to our research site: other North Atlantic salt marshes underwent substantial change in population density under the effect of rising sea level during the same period of time (Donnelly & Bertness, 2001; Morris *et al.*, 2002).

Daytime NEE stimulation by elevated *Ca* progressively dropped from 80% at the onset of the experiment to about 35% during the third year of treatment (Fig. 2). This 35% stimulation was maintained on average throughout the remaining 15 years of the experiment. Shoot density was increasingly stimulated by elevated *Ca* during the course of the experiment (Fig. 2). For the first 5 years of the experiment, shoot-density stimulation by elevated *Ca* was nearly constant and averaged only 16%. Beyond this initial 5-year phase, shoot-density stimulation increased nearly linearly with time, reaching 128% after 17 years of exposure to elevated *Ca*. Except for the initial 2 years of treatments, the response of shoot biomass to elevated *Ca* appeared fairly similar to that of shoot density: a sustained increase with duration of exposure (Fig. 2). Observations on all three curves suggest that initial responses should be treated separately from long-term ones. The most drastic

acclimation phase seems to have occurred within the initial 2 years of treatments, especially for daytime NEE and shoot biomass. We therefore excluded these initial 2 years from the rest of our analyses. Duration of exposure explained 67% and 89% of the variability in the elevated-*Ca* response of shoot biomass and density, respectively (Fig. 2). Daytime NEE response to elevated *Ca* did not correlate with duration of exposure ($r^2 = 0.00$).

Comparing the elevated-*Ca* stimulation curve of daytime NEE vs. that of shoot density reveals three remarkable features (Fig. 2). First, the two curves have in common that the initial responses were different from the long-term ones. Second, overall responses were nearly opposite, as clearly observable in Fig. 2. And third, the anomalies in the stimulation curves with time were often opposite. For example, 1995, 1999 and 2002 were local minima in the daytime NEE stimulation curve, while these years corresponded to high shoot-density stimulation values. A comparison with environmental databases indicated that these years were particularly dry in the spring and summer periods preceding our measurements (Fig. 2). In brackish wetlands, drought is likely to affect plant growth more through increased salinity of the pore water than through direct reduction in soil water content. Indeed, we observed that droughty springs and summers induced high salt contents of the wetland waters (Fig. 2), making these two variables highly correlated ($r = -0.79$ with $P \leq 0.001$, regression not shown). Increased salinity of the marsh, mostly induced by droughty conditions, negatively impacted the daytime NEE, the shoot biomass and the shoot density of the *Scirpus* plants in both ambient- and elevated-*Ca* chambers (Fig. 3). Therefore, increasing salinity appears as a major environmental stressor for *S. olneyi* communities.

Stimulation of daytime NEE by elevated *Ca* was positively correlated to precipitation (Fig. 4a) and inversely correlated to salinity of the salt marsh (Fig. 4B). Neither plant biomass nor shoot density correlated with salinity or precipitation (data not shown), which
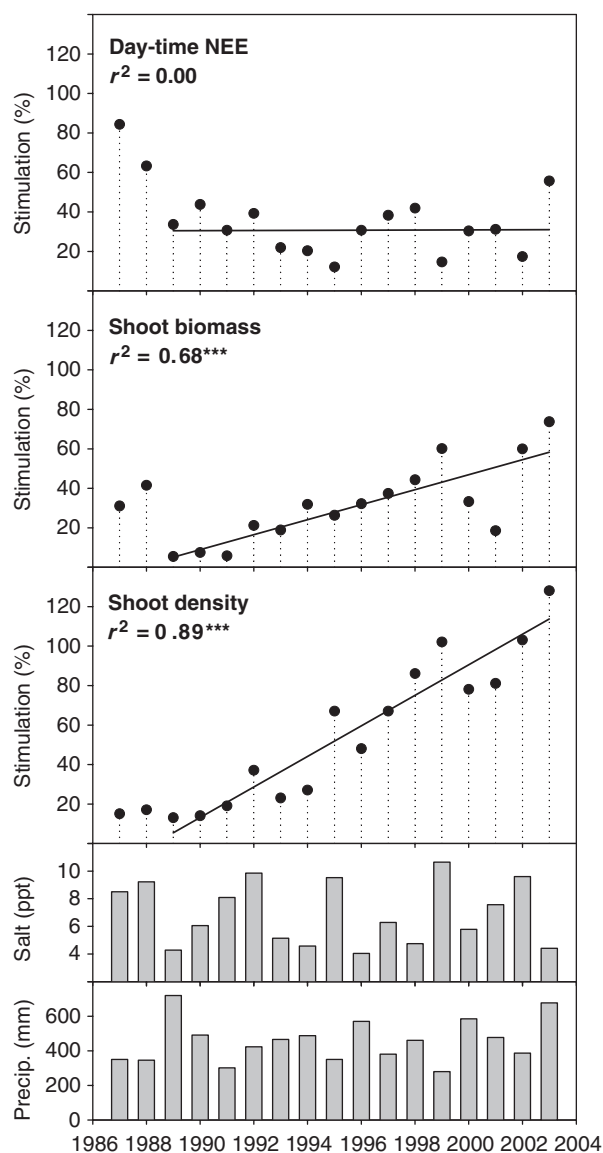
Fig. 2 Stimulation of daytime net CO_2 exchange (NEE), shoot biomass and shoot density of *Scirpus olneyi* by elevated CO_2, and March–July average salinity of the wetland, and March–July cumulative precipitation throughout the 17 years of treatment. Regression lines between stimulation values and years of treatment are represented for the 1989–2003 period. ***Significant at $P \leq 0.001$.

