

RESEARCH REVIEW

Rising sea level, temperature, and precipitation impact plant and ecosystem responses to elevated CO₂ on a Chesapeake Bay wetland: review of a 28-year study

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Abstract

An ongoing field study of the effects of elevated atmospheric CO₂ on a brackish wetland on Chesapeake Bay, started in 1987, is unique as the longest continually running investigation of the effects of elevated CO₂ on an ecosystem. Since the beginning of the study, atmospheric CO₂ increased 18%, sea level rose 20 cm, and growing season temperature varied with approximately the same range as predicted for global warming in the 21st century. This review looks back at this study for clues about how the effects of rising sea level, temperature, and precipitation interact with high atmospheric CO₂ to alter the physiology of C3 and C4 photosynthetic species, carbon assimilation, evapotranspiration, plant and ecosystem nitrogen, and distribution of plant communities in this brackish wetland. Rising sea level caused a shift to higher elevations in the *Scirpus olneyi* C3 populations on the wetland, displacing the *Spartina patens* C4 populations. Elevated CO₂ stimulated carbon assimilation in the *Scirpus* C3 species measured by increased shoot and root density and biomass, net ecosystem production, dissolved organic and inorganic carbon, and methane production. But elevated CO₂ also decreased biomass of the grass, *S. patens* C4. The elevated CO₂ treatment reduced tissue nitrogen concentration in shoots, roots, and total canopy nitrogen, which was associated with reduced ecosystem respiration. Net ecosystem production was mediated by precipitation through soil salinity: high salinity reduced the CO₂ effect on net ecosystem production, which was zero in years of severe drought. The elevated CO₂ stimulation of shoot density in the *Scirpus* C3 species was sustained throughout the 28 years of the study. Results from this study suggest that rising CO₂ can add substantial amounts of carbon to ecosystems through stimulation of carbon assimilation, increased root exudates to supply nitrogen fixation, reduced dark respiration, and improved water and nitrogen use efficiency.

Keywords: biomass production, ecosystem gas exchange, elevated CO₂, evapotranspiration, net ecosystem production, nitrogen, photosynthesis, rising sea level, wetland

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Introduction

Will terrestrial ecosystems be a sink for anthropogenic carbon as atmospheric CO₂ concentration continues to rise? This has been an open question since it was realized that rising emission of CO₂ from deforestation, fossil fuel burning has unbalanced the global carbon budget. Early observations were inconclusive: there was no discernible increase in the amplitude of seasonal atmospheric CO₂ concentrations during the first decade and a half of measurements suggesting that rising CO₂ and global warming had not altered either global photosynthesis or respiration (Hall *et al.*, 1975). Others concluded that the biosphere had been a CO₂ source for the past two millennia and that rising temperatures would shift the global carbon balance further

in that direction by increasing microbial respiration (Woodwell *et al.*, 1978).

Kimball's (1983) assessment of 430 studies of plant responses to CO₂ enrichment showed that production and yield increased an average of 30% for a doubling of CO₂ from preindustrial levels. The studies reviewed were heavily weighted by horticultural and crop species grown under ideal conditions in controlled environments over relatively brief periods of weeks to months. Although it was subsequently determined that in studies of seedlings in pots, photosynthetic capacity was regulated downward to accommodate the restricted sink (Arp, 1991; Sage, 1994), many researchers focused on acclimation of photosynthesis to elevated CO₂ and concluded that any increase in ecosystem productivity as a result of CO₂ stimulation would be transient.

Recognizing the limitations of our understanding of the effects of CO₂ on ecosystems, Lemon (1976) and

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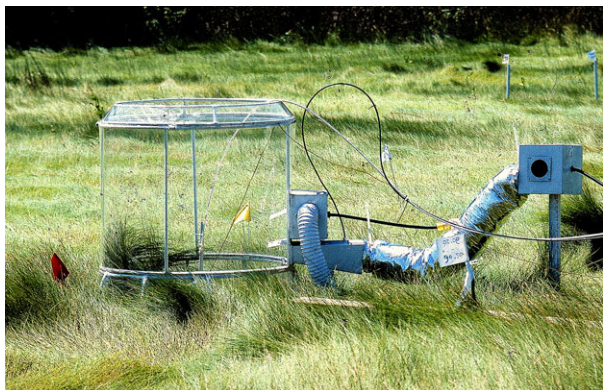


Fig. 1 Open top chamber for creating test atmospheres of elevated CO_2 in a Chesapeake Bay wetland here fitted with a flat top and exhaust chimney to prevent ambient air from mixing with air in the chamber. Details of the chamber design, microenvironment, and methods for measuring ecosystem gas exchange in Drake & Leadley (1991); Drake & Peresta (1993).

Strain (1978) emphasized the need for field studies to characterize responses of native ecosystems to increasing atmospheric CO_2 and climate change. Uncertainties about the land's response to rising atmospheric CO_2 are a central focus of efforts to understand the link between rising atmospheric CO_2 and climate processes (IPCC, 2007).

A Chesapeake Bay wetland was selected for a field study that began in 1987. This ecosystem has stands dominated by C4 grass *Spartina patens* and a C3 sedge, *Scirpus olneyi*.¹

Forty-five plots were established: 15 each in zones dominated by either C3 or C4 species and 15 in a zone where the two species occurred together. This situation presented a unique opportunity to test whether and to what degree elevated CO_2 stimulation of photosynthesis in the C3 sedge would favor this plant over the C4 grasses. Open top chambers (Fig. 1) provided the best approach available for elevating atmospheric CO_2 under the natural conditions of native plants in the field. In half of the chambers, atmospheric CO_2 was raised by 340 ppm, twice the daytime ambient concentration of CO_2 in the atmosphere in 1985 (Leadley & Drake, 1993). Elevated CO_2 was maintained 24 h per day. Whether or not raising the CO_2 level at night had any effect on plants or ecosystem processes, it seemed at the time we started that high CO_2 at night is a closer representation of the higher CO_2 world expected in the 21st century. The effect on the microenvironment

¹*Scirpus olneyi* is now *Schoenoplectus americanus* (pers.). Throughout this article, I will continue to refer to this species as *Scirpus olneyi* to be consistent with previous publications from this study.

within the open top chamber has been studied (Drake *et al.*, 1989; Drake & Peresta, 1993). Throughout the study, we found no systematic effect of the chamber environment on growth of shoots or roots (Rasse *et al.*, 2005). For details of chamber construction and operation see Drake & Leadley (1991), Arp *et al.* (1993), and Drake & Peresta (1993).

The floristic simplicity of stands of a C3 sedge, a C4 grass, and mixtures of these two make it possible to interpret results in terms of the photosynthetic responses to elevated CO_2 . The C4 grasses have high photosynthetic capacity, a requirement for salt, and fundamentally different responses from the C3 sedge to flooding, variable salinity, and temperature (Drake, 1989) as well to rising atmospheric CO_2 . Elevation differences in a few centimeters on the wetland surface create different edaphic environments: lower, less saline zones are dominated by the C3 Sedge and the higher, saltier zones by the C4 grasses Fig. 2 (Arp *et al.*, 1993). As C4 photosynthesis is considered saturated at the current CO_2 level, but not C3 photosynthesis, an expectation at the outset of the study was that the elevated CO_2 would give the *Scirpus* C3 advantage in competition with the *Spartina* C4. Environmental stresses of this wetland (i.e. anoxic soils, periodic flooding, variable salinity, high solar radiation and temperature, and desiccation of foliage) reduce photosynthesis of the native species below their genetic capacity. Rates of photosynthesis for the species in this field study were typically in the range $10\text{--}15 \mu\text{molCO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (leaf area basis; DeJong *et al.*, 1982). In a greenhouse study, under conditions that lacked the severe stress of the wetland habitat, photosynthetic capacity of *S. olneyi* exceeded $50 \mu\text{mol m}^{-2} \text{ s}^{-1}$ (DeJong *et al.*, 1982). The *Spartina* C4 grass had a higher photosynthetic capacity than the *Scirpus* C3 sedge under native habitat conditions but in elevated CO_2 , the sedge had rates of photosynthesis equal to or greater than the C4 grasses (DeJong *et al.*, 1982).

