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Direct and indirect effects of elevated atmospheric CO_2 on net ecosystem production in a Chesapeake Bay tidal wetland

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Abstract

The rapid increase in atmospheric CO_2 concentrations (C_a) has resulted in extensive research efforts to understand its impact on terrestrial ecosystems, especially carbon balance. Despite these efforts, there are relatively few data comparing net ecosystem exchange of CO_2 between the atmosphere and the biosphere (NEE), under both ambient and elevated C_a. Here we report data on annual sums of CO_2 (NEE_{net}) for 19 years on a Chesapeake Bay tidal wetland for *Scirpus olneyi* (C_3 photosynthetic pathway)- and *Spartina patens* (C_4 photosynthetic pathway)-dominated high marsh communities exposed to ambient and elevated C_a (ambient + 340 ppm). Our objectives were to (i) quantify effects of elevated C_a on seasonally integrated CO_2 assimilation ($NEE_{net} = NEE_{day} + NEE_{night}$, kg C m^{-2} y^{-1}) for the two communities; and (ii) quantify effects of altered canopy N content on ecosystem photosynthesis and respiration. Across all years, NEE_{net} averaged 1.9 kg m^{-2} y^{-1} in ambient C_a and 2.5 kg m^{-2} y^{-1} in elevated C_a, for the C_3-dominated community. Similarly, elevated C_a significantly ($P < 0.01$) increased carbon uptake in the C_4-dominated community, as NEE_{net} averaged 1.5 kg m^{-2} y^{-1} in ambient C_a and 1.7 kg m^{-2} y^{-1} in elevated C_a. This resulted in an average CO_2 stimulation of 32% and 13% of seasonally integrated NEE_{net} for the C_3- and C_4-dominated communities, respectively. Increased NEE_{day} was correlated with increased efficiencies of light and nitrogen use for net carbon assimilation under elevated C_a, while decreased NEE_{night} was associated with lower canopy nitrogen content. These results suggest that rising C_a may increase carbon assimilation in both C_3- and C_4-dominated wetland communities. The challenge remains to identify the fate of the assimilated carbon.

Keywords: carbon storage, ecosystem respiration, elevated CO_2, net ecosystem CO_2 exchange, nitrogen, photosynthesis, tidal wetlands

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Introduction

As atmospheric CO_2 concentrations (C_a) continue to rise, resultant consequences for terrestrial ecosystems remain unclear (Karl & Trenberth, 2003). Thus, research efforts have been focussed on understanding the interaction between rising atmospheric CO_2 and global climate change on ecosystem carbon cycling. Despite these efforts, relatively few studies have reported the net exchange of CO_2 between ecosystems and the atmosphere (NEE) under both ambient and elevated C_a conditions. Long-term studies (i.e. >10 years) that can be used to validate ecosystem models and examine how interannual climate variability interacts with elevated C_a to affect NEE are needed. This lack of data is partly a result of the fact that enclosure methods remain the only way to measure NEE in field experiments and these approaches have generally been excluded in studies using the Free Air Carbon Enrichment method. The limited data available have generally shown increased NEE under elevated C_a (Drake *et al.*, 1996a; Stocker *et al.*, 1999; Hymus *et al.*, 2003; Rasse *et al.*, 2005). In some studies, the stimulation of NEE under elevated C_a disappeared through time (Oechel *et al.*, 1994; Diemer & Körner, 1998). Short-term studies of a year to a few years have the liability that environmental factors that limit or amplify the effects of elevated CO_2 such as drought, high precipitation, and disturbance such as severe storms, do not occur during the course of the study.

Elevated C_a has the potential to affect NEE both directly and indirectly through a number of mechanisms. It can increase NEE directly by enhancing leaf-level carbon assimilation in C_3 plants through enhanced carboxylation and reduced photorespiration (Drake *et al.*, 1997; Ainsworth & Long, 2005). Elevated C_a can also affect NEE indirectly through increased growth and/or leaf area production (Körner *et al.*, 2005; Norby *et al.*, 2005; Rasse *et al.*, 2005), altered plant and/or ecosystem respiration (Amthor, 1991; Drake *et al.*, 1999; Davey *et al.*, 2004; Gonzalez-Meler *et al.*, 2004;

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Carney *et al.*, 2007) altered senescence (Curtis *et al.*, 1989; Sicher & Bunce, 1998; Rae *et al.*, 2006), improved plant water relations (Owensby *et al.*, 1999; Wullschleger *et al.*, 2002; Zavaleta *et al.*, 2003), and altered soil processes (Zak *et al.*, 2000; Luo *et al.*, 2004). Thus, the processes potentially affected by elevated C_a are numerous and likely have contributed to the wide range of photosynthetic and plant growth responses reported in the literature (e.g., Poorter, 1993; Long *et al.*, 2004). Thus, the number of processes affecting carbon cycling has illustrated the need for long-term data to gain a better understanding of how ecosystems will respond to rising C_a.