was expected because most of the variability is explained by correlation with time, reaching 89% in the case of shoot density. Detrending the data by removing the linear time increase also failed to produce significant correlations with either salinity or precipitation. In a second attempt, we used the time derivatives from 1 year to the next for salinity and density stimulation, thereby detrending all data from their long-term responses with time. Increases in the salinity

of the salt marsh from one growing season to the next significantly increased the response of the shoot density to elevated Ca (Fig. 5).

Discussion

While our results leave no doubt as to the sustained response of the salt marsh sedge to elevated Ca, they also point to the complexity of this response. Plant acclimation to elevated Ca was only transient and partial in the salt marsh ecosystem, as demonstrated by the long-term positive responses to elevated Ca of daytime NEE and plant shoot biomass and density. Our findings confirm recent results from long-term studies indicating that most terrestrial plant species sustain positive responses to long-term exposure to elevated Ca (Idso & Kimball, 2001; Ainsworth *et al.*, 2002, 2003a, b; Temperton *et al.*, 2003). Other studies lasting from 3 to 7 years have suggested that acclimation does occur and that biomass accumulation does not respond to elevated Ca after a few growing seasons (Oren *et al.*, 2001; Marissink *et al.*, 2002; Calfapietra *et al.*, 2003). Nevertheless, our results show that 3–7 years is probably not long enough to ascertain the long-term trend. In our study, the average shoot-density stimulation for the first five growing seasons was only 16% (Fig. 2). This initial stimulation value is comparable with the 15–20% increase in tiller density of low input rice (Kim *et al.*, 2003) and wheat (Ziska *et al.*, 1997) subjected to elevated-Ca treatments. In our study, it took about 10 growing seasons to clearly observe the increasing trend of shoot-density stimulation by elevated Ca. The same was true for photosynthesis, which displayed a strong acclimation trend during the first 2 years of study and an apparent milder one for the next 7 years, while the long-term trend stabilized at about + 35% stimulation (Fig. 2). The initial response of shoot biomass was also quite different from the longer-term one (Fig. 2). Most *in situ* multiannual studies are in the range of 2–5 years in duration (Norby *et al.*, 1999). Based on mechanistic simulation analyses, Rasse (2002) suggested that the initial 4-year response of trees to elevated CO_2 is unstable because of the progressive acclimation of plant allocation patterns that are not yet adapted to the new environment, which potentially generates transitory overcompensation lasting for one or two growing seasons.