The concept of limiting factors suggests that for ecosystems in which plant growth is constrained by many factors, elevated CO_2 might have little sustained effect on plant production (i.e. ecosystems are not carbon limited). Applied to the requirement for nutrients, this concept leads to the idea of progressive nitrogen limitation and implies that CO_2 stimulation of carbon assimilation and growth, often seen at the outset of elevated CO_2 studies, would not be sustained because the supply of nitrogen would soon be overwhelmed by demand (Luo *et al.*, 2004; Hungate *et al.*, 2005).

During the life of this study, atmospheric CO_2 has risen nearly 18%, sea level during the growing season rose 20 cm, and maximum growing season temperature has varied across a range equivalent to the projected

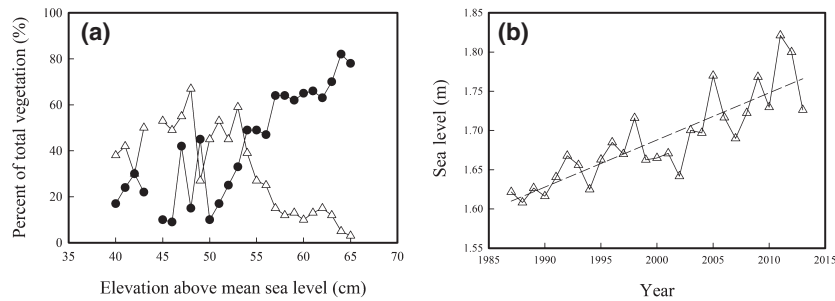


Fig. 2 (a) The distribution of *Scirpus olneyi* C3 (Δ) and *Spartina patens* C4 (\bullet) across the elevation gradient of the marsh in 1986 at the outset of the study (Arp *et al.*, 1993). *Scirpus* C3 occupies the lowest and *Spartina* C4 the highest elevations. (b) The average sea level during May, June, and July, the first 3 months of the growing season, from the outset of the study until 2013. Between 1988 and 2011, sea level has risen 20 cm, the full range of elevation for the distribution of the two species on the wetland.

rise in temperatures during the 21st century. The species in this study are perennials. Although the roots and rhizomes live from year to year and are thus affected by the CO₂ treatment and past history, the green shoots die back in the fall and reappear 6 months later in spring. The project is unique in that it is the only one to look at the simultaneous effects of two major environmental impacts of climate change on ecosystem processes, rising sea level, and temperature, as covariates with elevated CO₂. Data are used here to examine the impact of these critical climate change elements in the presence of atmospheric CO₂ levels expected during this century. In spite of large interannual variability, elevated CO₂ stimulated photosynthesis and growth of the *Scirpus* C3 throughout the course of the study.

Rising sea level and plant distribution at the field site

During the study, mean sea level during the summer growing season rose from about 160 cm to 180 cm (measured at Annapolis, Maryland 20 miles northeast of the site, tidesandcurrents.noaa.gov) (Fig. 2), an average of over 7 mm yr⁻¹. This is more than twice the long-term average 3.4 mm yr⁻¹ for the 80 year record of sea level at Annapolis on the Chesapeake Bay. Unless the surface elevation can keep pace with sea level rise, flooding in wetlands on the Chesapeake Bay is expected to accelerate dramatically as the rate of rising sea level accelerates in the next 40 years (Boon, 2012; Boesch *et al.*, 2013).

Elevated CO₂ stimulation of shoot density and biomass production

Distribution of C3 and C4 species was determined by the elevation of the surface above mean sea level

(Fig. 2; Arp *et al.*, 1993). Throughout the study, the plant communities on the wetland shifted in response to rising sea level (Figs 2 and 3): the *Scirpus* C3 component of the Mixed community, which occurs at an intermediate elevation, increased substantially as rising sea level increased the flooding. *Scirpus* C3 is better adapted to flooding, with its abundant aerenchyma and deeper rooting system that taps into less salty water at depth, than the *Spartina* C4 (Fig. 2). Rising sea level combined with elevated CO₂ increased shoot density of the *Scirpus* C3 in the Mixed community. The elevated CO₂ treatment reduced shoot density of the less flood-tolerant *Spartina* C4 in both Mixed and pure *Spartina* C4-dominated communities (Fig. 3).

The CO₂ effect on shoot density (Fig. 3) and biomass production (Fig. 4) was sustained throughout the study. In the Mixed community the CO₂ effect on shoot density of *Scirpus* C3 was nearly constant, but in the *Scirpus* C3-dominated community, the CO₂ effect increased gradually to a peak in 2003 and declined thereafter, perhaps reflecting the fact that rising sea level had begun to have a major effect on the capacity of *Scirpus* C3 to tolerate flooding. Interannual variation in the CO₂ effect of *Scirpus* C3 was caused mostly by precipitation, temperature, and sea level rise (discussed below). In the *Scirpus* C3 and Mixed communities, there was no statistically significant difference between the shoot density in the ambient chambers and the unchambered control sites (see also Rasse *et al.*, 2005).

Stimulation of shoot density and biomass production by elevated CO₂ (Figs 3 and 4) continued throughout the study with periods of very little response preceded and followed by periods of very large response (Erickson *et al.*, 2006, 2013). Rasse *et al.* (2005) reported that stimulation of shoot density in the *Scirpus* C3 community by elevated CO₂ rose from about 15% during the first 4 years of the study to 120% by 2003.

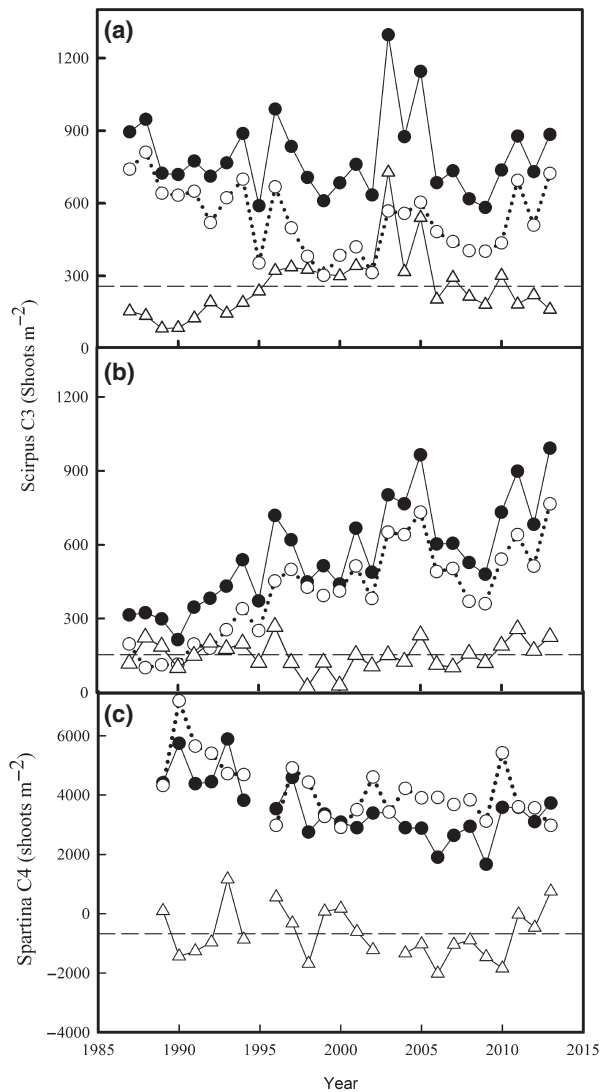


Fig. 3 Shoot density (shoots m^{-2}) measured at the peak of the growing season in the three communities: (a) *Scirpus olneyi*, (b) Mixed (only the *Scirpus* component is shown) and (c) *Spartina patens*. Values are mean of five chambers in each community. Closed circles (\bullet) for shoot density in chambers at elevated CO_2 , open circles (\circ) for shoot density in chambers at ambient CO_2 , and triangles (Δ) for the CO_2 effect (El-Am). The dashed line is the mean value of the CO_2 effect on shoot density: a. *Scirpus* C3, 263; b. Mixed C3, 150; c. *Spartina* C4, -685. The record spans 28 years. Elevated CO_2 increased *Scirpus* C3 shoot density in both the pure *Scirpus* (a) and mixed (b) communities ($P < 0.001$; $P < 0.001$), but decreased shoot density in the pure *Spartina* C4 (c, $P = 0.008$).