This study examined annual sums of diurnal ecosystem gas exchange in C_3- and C_4-dominated wetland communities over a 19-year study period. Despite occupying only a small fraction of land area, wetlands are an important source and sink of greenhouse gases (Whiting & Chanton, 1993; Bridgham *et al.*, 2006). For example, previous short-term (<3 years) annual carbon flux data estimated that a C_3-dominated wetland community assimilated approximately 1.5 kg C m^{-2} under ambient C_a conditions (Drake *et al.*, 1996b). In addition, other studies have shown long-term (>15 years) mid-season daily instantaneous NEE (Rasse *et al.*, 2005), long-term relations in biomass and nitrogen dynamics (Erickson *et al.*, 2007), short-term carbon pools and fluxes (Marsh *et al.*, 2005), and short-term daily and annual carbon flux estimates (Drake & Leadley, 1991; Drake *et al.*, 1996a).

What is missing from the literature, however, is an analysis of long-term data on annual NEE in both C_3- and C_4-dominated wetlands. We also analyzed components of NEE – ecosystem carbon assimilation during the day (NEE_{day}, mol CO_2 m^{-2} d^{-1}) and ecosystem respiration at night ($NEE_{night,}$ mol CO_2 m^{-2} d^{-1}). We hypothesized that elevated C_a would increase NEE in the C_3-dominated community, but not the C_4-dominated community (Drake *et al.*, 1996a). We further hypothesized that total aboveground plant nitrogen content would be lower under elevated C_a (Drake *et al.*, 1996b; Erickson *et al.*, 2007) and that this would lead to reductions in ecosystem respiration, further enhancing C assimilation under elevated C_a.

Materials and methods

Site description and experimental design

This study was conducted on Kirkpatrick Marsh on the Rhode River (38°53′N, 76°33′W), a brackish subestuary on the western shore of Chesapeake Bay. The study site was located in the high marsh (40–60 cm above mean low water), which is completely flooded approximately 2% of the time and is representative of brackish high marshes along Mid-Atlantic North America (Jordan & Correll, 1991). Dominant vegetation in the high marsh includes the C_3 sedge *Scirpus olneyi* (A.) Gray (a.k.a. *Schoenoplectus americanus* (Pers.) Volk. Ex Schinz & R. Keller) and the C_4 grass *Spartina patens* (Aiton) Muhl. Within the high marsh, *S. patens* and *S. olneyi* occur in near mono-specific swards as well as in intermingled communities (Arp *et al.*, 1993). As part of an ongoing study in this native wetland, a *S. olneyi*-dominated community and a *S. patens*-dominated community have been exposed to elevated atmospheric carbon dioxide since 1987 (Drake *et al.*, 1989).

Within each community, 15 circular plots of 0.47 m^2 were established according to a randomized block design ($n = 5$) with three treatments per block (Curtis *et al.*, 1989). Blocks were imposed according to proximity in the marsh. Using open-top chambers (OTC), one plot per block was ventilated with ambient air (Ambient treatment) and another plot per block was ventilated with ambient air + 340 ppm CO_2 (Elevated treatment) (Fig. 1). The remaining plot in each block had no chamber but was otherwise treated like the chambered plots (Control treatment). Since 1987, CO_2 exposure began each year when the plants emerged in late April and continued 24 h per day through October following total senescence. A survey of all plots was conducted in 1986 before initiation of the treatments and showed no significant differences in biomass assigned to the three treatments in each community (Arp *et al.*, 1993).

Measurement of net ecosystem exchange

Mean monthly air temperature (T_{air}) and precipitation data were collected from the National Climatic Data Center at nearby Baltimore-Washington International airport (http://www.ncdc.noaa.gov/). Mean hourly water level (MSL) data measured relative to a NOAA/NOS tidal gauge were obtained from the Severn River in Annapolis, Maryland (http://tidesandcurrents.noaa.gov/- station 8575512). No water level data were available for 1995. Incident photosynthetically active radiation (PAR) was measured continuously on site throughout the study. At a central location, a pair of Eppley radiometers fitted with cutoff filters for PAR (400–700 nm) recorded average incident radiation every 15 min. During periods where radiation data were lost at the site, surrogate radiation data from a nearby (<3 km) weather station were used. As ca. 2/3 of annual carbon uptake occurred during the summer months of June, July, and August, climate data are presented for these months (peak growing season) and on annual basis, with the exception of radiation, which was not available on an annual basis.