Past the initial acclimation phase, the shoot density and biomass responses kept increasing during the course of the experiment, while the daytime NEE remained at an average of 35% stimulation. These responses are not only reconcilable but logically expected if we consider that the sustained positive response of photosynthesis to elevated CO_2 had effects
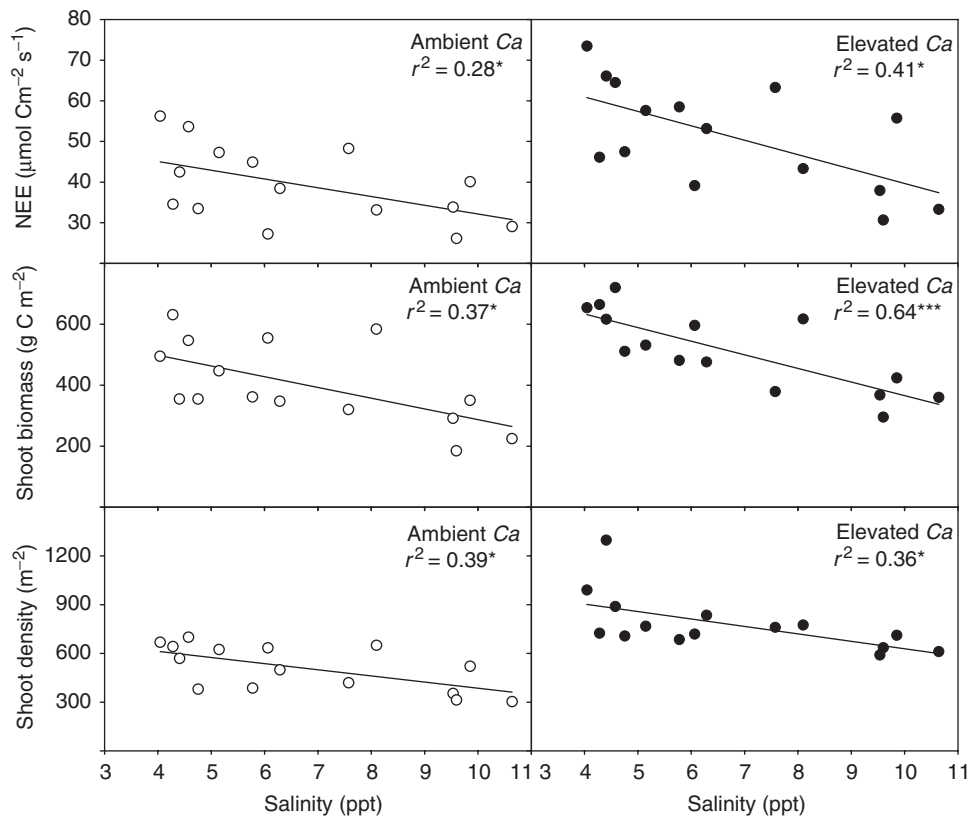
Fig. 3 Correlations between the salinity of the marsh and the daytime net CO_2 exchange (NEE), shoot biomass and shoot density measured in the ambient- and elevated-Ca chambers from 1989 to 2003. *,***Significant at $P \leq 0.05$ and 0.001, respectively.

on plant growth parameters that accumulated from one year to the next. Maintaining the NEE with reduced photosynthetic shoot biomass implies that other species replaced some of the *Scirpus* plants in the chambers. This replacement is likely, if anything, to make us underestimate the long-term NEE stimulation of *S. olneyi* by elevated Ca, because the invading species are mostly C4 plants such as *Spartina patens* and *Distichlis spicata*. Notwithstanding this community composition effect, the measured NEE response through time is consistent with periodic leaf-level studies on *S. olneyi* acclimation conducted at the site. Indeed, we observed a high NEE stimulation at the beginning of the experiment (Fig. 2), in agreement with previous findings that leaf-level photosynthesis was not significantly downregulated during the first two to four growing seasons of exposure to elevated Ca (Ziska et al., 1990; Arp & Drake, 1991; Long & Drake, 1991). From 7 to 9 years after the beginning of the experiment (1993–1995), photosynthesis per leaf area in elevated-Ca grown plants was downregulated by 35–50% as compared with that of ambient-grown plants (Jacob et al., 1995; Drake et al., 1996). Our data show that the minimum plateau of NEE stimulation had been reached

by that time (Fig. 2). Two point measurements conducted in 1997 and 2001 (unpublished data) indicate that the downregulation of photosynthesis was maintained at about 35% for both years, while for 2003, the wettest during the 17-year record, photosynthesis was downregulated only 18%, or about half the amount of downregulation during 2001, a moderate year (unpublished data).