A decline in the effects of CO_2 with time in field studies is well known if poorly understood (Norby *et al.*, 2005). The Chesapeake Bay wetland study is not the only study in which the growth and other responses to elevated CO_2 persisted throughout the entire study

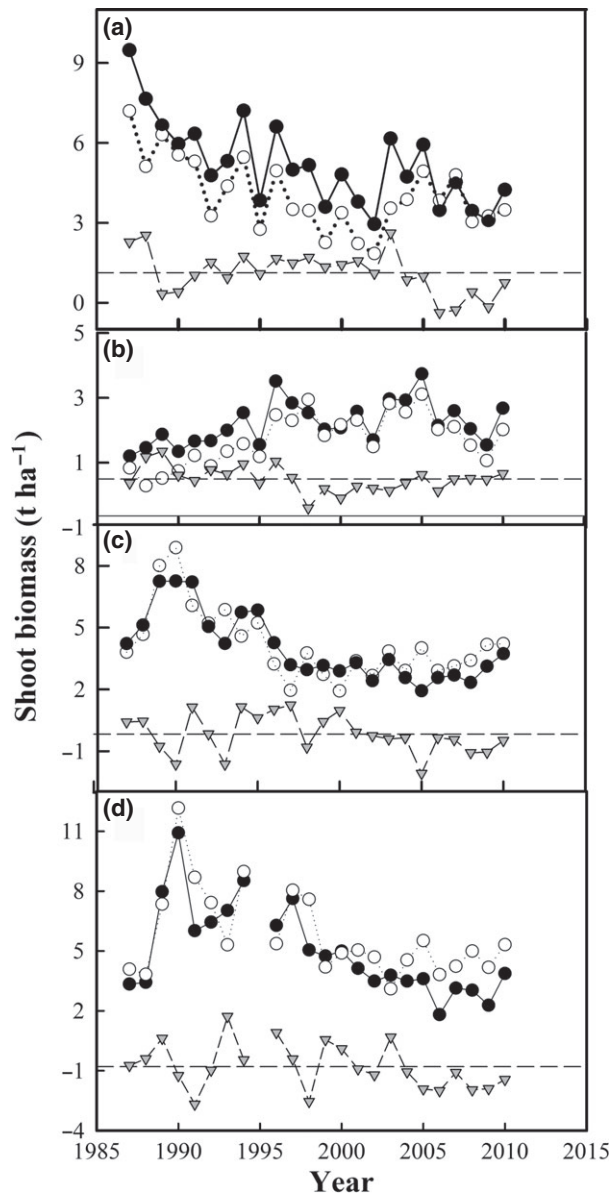


Fig. 4 Shoot biomass ($t\ ha^{-1}$). Symbols and values as in Fig 3. (a) The mean value of the CO_2 effect throughout the study on (a) *Scirpus* C3 was 1.2; (b) Mixed C3, 0.5, (c) Mixed C4, -0.2; (d) *Spartina* C4, -0.8 ($t\ ha^{-1}\ yr^{-1}$). The CO_2 effect was statistically significant for the *Scirpus* in both the *Scirpus* (a; $P < 0.011$), and Mixed C3 (b; $P = 0.024$), but not in the *Spartina* C4 in the Mixed community (c; $P = 0.571$). The CO_2 effect was significant ($P < 0.10$) in the pure *Spartina* C4 (d; $P = 0.099$) community.

(discussed in Norby *et al.*, 2005). The recovery of interacting processes from disturbance may be critical to the responses of ecosystems to rising CO_2 and climate change. Processes acting at the ecosystem level have very different time response functions. Photosynthesis scrubs CO_2 from the spaces within the leaf in a small fraction of a second; delivery of carbon skeletons from

the leaf to microbes in the soil requires hours; acquisition of nutrients takes hours to days; and full recovery of both plant and soil process from major disturbances such as violent storms takes months to years. We don't know how long it will take the Chesapeake Bay Wetland ecosystem to reach a new equilibrium after the sea level rises an estimated 100 cm and the atmospheric CO₂ concentration doubles by the end of the 21st century (Boesch *et al.*, 2013).

Stimulation of biomass production (Fig. 4) by elevated CO₂ was caused by both increases in shoot density and effects on mass per unit area of shoot (Rasse *et al.*, 2005; Erickson *et al.*, 2006). Shoot biomass at the peak of growing season in late July declined during years of low rainfall and high salinity (Rasse *et al.*, 2005; Erickson *et al.*, 2006). During the 5 months from March to July, salinity in pore water at the study site and in the nearby estuary ranged from about 4 ppt during the four highest rainfall years to near 10 ppt during the 4 years of lowest rainfall (Erickson *et al.*, 2006).

Keeping up with rising sea level

Rising sea level correlated with increasing biomass of *Scirpus C3* in the Mixed community at higher elevations (Fig. 5; Erickson *et al.*, 2006). Are the wetland plants in this study capable of supplying the biomass needed for the surface of the marsh to keep pace with predicted sea level rise in Chesapeake Bay throughout the 21st century (Boesch *et al.*, 2013)? Elevated CO₂ stimulated growth of shoots 5–37% and increased roots of the *Scirpus C3* but not the *Spartina C4* (Curtis *et al.*,

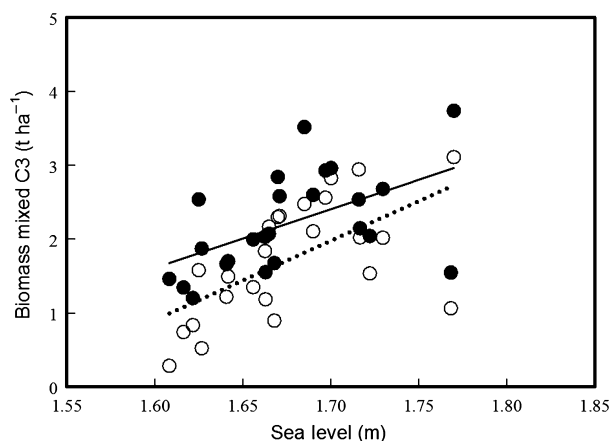


Fig. 5 The correlation of rising sea level and biomass of the *Scirpus C3* in the Mixed community. Symbols as in Fig. 3. Values are mean of five chambers. (see Rasse *et al.*, 2005; Erickson *et al.*, 2006; for methods of estimating biomass). The CO₂ treatments are significantly different ($P = 0.024$), but the slopes of the regressions are not different ($t = 12.32$).

1989a, 1990; Arp *et al.*, 1993; Rasse *et al.*, 2005; Erickson *et al.*, 2006). There was a much larger relative increase in the shoot growth of *Scirpus C3* in the mixed community where elevated CO₂ also caused growth of roots to increase 83% over the biomass of roots in the plots exposed to ambient CO₂ (Erickson *et al.*, 2006). Elevated CO₂ effects on growth in the C3 *Scirpus*-dominated community added an average of 0.53 kg C m⁻² yr⁻¹ as biomass in the C3 *Scirpus* community (Erickson *et al.*, 2006).

In a different study designed to measure increasing soil surface elevation on the same marsh in response to elevated CO₂-stimulated growth of *Scirpus C3* and *Spartina C4*, Langley *et al.* (2009) showed that in the short term of 2 years, elevated CO₂ stimulation of growth of fine roots was sufficient to raise the elevation of the marsh by 4.0 mm yr⁻¹. Although this is more than the long-term average of sea level rise, it is not clear whether the gradual increase in atmospheric CO₂ can stimulate biomass sufficient to keep pace with accelerating sea level rise in the 21st century.

Acclimation of photosynthesis and stomatal conductance to chronic elevated CO₂

The CO₂ stimulation of growth occurs because photosynthesis is increased by elevated CO₂. Plants sense CO₂ at two known targets: photosynthetic carbon reduction by Rubisco; and some as yet unknown system within the guard cells surrounding stomata of most angiosperms. In C3 plants, elevated CO₂ usually reduces the rate of carbon oxidation (photorespiration) and increases the rate of photosynthetic carbon reduction (Long, 1991). With some exceptions, plants having the C4 photosynthetic pathway do not show increased photosynthetic carbon reduction when exposed to atmospheric CO₂ much above 350 ppm (Drake *et al.*, 1997). Stomata in angiosperms respond to elevated atmospheric CO₂ concentration by reducing the aperture and transpiration (Drake *et al.*, 1997; Brodribb & McAdam, 2013). Stomata in conifers show no effect of CO₂ on stomatal opening but acclimation to chronic exposure to elevated CO₂ alters reduces stomatal density in conifers (Kouwenberg *et al.*, 2003), which would also result in reduced transpiration in conifers grown in elevated atmospheric CO₂.