One advantage of the OTC method for assessing ecosystem responses to elevated C_a is the ability to directly measure the net CO_2 exchange between the ecosystem and the atmosphere per unit ground area (NEE μmol CO_2 m^{-2} s^{-1}); here positive values represent a net flux of CO_2 from the atmosphere into the ecosystem). Acrylic lids with exit chimneys were placed on top of the OTCs to measure NEE calculated as the difference in CO_2 concentrations between inlet ($C_{a,in}$) and outlet ($C_{a,out}$) sampling points multiplied by the flow rate of air through the chambers (Fig. 1). Air from the two sampling points was

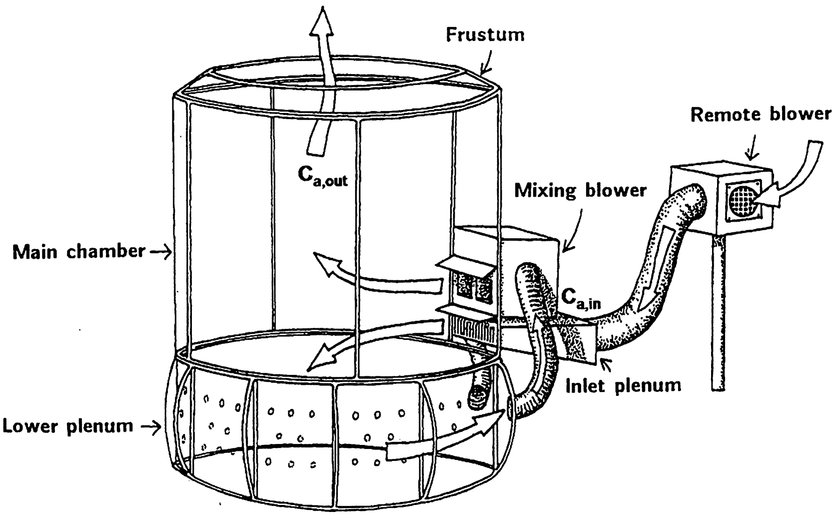

Fig. 1 Diagram of open-top chamber (OTC) used to expose wetland plant communities to elevated C_a and to measure net ecosystem gas exchange (NEE, μmol CO_2 m^{-2} ground s^{-1}). Air is drawn in at the remote blower and exits the chamber through the frustum. NEE was determined from the difference in measured CO_2 concentrations in the air stream from air samples collected the near the frustum ($C_{a,out}$) and the inlet plenum ($C_{a,in}$). Figure modified from Drake *et al.* (1989). Not shown on the drawing is a chimney used on top of chamber to prevent mixing of air in the chamber with air outside chamber during NEE measurements.

pumped continuously from each chamber to a laboratory on the margin of the wetland where CO_2 concentrations and differences ($C_{a,in}-C_{a,out}$) were measured by infrared gas analyzers (Li-Cor, Lincoln, NE, USA). Approximately every 90 s, data from one chamber were measured so that in the course of 15 min, all 10 chambers in one stand could be recorded. Data on NEE were collected over a 3–5 day period during each measurement interval, which occurred approximately every 3 weeks during the growing season (April through November). A subset of each of these measurement periods covering the years from 1987 to 2005 was used in our analysis here. Detailed descriptions of the OTC facility and measurements of NEE are provided in Drake *et al.* (1989), Drake & Leadley (1991) and Drake & Peresta (1994).

While the chambers used in this study have been shown to have effects on microenvironment (Drake *et al.*, 1989) and may slightly overestimate NEE under elevated CO_2 (Niklaus *et al.*, 2000), studies have shown good agreement between measured and modeled NEE data in the wetland study (Rasse *et al.*, 2003) and between NEE data from ambient chambered plots and from nearby eddy covariance data in a scrub oak ecosystem (e.g., Dore *et al.*, 2003). Thus, the 19-year data record presented in this article represents a key contribution to our understanding of NEE under elevated C_a as well as a valuable dataset for modeling ecosystem responses to elevated C_a.

Calculation of net ecosystem production

NEE data, collected periodically from each chamber throughout the growing season, were separated into daytime NEE_{day} and nighttime NEE_{night} based on local sunrise and sunset data. We determined ecosystem respiration during nighttime to be equal to measured nighttime NEE when average wind speed was greater than 0.8 m s^{-1}. As we were unable to identify statistically significant differences between either soil or air temperature and instantaneous rates of ecosystem respiration at night (e.g., Lloyd & Taylor, 1994; Falge *et al.*, 2001), we estimated annual sums (i.e. from beginning of April to end of November) of ecosystem respiration from polynomial regressions of total nightly respiration and day of year (Drake *et al.*, 1996b). Few data were available on NEE over the winter, but data that were collected indicated very little activity (e.g., Marsh *et al.*, 2005) in the winter months.