Declining populations of *S. olneyi* in their natural environment appear to be the main driver of the increasing response with time of shoot density to elevated Ca. Environmental stress has been reported to induce a larger response to elevated Ca (Idso & Idso, 1994; Hamerlynck et al., 2000). Salinity, which was tightly coupled to the precipitation pattern, appeared as the main environmental stress that affected shoot density, biomass and daytime NEE in the *S. olneyi* community (Fig. 3). High salinity, associated with high tides, has been reported to have detrimental effects on the growth of *Scirpus* plants (Broome et al., 1995; Howard & Mendelssohn, 1999). Salinity stress is similar to water stress in that it reduces the ability of plants to absorb water (Munns, 2002). Our results suggest that water and salinity stresses significantly decreased the
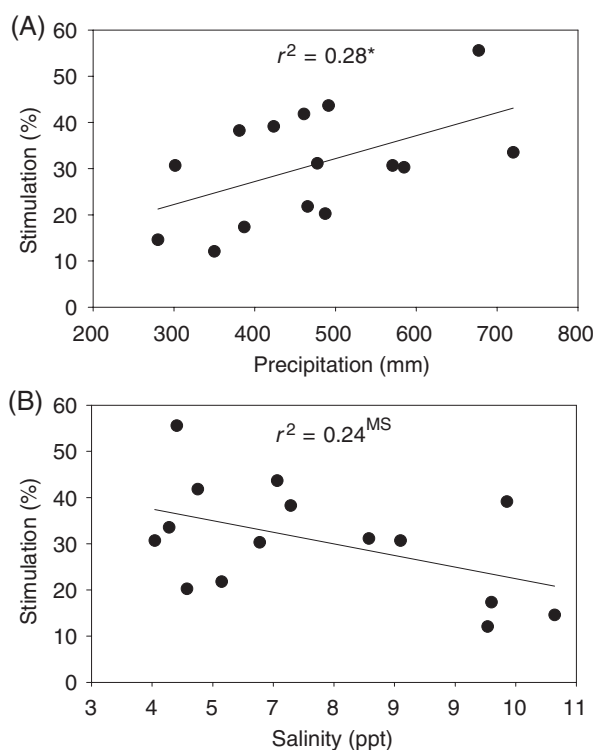
Fig. 4 Correlation between the stimulation of the daytime net CO$_2$ exchange (NEE) by elevated *Ca* and the March–July total precipitation (a) and March–July average salinity (b), for the 1989 to 2003 period. *Significant at $P \leq 0.05$; MS, marginally significant ($P \leq 0.1$).
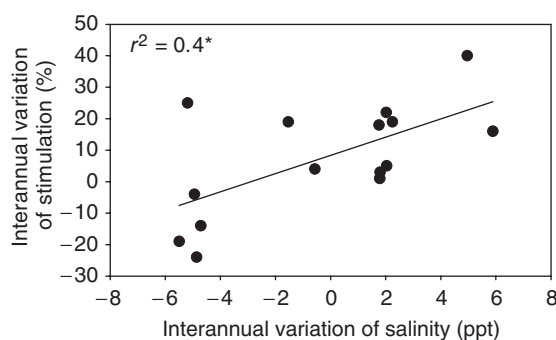

Fig. 5 Correlation between interannual salinity changes in the salt marsh and interannual changes in shoot density, for the 1989–2003 period. *Significant at $P \leq 0.05$.

stimulation of NEE by elevated *Ca* (Fig. 4). Not only was this effect observed for neither shoot biomass nor density, but we have circumstantial evidences suggesting that salinity stress increased the stimulation of shoot density by elevated *Ca*. Years with high salinity had high stimulation of shoot density by elevated *Ca* (Fig. 2), and we observed that increases in the salinity of the salt marsh from one growing season to the next significantly increased the response of the shoot density to elevated *Ca* (Fig. 5). These contrasting results, although circumstantial, highlight the complexity of the interaction between water-related stress and the response of plant communities to elevated *Ca*. Wullschleger *et al.* (2002) commented that despite considerable study the effects of water stress on plant responses to elevated *Ca* remain quite uncertain. On the one hand, several studies observed that plant morphological and growth responses to elevated *Ca* are stimulated by salinity stress (Ball & Munns, 1992; Li *et al.*, 1999; Bray & Reid, 2002) and water stress (Ottman *et al.*, 2001; Marissink *et al.*, 2002; Wullschleger *et al.*, 2002). Some other studies reported no interaction between salinity/water stresses and elevated *Ca* on plant growth (Yeo, 1999; Centritto, 2002; Centritto *et al.*, 2002). On the other

hand, Ball *et al.* (1997) reported maximum elevated-*Ca* benefits to mangrove-species growth under low-salinity conditions. Water stress was reported to decrease the stimulation of photosynthesis by elevated CO$_2$ for sweetgum trees (Gunderson *et al.*, 2002). Similarly, and in agreement with our results, Hymus *et al.* (2003) report that NEE stimulation by elevated *Ca* is decreased by water stress.

Elevated *Ca* modifies plant hormone levels and cell division (Urban, 2003), which potentially affects shoot density in a manner quite independent of the more direct effect of elevated *Ca* on photosynthesis. Therefore, it is possible that various physiological and biochemical processes within a same species are affected quite differently by elevated-*Ca* conditions, as suggested by our circumstantial evidences. If contrasted physiological responses occur within a same species, then the combination of these responses is the likely source of the variability of the biomass response to elevated *Ca* among plant species as observed even within plant functional groups (Hanley *et al.*, 2004).

Notwithstanding the effects of salinity stress, we believe that the most important finding of the present research is that a species response to elevated *Ca* can continually increase when this species is under stress and declining in its natural environment. This is particularly important because climate changes associated with elevated *Ca* are likely to increase environmental stresses on numerous species and modify their present distribution (Walther *et al.*, 2002; Thuiller, 2003). Our results point to an increased resilience to change under elevated *Ca* when plants are exposed to adverse environmental conditions.

Acknowledgements

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