Quantum yield (low light responses) was measured in the field using an integrating sphere (adapted as a leaf gas exchange cuvette) to determine absorbed photosynthetically active radiation near the light compensation values in the *Scirpus C3* (Long & Drake, 1991). Elevated CO₂ increased the maximum quantum yield 20%, as a measure of light-limited photosynthesis, and reduced the light compensation point about 40%. There

was no evidence for acclimation of the light harvesting apparatus in *S. olneyi* (Long & Drake, 1991).

However, exposure of *Scirpus* C3 to elevated CO₂ resulted in reduced light-saturated photosynthetic capacity when compared with plants grown and measured at ambient CO₂ levels (Jacob & Drake, 1995). Elevated CO₂ had little or no effect on photosynthesis in *Spartina* C4 plants (Ziska *et al.*, 1990). The high CO₂-grown *Scirpus* C3 plants also had lower protein content (Jacob & Drake, 1995). Rubisco, which accounted for a little over 50% of soluble protein in *S. olneyi* was reduced along with total protein, but there was no effect of elevated CO₂ on the Rubisco as a proportion of total protein (Jacob & Drake, 1995) suggesting that acclimation was not a property of specific components of photosynthetic carbon reduction but a consequence of reduced protein content. The CO₂ effect on protein was associated with lower nitrogen concentration in plant tissues of 5–30% at midseason (Curtis *et al.*, 1989b; Erickson *et al.*, 2013). Moreover, the reduction in nitrogen was also seen in root tissues of *Scirpus* C3 as well as shoots of *Spartina* C4 (Erickson *et al.*, 2013).

CO₂ stimulation of net ecosystem production

Net ecosystem CO₂ exchange (NEE, $\mu\text{molCO}_2 \text{ m}^{-2} \text{ s}^{-1}$, ground area basis) was measured using the open top chambers modified with addition of a chimney (Fig. 1) to prevent back flow of outside air into the chamber (Drake *et al.*, 1989). Elevated CO₂ increased total assimilation rate of stands of *S. olneyi* compared to stands at ambient levels of CO₂ when measured at their respective growth concentrations of CO₂ (Drake *et al.*, 1997), but the effect on the *Spartina* C4 was smaller (Fig. 6). Periodic measurements (ca. 10–20 times per growing season) were made to obtain ecosystem light response characteristics under different environmental conditions (see Erickson *et al.*, 2013 for full description of methods for reducing data and filling gaps). Data for net ecosystem production ($\text{NEP} = \sum (\text{NEE}_{\text{day}} + \text{NEE}_{\text{night}})$ sum of 24 h carbon assimilation and loss) each year of the study for 1988 through 2004 are shown in Fig. 7 (Erickson *et al.*, 2013).

The CO₂ stimulation of NEP in the C3 *Scirpus* averaged 35%, but was highly variable with a range of 0 to

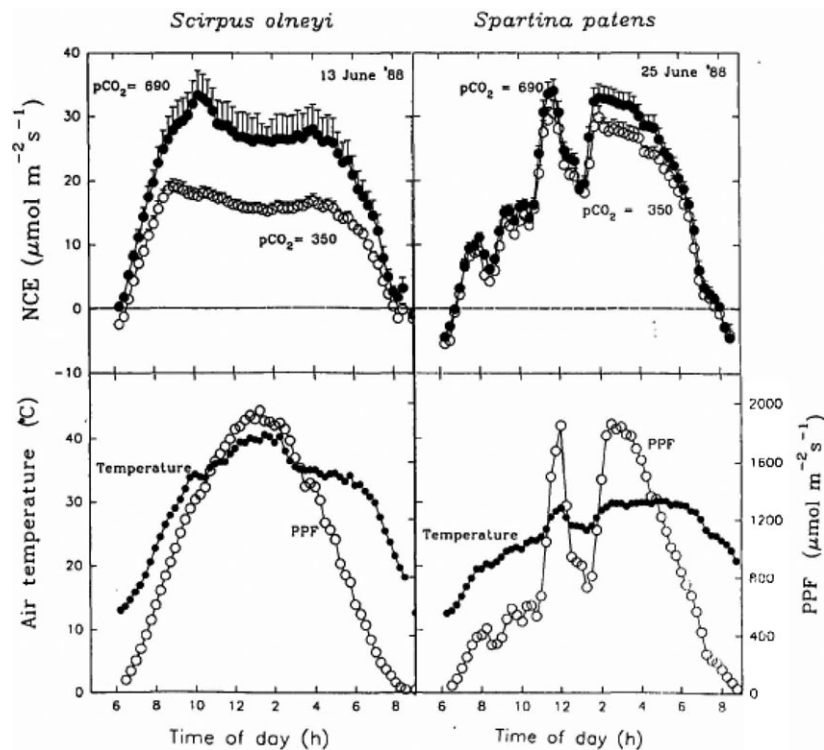


Fig. 6 Ecosystem gas exchange data for 2 days in 1988. Left panels 13 June, right panels 28 June. Upper panels: Net ecosystem gas exchange per unit ground area ($\mu\text{molCO}_2 \text{ m}^{-2} \text{ s}^{-1}$) for *Scirpus* C3 and *Spartina* C4 grown and tested in elevated (● closed circles) or ambient (○ open circles) atmospheric [CO₂]. Lower panels, photosynthetically active photon flux (○ open circles, $\mu\text{mol m}^{-2} \text{ s}^{-1}$) and air temperature (● closed circles, °C) within the chambers. Values of gas exchange data are means and standard errors ($n = 5$) determined every 15 min throughout the day. The biomass for *Scirpus* C3 was equal in both elevated and ambient CO₂ treatments for the day these measurements were made (Drake & Leadley, 1991).

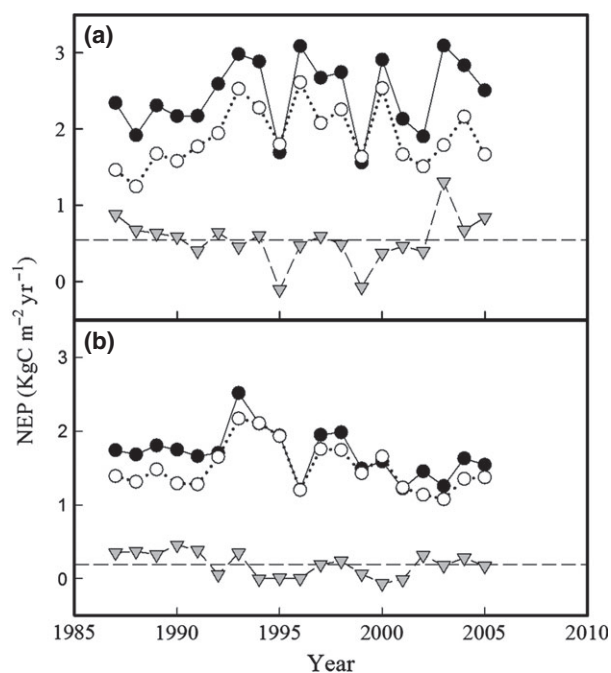


Fig. 7 Net ecosystem production (NEP, kg C m^{-2}), the sum of 24 h net ecosystem CO₂ exchange for the 200 day growing season (after Erickson *et al.*, 2013). Daily NEE as in Fig. 6 were used to create light response curves for each day that measurements were taken. The coefficients from these curves were used with solar radiation to estimate daily NEE for every day between measurement campaigns. Symbols as in Fig. 3. The mean CO₂ effect for the (a) *Scirpus* C3 was 0.55 and (b) for *Spartina* C4 0.20 $\text{kg C m}^{-2} \text{yr}^{-1}$. The CO₂ effect was statistically significant in both communities ($P < 0.001$; $P < 0.001$).

88%. Nevertheless, the capacity of ecosystem CO₂ assimilation to respond vigorously to elevated CO₂ was sustained from 1987 through 2004 (Fig. 7). Ecosystem gas exchange measurements were discontinued after 2005. Greatest CO₂ stimulation, as percent of NEP at ambient CO₂ level, occurred during wet years (e.g. 1996 and 2003) and the least in extremely severe drought years (e.g. 1995 and 1999) when there was no response to elevated CO₂ (Erickson *et al.*, 2013). The record for 1988 showed that elevated CO₂ increased NEP 48% per unit green biomass or leaf area, which, when combined with increased leaf area, translates to an increase of 88% per unit ground area (Drake & Leadley, 1991).