Annual sums of net ecosystem exchange of CO_2 (NEE_{net}; kg C m^{-2} y^{-1}) were calculated using measured NEE data for days where data were available and modeled data for days where no measurements were made. Modeled data for daytime NEE were estimated using a modified rectangular hyperbola light response equation (e.g., Falge *et al.*, 2001; Powell *et al.*, 2006):

$$\mathrm{NEE} = \frac{\phi_{\mathrm{NEE}}\mathrm{PAR}}{\left(1 - \left(\frac{\mathrm{PAR}}{2000}\right) + \left(\frac{\phi_{\mathrm{NEE}}\mathrm{PAR}}{\mathrm{NEE}_{2000}}\right)\right)} + R_{\mathrm{d}} \qquad (1)$$

where PAR is measured incident photosynthetically active radiation, ϕ_{NEE} is apparent ecosystem quantum yield (μmol CO_2 μmol $quantum^{-1}$), NEE_{2000} at light saturation (2000 μmol m^{-2} s^{-1}), and R_d (μmol CO_2 m^{-2} s^{-1}) is ecosystem respiration during the day. Model parameters (ϕ_{NEE}, NEE_{2000}, and R_d) were estimated from measured NEE vs. PAR (15 min averages, see Fig. 3) using the above equation in PROC NLIN of the SAS system (SAS Institute Inc., 1999) for days with sufficient data. See (Data S1) on details of the light response curve and the seasonal trends in $\phi_{NEE,}$ $GPP_{2000,}$ and $NEE_{day.}$ To account for seasonal variation in modeled parameters (Powell *et al.*, 2006), time-weighted averages of model parameters were used between measurement intervals. These derived parameters were subsequently combined with measured PAR to estimate NEE for days where no measured data were available. (See Data S1) Daily NEE estimates were summed over the course of the year for months when plants were active (approximately May through October) to estimate annual sums for NEE_{day}. Finally, seasonally integrated ecosystem gas exchange, NEE_{net} (kg C m^{-2} y^{-1}) was estimated as the sum of NEE_{day} and NEE_{night}. This approach allowed us to use physiologically meaningful parameters for estimating annual net carbon exchange.

Biomass and nitrogen estimates

During annual harvests, data were collected on *S. olneyi* shoot properties from 1987 to 2005. At the peak of the growing season, which occurred during the last week of July to the first week in August (Curtis *et al.*, 1989), photosynthetically active (green tissue) *S. olneyi* shoots in each plot were counted and measured for length and width at ½ shoot length. Each year, shoots from random quadrats in each plot were harvested (ca. 10 shoots per plot) and shoot biomass was estimated using census data and allometric relations from harvested subsamples as described in Curtis *et al.* (1989). Aboveground biomass of C_4 grasses was estimated by subsampling five randomly selected 25 cm^2 quadrats in each plot. Shoots chosen for subsampling from each of the plots were oven dried at 60 °C to a constant mass, weighed, ground to pass through a 60 mesh screen and analyzed for tissue carbon and nitrogen concentrations (see Drake *et al.*, 1996a). Total canopy nitrogen content was determined from estimates of shoot biomass at peak season combined with tissue nitrogen concentrations.

Data analyses

Treatment effects on annual daytime and nighttime net ecosystem exchange of CO_2 (NEE_{day}, NEE_{night}) over 19 consecutive years (1987–2005) were analyzed using a repeated-measures (treating year as a repeated categorical variable) approach in PROC MIXED of the SAS statistical software system (e.g., Littell *et al.*, 1998; SAS Institute Inc., 1999). CO_2 treatment was treated as a fixed effect and the block x treatment (chamber) interaction was treated as a random effect. To assess treatment effects on response variables, data from elevated C_a plots were compared to data from ambient chambered plots. To account for potential dependence among observations through time, a discrete autoregressive correlation model was used to model dependence among the within-group errors. Degrees of freedom were determined using the Satterthwaite approximation. In addition, relations between canopy nitrogen content and ecosystem respiration were analyzed using standard regression procedures for years data were available in the C_3-dominated community. Treatment effects were considered significant at $P < 0.05$ for all analyses.

Results

Climate data

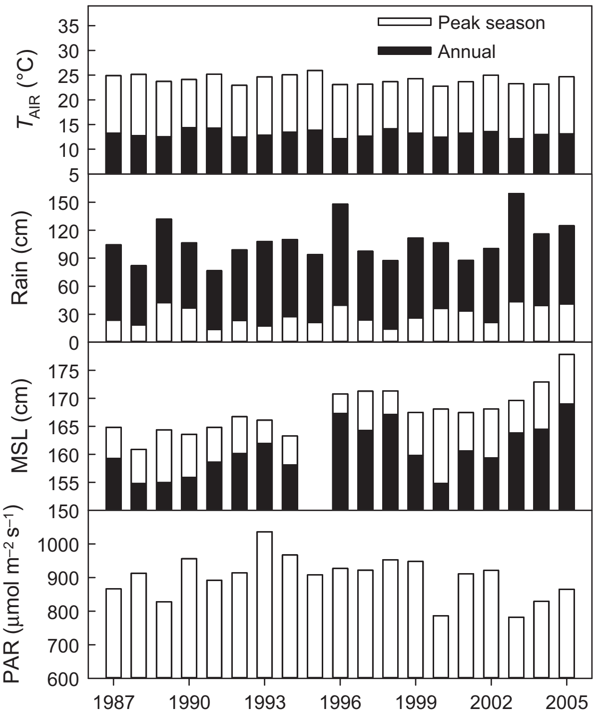

Fig. 2 Seasonal climate data during the 19-year study period. Air temperature (T_{air}), Mean hourly water level (MSL) and photosynthetically active radiation (PAR) represent mean data for a given year (annual) or for the growing season months of June, July and August (peak season). Similarly precipitation data represent the sum of precipitation received during the year and during peak growing season months.

Throughout the 19-year data collection period, variation in T_{air} and PAR was relatively modest (CV < 10%) compared to precipitation and water level (Fig. 2). Over threefold variation in precipitation was observed during the peak growing season months ranging from 13.6 cm in 1991 to 43.5 cm in 2003. Mean water level varied over 14 cm during the course of the study and showed an increasing trend with time. Precipitation, T_{air} and PAR were all loosely correlated as years that had high precipitation had relatively low T_{air} and low PAR. However, MSL was not strongly correlated with other climate variables.

Daytime net ecosystem exchange

Data on instantaneous diurnal NEE (μmol CO_2 m^{-2} s^{-1}) showed the influence of plant species for carbon exchange (Fig. 3). Generally, NEE was higher in the C_3 (*S. olneyi*)-dominated community compared to the C_4 (*S. patens*)-dominated community. The two communities also responded differently to precipitation, as the C_3-dominated community showed greatly increased NEE in response to abundant precipitation (2003 shown), while the C_4-dominated community appeared to be relatively insensitive to precipitation.

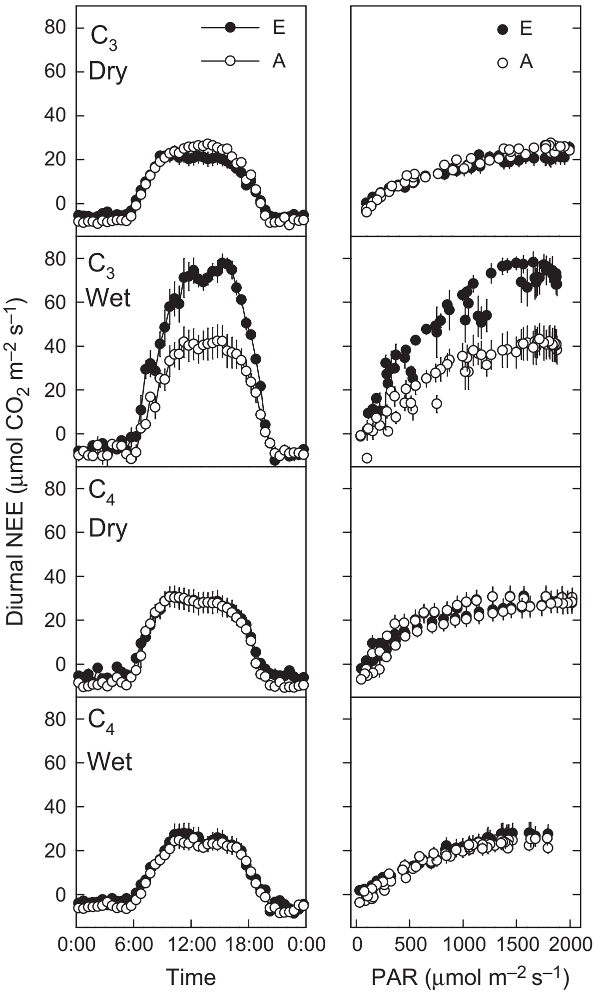

Fig. 3 Fluxes of carbon (NEE) during peak growing season for C_3- and C_4-dominated wetland communities during a dry year (1999) and a wet year (2003). The first panel presents diurnal course of NEE, while the second panel presents daily NEE vs. PAR, which was used to determine physiological response parameters. Open circles represent the mean of the chambered ambient C_a treatment (A) and the filled circles represent the mean of the elevated C_a treatment (E). Vertical bars represent standard error (n = 5).