Why is the rate of net ecosystem CO₂ exchange in the wetland high?

We compared ecosystem gas exchange measurements with a model parameterized for this ecosystem with physiological data (Rasse *et al.*, 2003). Model simulations suggested that numerous factors contributed to

the relatively high stimulation of net ecosystem photosynthesis in the C3 community. Higher quantum yield and reduced light compensation point (Long & Drake, 1991), stimulation of maximum photosynthesis (Ziska *et al.*, 1990; Jacob & Drake, 1995), increased numbers of green shoots (Curtis *et al.*, 1989a; Rasse *et al.*, 2005), relatively high nitrogen concentration (Rasse *et al.*, 2003), and reduced water stress (Arp *et al.*, 1993) all contributed to the relatively high rates of ecosystem NEP. Seasonal increase in salinity (Rasse *et al.*, 2005; Erickson *et al.*, 2006), flooding (Erickson *et al.*, 2006), and extreme temperatures reduced ecosystem gas exchange. Compared to upland systems where soil respiration is a dominant fraction of net ecosystem CO₂ exchange, at our site, a large fraction of the primary productivity is stored as soil organic matter due to anaerobic conditions that inhibit decomposition. Soil organic matter content at the site is >80% to a depth of 5 m. Although wetlands generally export more dissolved organic or inorganic carbon than other systems, there may be negligible hydrological export from the soils in this experiment because of low soil hydraulic conductivity and the site location about ca. 300 m from the nearest tidal creek (Marsh *et al.*, 2005).

The temperature dependence of photosynthesis interacts strongly with the background CO₂ level (Long, 1991; Drake *et al.*, 1997). Compared with 350 ppm, the temperature optimum for simulated leaf photosynthesis will be 5 °C higher at 650 ppm atmospheric CO₂ based on simulations with the Farquhar equation (i.e. Bernacchi *et al.*, 2001). Simulations also showed that at temperatures above 30 °C (often found inside the chambers in this study), elevated CO₂ increased light-saturated net photosynthesis of canopies by more than 100% above the rate at present ambient CO₂ levels (Drake *et al.*, 1997). Thus, theory would suggest that the CO₂ effect might increase ecosystem photosynthesis at increased temperature compared with gas exchange in plants exposed to normal ambient CO₂. In the wetland study, increasing temperature had a significant negative effect on net ecosystem CO₂ exchange carbon (Fig. 8): higher temperature reduced net ecosystem production at both ambient and elevated CO₂ and elevated CO₂ did not compensate or mediate a greater effect on net ecosystem production.

But which environmental or physiological factors mediating ecosystem level gas exchange are sensitive to rising temperature at high CO₂? At the leaf level, the stimulation of photosynthesis in *Eucalyptus* was more sensitive to increasing temperature at elevated CO₂ than photosynthesis at lower CO₂ levels (Roden & Ball, 1996) and in *Quercus* leaves, the temperature sensitivity was attributed to effects on Rubisco activase (Haldimann & Feller, 2004). The simulations discussed above

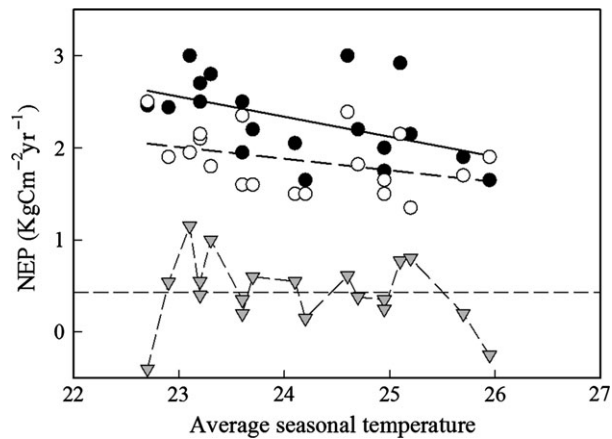


Fig. 8 The effect of mean daytime growing season temperature ($^{\circ}\text{C}$) and elevated CO_2 on net ecosystem production in the *Scirpus* C3 community. Temperature effect, elevated CO_2 (\bullet , solid line, $\text{NEP}_e = 7.54 - 0.21(T)$, $r^2 = 0.23$); ambient CO_2 (\circ , dashed line, $\text{NEP}_a = 4.91 - 0.126(T)$, $r^2 = 0.13$). The CO_2 effect (Δ ; mean is dashed line, $0.44 \text{ kg C m}^{-2} \text{ yr}^{-1}$). NEP declined about $8\% \text{ C}^{-1}$ in elevated CO_2 and $5\% \text{ C}^{-1}$ in the ambient treatments. The two treatments are different ($P < 0.001$), but the slopes are not different ($t = 5.0$).

(Drake *et al.*, 1997) did not include a way to account for the impacts of prolonged exposure of ecosystem level processes (such as shoot density or leaf area) to elevated temperature that can alter photosynthesis on several levels of organization. High temperature is often associated with higher solar radiation, higher VPD, reduced precipitation, and, in the tidal wetland, higher salinity, all of which can reduce photosynthesis directly at the cellular level and indirectly by dehydration of green tissues, failure of leaf expansion, or accelerated senescence of leaf area. Sharply reduced yield of corn, soybeans, and cotton in the United States that occurs at temperatures above $28\text{--}31\text{ }^{\circ}\text{C}$ (Schlenker & Roberts, 2009) is responses to temperature that probably involve growth and development as well as photosynthesis.

Simulations of the effect of elevated CO_2 on leaf and canopy photosynthesis (Drake *et al.*, 1997) cannot account for the temperature inhibition of photosynthesis in leaves (Haldimann & Feller, 2004; Salvucci & Crafts-Brandner, 2004). In some crop species, deactivation of Rubisco activase after exposure of plants to high temperature inhibits carboxylation capacity (Salvucci & Crafts-Brandner, 2004).

Our analysis of temperature effects also indicated that leaf area index and ecosystem respiration were reduced as temperature increased (data not shown). This is counterintuitive in that one expects ecosystem respiration to increase as temperature increases. Effects

of temperature also correlate with effects of drought and salinity and separating the effects of these factors in this study was not possible.

Evapotranspiration (ET) and water stress

Drake *et al.* (1997) reported that elevated CO_2 reduced stomatal conductance 20–40% and reduced transpiration in leaves and canopies. The relative effect generally declined as the scale increased from stomatal opening to ecosystem evapotranspiration. Acclimation to the elevated CO_2 treatment in *Scirpus* C3 reduced numbers and density of stomata (unpublished data). The net effect of acclimation to elevated CO_2 gave a 35–66% reduction in stomatal conductance. Acclimation to elevated CO_2 also made stomata in the *Scirpus* C3 less sensitive to environmental effects than stomata in plants under normal ambient CO_2 (Li *et al.*, 2009). Compared with the *Scirpus* C3, elevated CO_2 reduced ET about 50% more in the *Spartina* C4 (Li *et al.*, 2009).

Evapotranspiration in plots of both *Scirpus* C3 and *Spartina* C4 plants was significantly reduced: on average, 19% in the C3 *Scirpus* and 34% in the C4 *Spartina* community (Fig. 9; Li *et al.*, 2009). The smaller reduction in ET in the *Scirpus* C3 was due to increased leaf area index in the C3 *Scirpus* community but not in the C4 *Spartina*, where leaf area was decreased by elevated CO_2 (Fig. 4; Li *et al.*, 2009). Elevated CO_2 increased ecosystem water use efficiency (EWUE) about the same in both *Scirpus* C3 and *Spartina* C4, but this came about as a result of a different combination of factors in the two species. An increase of 36% in NEE, 34% in LAI, and a 19% reduction in ET for the *Scirpus* C3 community, increased EWUE by about 82%, while a 13% increase in NEE and 34% reduction in ET increased EWUE in the C4 community by 83% (Fig. 9 (Li *et al.*, 2009). Evapotranspiration decreased relatively more in the *Spartina* C4 than *Scirpus* C3, which suggests that stomatal conductances decreased more in the C4 than C3 as would be expected (Li *et al.*, 2009).

A greenhouse experiment showed that the effect of elevated CO_2 on ET in the C3 *Scirpus* species was reduced by increased salinity: elevated CO_2 reduced canopy transpiration 30% at very low salinity but only 10% when pore water salinity was nearly 2/3 sea water strength (Li *et al.*, 2009).