Furthermore, the CO_2 effect on NEE was often greater during wet years in the C_3-dominated community, but response of NEE to elevated C_a in the C_4-dominated community was similar in both wet and dry years. Finally, we saw good relationships between incident PAR and NEE during the day, although there was evidence of depressed NEE in the afternoon (compared to similar PAR values in the morning), likely related to stomatal closure caused by high vapor pressure deficits (Fig 3).

Elevated C_a significantly ($P < 0.01$) enhanced seasonally integrated daytime, NEE_{day}, in both the C_3- and C_4-dominated communities, but to a greater extent in the C_3-dominated community (Table 1). NEE_{day} was also significantly ($P < 0.01$) affected by year, with greater variance in the C_3-dominated community. For the C_3-dominated community, NEE_{day} averaged 2.3 kg C m^{-2} y^{-1} in ambient C_a and 2.9 kg C m^{-2} y^{-1} in elevated C_a, while for the C_4-dominated community, NEE_{day} averaged 1.9 kg C m^{-2} y^{-1} in ambient C_a and 2.1 kg C m^{-2} y^{-1} in elevated C_a. A significant CO_2 × year interaction was seen in the C_3-dominated community, but not in the C_4-dominated community. Variation in NEE_{day} was significantly ($P < 0.01$) correlated with canopy nitrogen content at peak biomass in the C_3-dominated community for both treatments (Fig. 5). Elevated C_a significantly ($P < 0.01$) increased the intercept of the relationship between NEE_{day} and canopy nitrogen content, but did not significantly affect the slope of this relationship. In the C4 community, variation in NEE_{day} was not correlated with variation in N (Fig. 5).

Increased NEE_{day} under elevated C_a resulted from significantly ($P < 0.01$) increased ϕ_{NEE} and GPP_{2000} at light saturation in both communities (Tables 2 and 3). However, elevated C_a effects on ϕ_{NEE} were relatively greater (approximately twofold) in the C_3-dominated community. Finally, within a given year, seasonality did not appear to strongly influence elevated C_a effects on NEE_{day} (bimonthly), although it was larger late in the season for a couple of years (data not shown).

Table 1 P-values resulting from repeated-measures analysis assessing treatment effects (ambient or elevated C_a treatment) on net ecosystem production during the day (NEE_{day}, kg C m^{-2} y^{-1}), net ecosystem production during nighttime (NEE_{night}, kg C m^{-2} y^{-1}) and net ecosystem production (NEE_{net}, kg C m^{-2} y^{-1}) in C_3-dominated (*S. olneyi*) and C_4-dominated (*S. patens*) marsh communities on a sub-estuary of Chesapeake Bay.

	C_3-dominated (*S. olneyi*)			C_4-dominated (*S. patens*)		
	NEE_{day}	NEE_{night}	NEE_{net}	NEE_{day}	NEE_{night}	NEE_{net}
CO_2	<0.01 (+)	<0.01 (−)	<0.01 (+)	<0.01 (+)	<0.01 (−)	<0.01 (+)
Yr	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
CO_2 × Yr	0.03	<0.01	0.01	0.35	<0.01	0.69

Note: (+) denotes a significant increase and (−) a decrease due to elevated CO_2

Table 2 Overall means ($n = 19$ y) for light response parameters statistically derived from measures of incident radiation and NEE at peak biomass (approximately the last week of July) for ambient and elevated C_a treatments in the *S. olneyi*- and *S. patens*-dominated communities. Model parameters include ecosystem quantum yield (ϕ_{NEE}, μmol CO_2 μmol^{-1} quanta), gross primary productivity at light saturation (NEE_{2000}, μmol CO_2 m^{-2} s^{-1}) and ecosystem respiration during the day (R_d, μmol CO_2 m^{-2} s^{-1})

	C_3-dominated (*S. olneyi*)			C_4-dominated (*S. patens*)		
	ϕ_{NEE}	NEE_{2000}	R_d	ϕ_{NEE}	NEE_{2000}	R_d
Ambient	0.058	43	−7.8	0.046	34	−7.0
Elevated	0.087	54	−7.0	0.057	38	−6.2

Table 3 *P*-values resulting from repeated-measures analysis assessing treatment effects (ambient or elevated C_a treatment) on ecosystem quantum yield (ϕ_{NEE}, μmol CO_2 μmol^{-1} quanta), gross primary productivity at light saturation (NE_{2000}, μmol CO_2 m^{-2} s^{-1}) and ecosystem respiration during the day (R_d, μmol CO_2 m^{-2} s^{-1}) in C_3-dominated (*S. olneyi*) and C_4-dominated (*S. patens*) marsh communities on a subestuary of Chesapeake Bay. Above analyses done on parameter estimates determined from radiation and NEE data measured at peak biomass around late July.

	C_3-dominated (*S. olneyi*)			C_4-dominated (*S. patens*)		
	ϕ_{NEE}	NEE_{2000}	R_d	ϕ_{NEE}	NEE_{2000}	R_d
CO_2	<0.01 (+)	<0.01 (+)	<0.01 (−)	<0.01 (+)	<0.01 (+)	<0.01 (−)
Yr	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
CO_2 × Yr	0.33	0.04	<0.01	0.96	0.84	<0.01

Note: (+) denotes a significant increase and (−) a decrease due to elevated CO_2

Ecosystem respiration (NEE_{night})

Elevated C_a reduced fluxes of carbon from the ecosystem to the atmosphere at night, and thus significantly ($P < 0.01$) reduced seasonally integrated NEE_{night}, in both communities (Tables 1 and 4; Fig. 4). In addition, year and CO_2 × year both significantly ($P < 0.01$) affected NEE_{night} during the study. Overall, NEE_{night} averaged −0.44 and −0.40 kg C m^{-2} y^{-1} in ambient and elevated C_a for the C_3-dominated community, and averaged −0.39 and −0.35 kg C m^{-2} y^{-1} in ambient and elevated C_a for the C_4-dominated community. Thus, NEE_{night} as a fraction of NEE_{day} ranged from about 14 to 20%. Significantly lower NEE_{night} (i.e. less C loss at night) in both communities at elevated CO_2 was also associated with lower canopy nitrogen content of the vegetation (Fig 5; Table 4). Total N in the canopy (g N m^{-2} ground area) of the Scirpus C3 community was, on average 1.02 g N m^{-2} lower in the elevated CO_2 treatment, about 15% of mean canopy N, and 0.44 g N m^{-2} or 9.7% of mean canopy N in the C4 community (Fig 6; Table 4).

Seasonally integrated net ecosystem exchange

Throughout the 19-year data collection period, seasonally integrated NEE_{net} (= Nee_{day} + Nee_{night}) in the C_3-dominated community ranged from 1.3 to 2.5 kg C m^{-2} y^{-1} in ambient C_a and from 1.6 to 3.1 kg C m^{-2} y^{-1} in elevated C_a (Fig. 3). Across all years, NEE_{net} averaged 1.9 kg C m^{-2} y^{-1} in ambient C_a and 2.5 kg C m^{-2} y^{-1} in elevated C_a, resulting in an average CO_2 stimulation of 31% throughout the study. Year significantly affected NEE_{net} ($P < 0.01$), which indicated environmentally mediated variability in NEE_{net}. For example, when precipitation was relatively high and PAR relatively low in 1996 and 2003 (Fig. 2), NEE_{net} was relatively high (Fig. 4), whereas it was relatively

Table 4 Effect of elevated CO_2 on NEE_{night} (kg C m^{-2} y^{-1}) and canopy N content (g N m^{-2}) at peak biomass. Data are for individual chambers for all years that data were available, about 73% of possible values. Equality of variances was tested with Hartley's F_{max} test and found to be nonsignificant in each case

	Scirpus (C3)			Spartina (C4)		
	n	Mean	SD	*n*	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}	$P < 0.01$