Severe water stress was indicated by midday leaf water potential of -1.8 MPa for *Scirpus* C3 and -2.8 MPa for the *Spartina* C4 in ambient CO_2 (Arp *et al.*, 1993). Elevated CO_2 reduced water stress as indicated measurements of daytime water potential. In the C3 *Scirpus*, water potential was improved by 0.4 MPa and in C4 *Spartina*, 0.7 MPa (Arp *et al.*, 1993). The more severe water stress for *Spartina* C4 (indicated by more

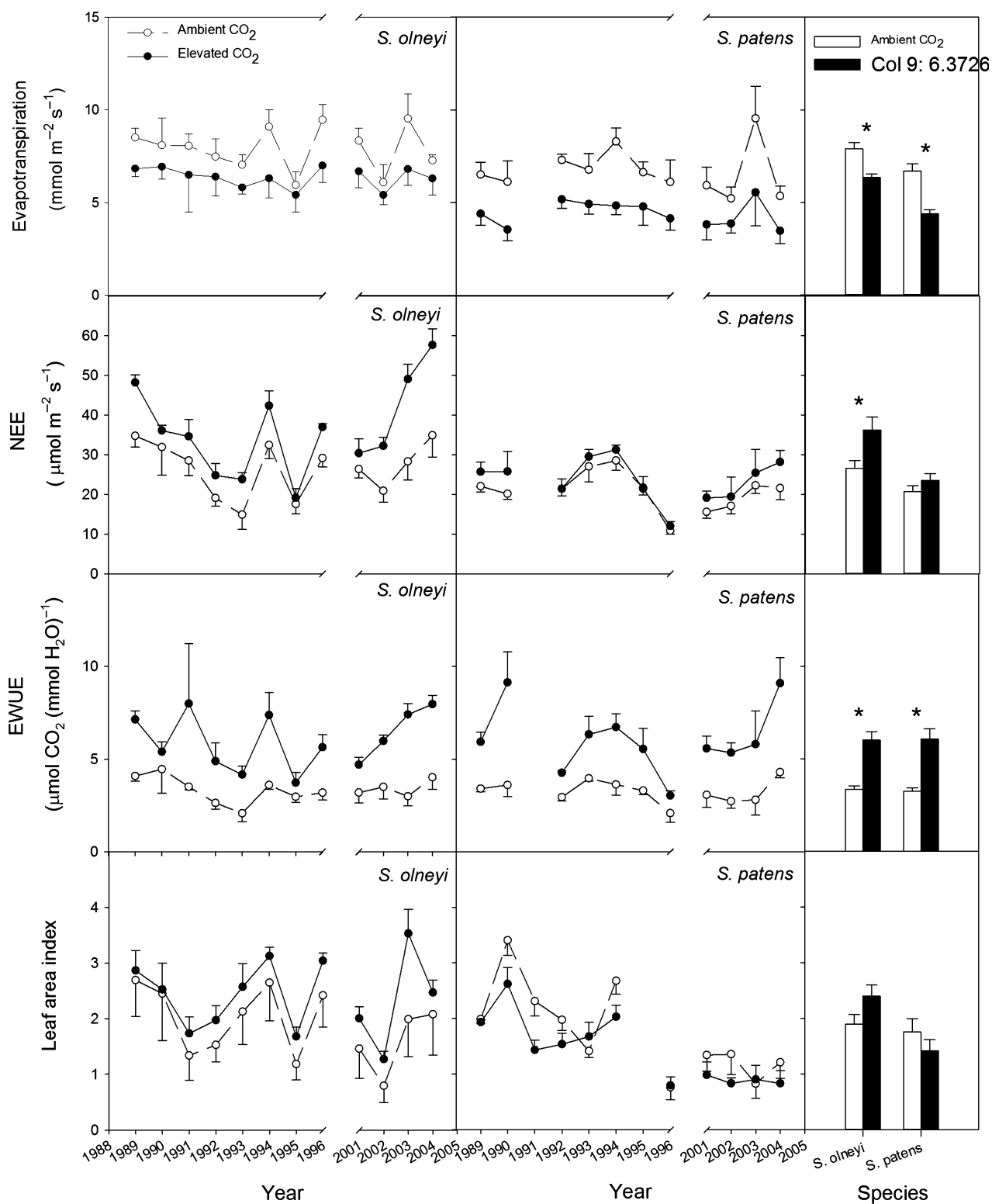


Fig. 9 Average seasonal values for evapotranspiration, net ecosystem CO₂ exchange (NEE), ecosystem water use efficiency (EWUE) measured between 13:00 and 15:00 hours, and leaf area index (LAI) measured during peak of growth (Li *et al.*, 2009). Data were taken during the last week in July and first week in August for each year ($n = 11-13$) for C3 Scirpus and C4 Spartina communities exposed to normal ambient (○, open circles and dashed lines) or elevated atmospheric CO₂ (●, closed circles and solid lines). Panels on right show means and standard errors. * indicates significant CO₂ effect ($P < 0.05$) between treatments for one way analysis of variance.

negative water potential) is consistent with shallow roots exposed to higher salinity than those of the *Scirpus* C3 with their deeper roots in less salty water. Severe water stress often occurred in both species even though roots of the plants were nearly always wet. The large daily excursion of water potentials (ca 1.5 MPa in *Scirpus* C3 and 2.0 MPa in *Spartina* C4) further emphasizes the greater salt tolerance of the C4 grass. Elevated CO_2 reduced the dawn water potential (i.e. reduced water stress) in both species (Arp *et al.*, 1993).

Relief of plant water stress may account for the fact that elevated CO_2 stimulated NEP in the C4 *Spartina* community 13% (Figs 6 and 7), even though in single leaves, there was no stimulation of assimilation by elevated CO_2 (Ziska *et al.*, 1990). In arid lands, the reduction in water loss delayed the drawdown of soil water in plots exposed to elevated CO_2 , which accounted in part for the greater effects of elevated CO_2 in these grasslands during drought than wet years (Morgan *et al.*, 2004).

Elevated CO_2 and nitrogen

The tissue nitrogen in both the *Scirpus* C3 and *Spartina* C4 was reduced by growth in elevated CO_2 (Fig. 10)

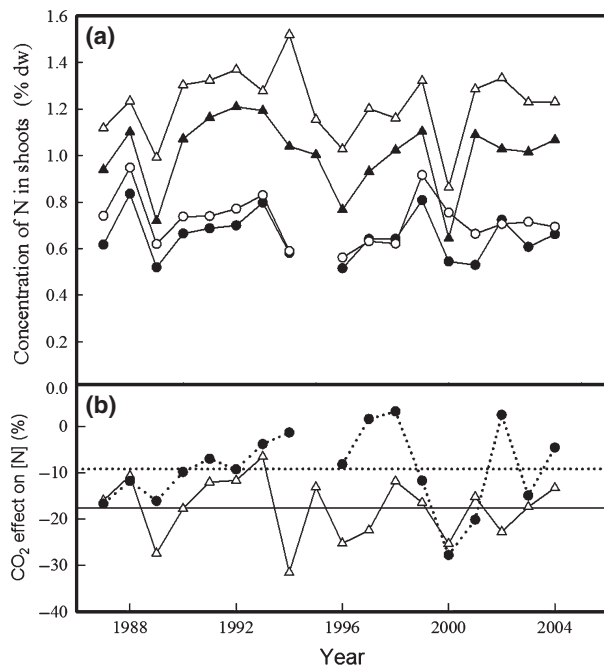


Fig. 10 (a) The nitrogen concentration (% dry weight) in shoots of the *Scirpus* C3, triangles (Δ), and for *Spartina* C4, circles (\circ); open symbols for ambient, closed for elevated CO_2 treatments. (b) The CO_2 effect on nitrogen concentration. It was significant for both species: *Scirpus* C3: mean -17.7% ($P < 0.001$); *Spartina* C4: mean -9.0% ($P = 0.062$).

(Curtis *et al.*, 1989b) and mediated by precipitation (Erickson *et al.*, 2006). Lower nitrogen concentration in elevated CO_2 -grown plants is often attributed to 'dilution', presumably of Rubisco which occupies a large fraction of soluble protein. But lower nitrogen concentration could not be attributed entirely to dilution of Rubisco because growth in elevated CO_2 also resulted in lower nitrogen concentration in roots of *Scirpus* C3 as well as in shoots of *Spartina* C4, in which Rubisco is a relatively small fraction of soluble protein (Jacob & Drake, 1995; Matamala & Drake, 1998; Erickson *et al.*, 2006). The range for the reduction in nitrogen (per unit dry weight) in shoots was 5% to 30% in the *Scirpus* C3 and 0 to 29% in the *Spartina* C4 (Fig. 11). The elevated CO_2 effect on nitrogen concentration was proportional to precipitation (Fig. 11) with the biggest reduction caused by elevated CO_2 during the wettest years (22–35%), while during the driest years, the reduction was only 5 to 10% (Erickson *et al.*, 2006).

These facts suggest that the elevated CO_2 effect on evapotranspiration was responsible for some fraction of the reduced assimilation of nitrogen. In *Spartina* C4, the reduction in evapotranspiration was about twice that in *Scirpus* C3, but the reduction in nitrogen concentration was only about half that in *Scirpus* C3. The effect in the *Spartina* C4 may represent the total effect of reduced transpiration on nitrogen concentration. The higher nitrogen demand of growth in *Scirpus* C3, in which elevated CO_2 stimulated photosynthesis and growth, was also correlated with greater reduction in nitrogen in shoots (Fig. 11). This could explain why the reduction in nitrogen was greater in the *Scirpus* C3, in which photosynthesis was stimulated increasing growth demand, than in the *Spartina* C4 (Fig. 11), in which photosynthesis was stimulated much less, resulting in a smaller demand for nitrogen. Comparing these two different species, one can speculate that reduction in transpiration might account for about half of the reduction in tissue N in species where elevated CO_2 also stimulates growth. McDonald *et al.* (2002) suggested that about 44% of the reduction in nitrogen in elevated CO_2 could be attributed to transpiration with the remaining 56% caused by stimulated photosynthesis and growth.

The mechanism for the reduction in tissue nitrogen concentration in plants grown in elevated CO_2 has been a source of considerable speculation. Taub & Wang (2008) review the literature and main hypotheses that might explain how elevated CO_2 could reduce tissue nitrogen concentration. They conclude that the hypothesis with the most support is that reduced transpiration reduces the supply of nitrogen either through reduction in movement through soil (as suggested by McDonald *et al.*, 2002), or by movement of nitrogen within the

transpiration stream in the plant. McDonald *et al.* (2002) showed that high humidity or high atmospheric CO₂ reduced both transpiration and the assimilation of ¹⁵N from soil in cottonwood seedlings.

Over the course of our study, plant nitrogen concentration was reduced proportional to evapotranspiration: in years of high precipitation, evapotranspiration was high and the reduction in plant nitrogen by elevated CO₂ was greatest (Fig. 11). The opposite was true in dry years.

Thus, the first order effects of elevated CO₂ on stomatal density, stomatal conductance, and transpiration have broad implications for second or third order effects, such as ecosystem processes like nutrient cycling, independent of stimulation of photosynthesis, and growth. The reduction in *Spartina* C4 plant density (Fig. 3) and growth (Fig. 4) by elevated CO₂ may be an example of this effect. Other ecosystem level impacts in which reduced plant nitrogen might have significant

effects include plant insect interaction in C3 species (Thompson & Drake, 1994), osmotic adaptation to salinity stress in halophytes (Drake, 1989), and competition between C3 and C4 species. Langley & Magonigal (2010) showed that *Spartina* C4 could successfully compete with *Scirpus* C3 in elevated CO₂ if supplied with additional nitrogen. This suggests that the nitrogen deficit induced by reduced transpiration in elevated CO₂ caused the reduction in shoot density and biomass of *Spartina* C4 (Figs 3 and 4).

In the sense that chronic exposure to elevated CO₂ induces nitrogen deficit in plants, the stimulation of photosynthesis and growth by elevated CO₂ in *Scirpus* C3 might also be seen to be nitrogen limited, although not sufficient to eliminate the stimulation of additional ecosystem carbon assimilation (Erickson *et al.*, 2006, 2013).

The interaction between elevated CO₂, transpiration, and nitrogen may have consequences for ecosystem carbon balance as a result lower ecosystem respiration (Erickson *et al.*, 2013). Total N in the canopy (g N m⁻² ground area) at the peak of the growing season was, on average, lower in plant canopies at elevated CO₂ treatment (Fig. 9) (Curtis *et al.*, 1989b; Erickson *et al.*, 2006, 2013) in spite of increased biomass in the *Scirpus* C3. Lower total canopy N in the elevated CO₂-treated plants was associated with lower ecosystem respiration Table 1 (Erickson *et al.*, 2013). Drake *et al.* (1999) reported an average of 15–18% reduction in respiration of leaves exposed to elevated CO₂ in three summaries of observations with total numbers of species ranging from 31 to 140 (see Table 1 in Drake *et al.*, 1999). This article also reported that reduced nitrogen in foliage of 15–19% (caused by elevated CO₂) would contribute

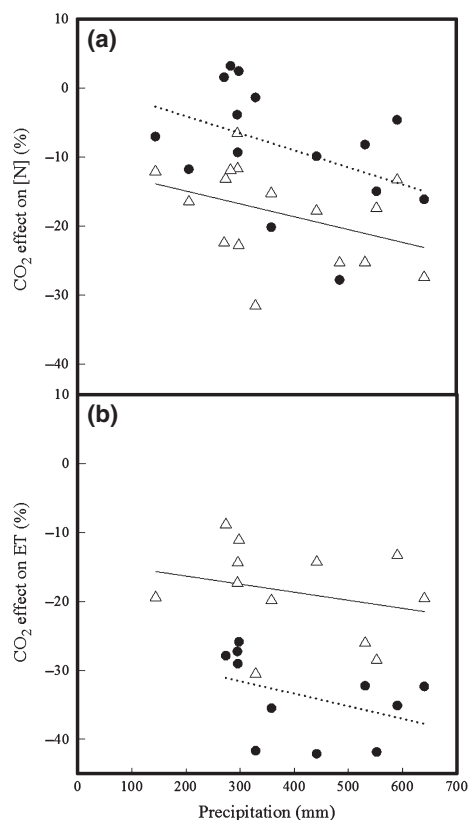


Fig. 11 The effect of annual precipitation during the growing season (mm) on (a) evapotranspiration (*Scirpus* C3: $r^2 = 0.15$, slope of line -0.18 ; *Spartina* C4: $r^2 = 0.18$, slope of line -0.024) and (b) the nitrogen concentration in shoots of *Scirpus* C3 ($r^2 = 0.07$; slope -0.011) and *Spartina* C4 ($r^2 = 0.17$; slope $= -0.018$). Elevated CO₂ reduced both ET and shoot Nitrogen concentration and this effect was proportional to increasing precipitation.

Table 1 Effect of elevated CO₂ on NEE_{night} ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and canopy N content (g N m⁻²) at peak biomass for individual chambers. Equality of variances was tested with Hartley's F_{max} test and found to be nonsignificant in each case (Erickson *et al.*, 2013)

	<i>Scirpus</i> (C3)			<i>Spartina</i> (C4)		
	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD
NEE _{night}						
Ambient	68	-0.442	0.089	73	-0.394	0.110
Elevated	62	-0.405	0.089	72	-0.349	0.089
CO ₂ effect		-8%			-11%	
	t_{128}	$P < 0.01$		t_{143}	$P < 0.01$	
Canopy N						
Ambient	69	6.96	2.06	74	4.55	1.36
Elevated	63	5.94	1.77	72	4.11	1.44
CO ₂ effect		-14.7%			-9.7%	
	t_{130}	$P < 0.01$		t_{144}	$P < 0.01$	

3.4–4.3 Gt C yr⁻¹ to the global carbon sink through reduction in the annual cost of global foliar maintenance respiration, an important impact on global carbon balance.

Higher nitrogen use efficiency was associated with high CO₂ which stimulated more carbon assimilation and biomass production in roots and shoots for the same amount of N in the *Scirpus* C3 than in *Spartina* C4 (Erickson *et al.*, 2006). Elevated CO₂ stimulation of biomass accumulation was greatest during rainy, low salinity years: average stimulation of carbon accumulation in roots and shoots was 2.9 t C ha⁻¹ during the three wettest years (1994, 1996, 2003) but less than half that, 1.2 t C ha⁻¹, in the three driest years (1995, 1999, 2002) (Erickson *et al.*, 2006).

The relative depression of nitrogen concentration in *Scirpus* C3 shoots correlated inversely with salinity and with the relative enhancement of total biomass production (Erickson *et al.*, 2006). Thus, the greatest amount of carbon was added to the *Scirpus* C3-dominated community during years when shoot nitrogen was reduced the most, suggesting that growth demand for nitrogen was a flexible limitation to elevated CO₂ stimulation of carbon assimilation. This suggests a constraint on the concept of progressive nitrogen limitation (Luo *et al.*, 2004).

Associative nitrogen fixation occurs on root surfaces and by free living nitrogen fixers in wetland soils (van Berkum, 1984). Elevated CO₂ increased nitrogen fixation (measured by acetylene reduction) in the C3 *Scirpus* plants but had very little effect on N fixation in C4 *Spartina* (Dakora & Drake, 2000). The level of fixation was sufficient to be important in the growth of the *Scirpus* C3 (Dakora & Drake, 2000) and it was estimated that elevated CO₂ doubled the amount of N fixed compared to plots at normal ambient CO₂ suggesting that excess carbon exudates were available to the N fixers.

Increased growth stimulated by elevated CO₂ reduced available N (NH₄-N) in 1994 by 55%, in the first 10 cm of soil in *Scirpus* C3 but not in the *Spartina* C4 emphasizing again the pervasive effect of elevated CO₂ stimulation of photosynthesis on ecosystem processes (Matamala & Drake, 1998). Available soil nitrogen was drawn down more during a wet year, when growth was very high, than during a drier year (Matamala & Drake, 1998). The trend for elevated CO₂ to drawdown soil nitrogen at 10 cm depth was persistent (Marsh *et al.*, 2005; Keller *et al.*, 2009). But a stronger trend was for higher soil nitrogen at depths of 30 cm or more (Keller *et al.*, 2009) suggesting that elevated CO₂ resulted in a net gain of available nitrogen in the communities where *Scirpus* C3 was dominant.

The wetland vegetation was flexible in allocation of nitrogen reserves and opportunistic in exploiting the

availability of new carbon from stimulation of photosynthesis for the energy needed for additional N fixation. Although there was a measureable depletion of nitrogen reserves in the soil (Matamala & Drake, 1998), elevated CO₂ had a synergistic effect on the nitrogen economy of the wetland: stimulation of nitrogen fixation coupled with increased nitrogen use efficiency combined to increase carbon assimilation. Luo *et al.* (2006) report that elevated CO₂ stimulated accumulation, not depletion, of nitrogen, in native ecosystems.

Methane emission

Methane emission is a major feature of greenhouse gas carbon balance in wetlands. Elevated CO₂ caused an increase in methane emissions from the Chesapeake Bay wetland (Dacey *et al.*, 1994) during the early part of the study, and later measurements of methane dissolved in pore water were consistent with this finding (Marsh *et al.*, 2005; Keller *et al.*, 2009). While the stimulation of methane production by elevated CO₂ was a relatively small component of the wetland carbon balance, increasing methane emission in wetlands may represent an important effect of increasing greenhouse gases on the climate (Poffenbarger *et al.*, 2011).

Where does the extra carbon go?

Stimulation of methane emission (Dacey *et al.*, 1994), nitrogen fixation (Dakora & Drake, 2000), and dissolved organic and inorganic carbon (Marsh *et al.*, 2005; Keller *et al.*, 2009) suggest that much of the carbon assimilated as net ecosystem production (NEP, Fig. 8) is utilized by microbial processes or exported. Losses from the wetland as dissolved organic and inorganic carbon in pore water was determined to be about 49 gC m⁻² yr⁻¹ (Jordan & Correll, 1991). The effects of elevated CO₂ clearly increased carbon in pore water but the rate of loss of carbon from the small CO₂ plots could not be determined because we have no data on the rate of exchange of pore water from sites within the marsh into the adjacent estuary. Freeman *et al.* (2004) report that the proportion of dissolved organic carbon derived from recently assimilated CO₂ in a peatland exposed to elevated atmospheric CO₂ was an order of magnitude higher than from a control study with no elevated CO₂ treatment.

After nearly three decades of exposure, it is clear that elevated CO₂ had a major impact on the plants and ecosystem processes in Chesapeake Bay wetland. These effects were highly variable depending on interaction with the key environmental factors, precipitation, salinity, temperature, and sea level. Elevated CO₂ had major

effects on the nitrogen economy of the plants and ecosystem processes through reduction in transpiration leading to reduced ecosystem respiration. Reduced foliar respiration as rising atmospheric CO₂ affects transpiration could represent a major impact on the land sink for carbon in a higher CO₂ world.

The high initial response to elevated CO₂ seen in ecosystems studies is often reduced or absent in subsequent years (Norby *et al.*, 2005). The duration of this study allows for another test of this observation and the idea that some process, such as progressive nitrogen limitation, may constrain ecosystem responses to elevated CO₂ in the native ecosystems. Elevated CO₂ was still increasing shoot density and biomass in the Scirpus C3 after 28 years. Moreover, the evidence from this study suggests that rising CO₂ may increase nitrogen in ecosystems.

As pointed out by Norby & Zak (2011), the question whether rising atmospheric CO₂ will cause the land sink for anthropogenic carbon to expand or contract has been the basis for most ecosystem studies to date. In the wetland study, we have strong evidence that shoot and root biomass and net ecosystem production increased significantly and I infer from the fact that methane emission (Dacey *et al.*, 1994) and nitrogen fixation were also stimulated by elevated CO₂ (Dakora & Drake, 2000) that inputs of soil carbon also increased. Results of this study and others (e.g. Norby *et al.*, 2005; Norby & Zak, 2011) imply that ecosystems will accumulate additional carbon as atmospheric CO₂ continues to rise as suggested by Luo *et al.* (2006).

Worldwide, there have been less than 50 studies of the effects of elevated CO₂ on ecosystem carbon cycling and most were in midlatitudes where the ambient temperature is 5–15 °C and annual precipitation is 550 to 1200 mm per year (Leakey *et al.*, 2012). Tropical ecosystems may account for the majority of annual CO₂ assimilation in land ecosystems, they exist mainly at the very narrow temperature range of 27–29 °C: there have been no extended studies of the combined impact of rising CO₂, temperature, and drought in them (Leakey *et al.*, 2012). While the data reported here give strong support to the idea that rising CO₂ may stimulate land ecosystems to absorb additional anthropogenic carbon, they also suggest that rising temperature and drought may moderate or even eliminate the effects of rising CO₂ on ecosystem carbon assimilation.

Conclusions

1. This review is based on a 28 year study, begun in 1985 and continuing, of the effects of elevated atmospheric CO₂ (+340 ppm above ambient) in 30 open

top chambers on three communities of C3 and C4 vegetation on a brackish wetland on Chesapeake Bay.

2. In shoots of the Scirpus C3, elevated CO₂ stimulated photosynthesis, increased quantum yield, and decreased the light compensation point, but not in Spartina C4.
3. Elevated CO₂ increased shoot density and biomass in Scirpus C3, but it decreased density and biomass Spartina C4.
4. Rising sea level shifted the Scirpus C3 community to higher elevations on the marsh and led to increased Scirpus C3 shoot biomass in the mixed community and decreased Spartina C4 biomass in both the mixed and pure Spartina C4 communities.
5. Elevated CO₂ reduced stomatal density, stomatal conductance, and transpiration of leaves and stems of both Scirpus C3 and Spartina C4. Evapotranspiration was reduced in both species, but about twice as much in Spartina C4 as in Scirpus C3.
6. Elevated CO₂ reduced nitrogen concentration in both Scirpus C3 and Spartina C4 and the reduction in nitrogen concentration was proportional to precipitation.
7. Elevated CO₂ reduced ecosystem respiration in both Scirpus C3 and Spartina C4 associated with reduced nitrogen in plants.
8. Elevated CO₂ increased net ecosystem production (measured by ecosystem gas exchange), 35% in Scirpus C3 and 15% in Spartina C4. The increased ecosystem CO₂ assimilation occurred in part by reduced dark respiration.
9. The effects of elevated CO₂ on tissue nitrogen concentration, total canopy nitrogen, and ecosystem respiration in both Scirpus C3 and Spartina C4 were related through reduced evapotranspiration.
10. Increasing temperature reduced net ecosystem production 6–8% C⁻¹.

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