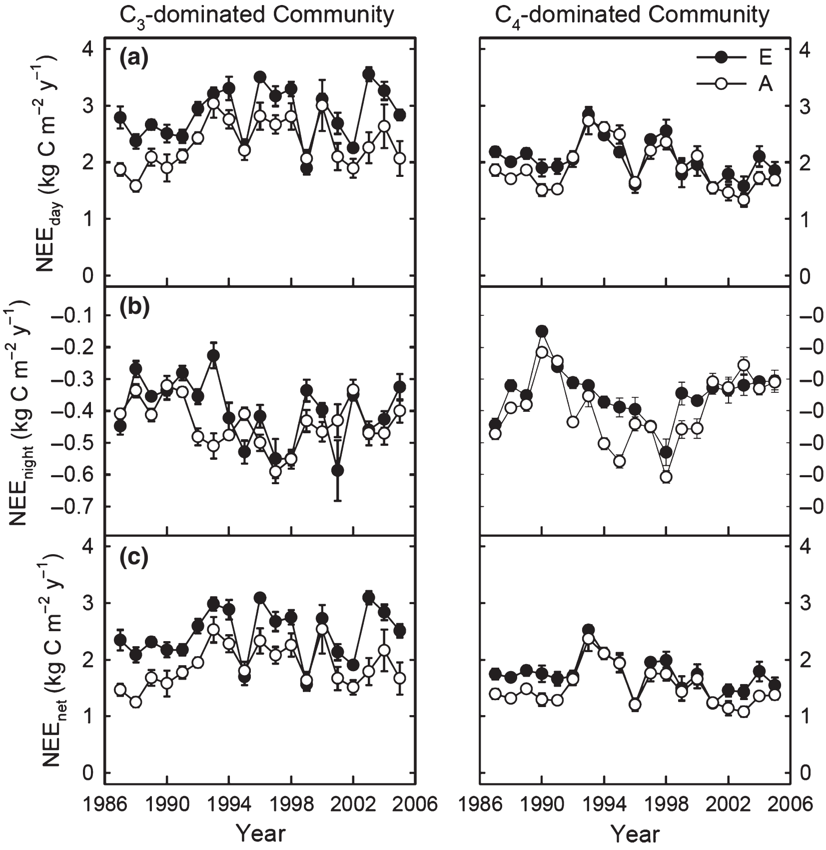

Fig. 4 (a). Mean (± SE; $n = 5$) daytime net ecosystem exchange (NEE_{day}; kg C m^{-2} y^{-1}) during the 19-year study period for C_3-dominated (*S. olneyi*) and C_4-dominated (*S. patens*) communities (b). Mean (± SE; $n = 5$) nighttime net ecosystem exchange (NEE_{night}; kg C m^{-2} y^{-1}) or ecosystem respiration. (c). Mean (± SE; $n = 5$) total seasonal net ecosystem exchange where $NEE_{net} = NEE_{day} + NEE_{night}$. Open circles represent ambient C_a chambered plots and filled circles represent elevated C_a chambered plots.

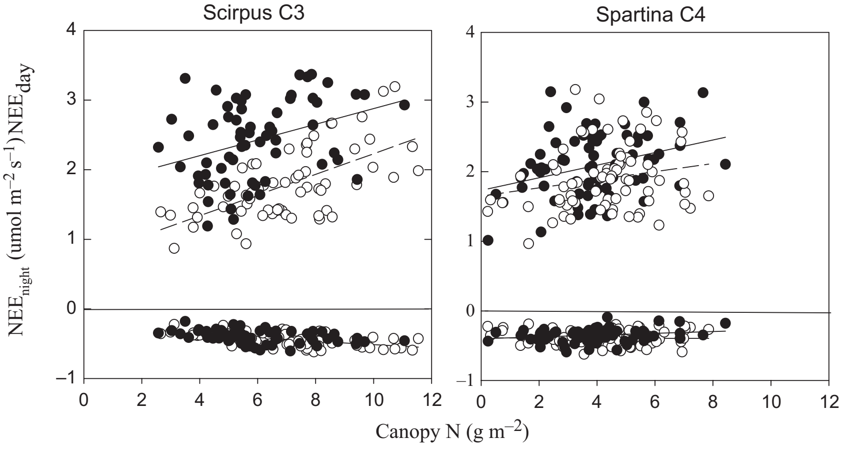

Fig. 5 Relations between total canopy nitrogen content (g N m^{-2}) at peak biomass and annual net carbon uptake during the day (NEE_{day}; kg C m^{-2} y^{-1}) and annual nighttime ecosystem respiration (NEE_{night}; kg C m^{-2} y^{-1}) for individual chambers in the C_3-dominated and C4-dominated communities from 1987 to 2004 where data were available. *Scirpus* C3:Regression equations for NEE_{day} are (Elevated): $y = 0.11x + 1.75$ ($R^2 = 0.12$; $P < 0.01$); (Ambient): $y = 0.15x + 0.75$ ($R^2 = 0.38$; $P < 0.01$). CO_2 significantly ($P < 0.01$) increased the intercept. Regression equation across all data for NEE_{night}: $y = -0.022x - 0.283$ ($R^2 = 0.22$; $P < 0.01$). Elevated C_a did not significantly affect slope ($P = 0.67$) or intercept ($P = 0.45$) of the relationship. *Spartina* C4: Regression equations for NEE_{day} (Elevated: $y = 0.09x + 1.73$, $R^2 = 0.098$); (Ambient: $y = 0.058x + 1.64$, $R^2 = 0.04$). CO_2 had no effect on intercept or slope. NEE_{night} Elevated ($y = 0.008x - 0.400$, $R^2 < 0.005$); Ambient ($y = 0.008x - 0.388$, $R^2 < 0.002$.) Elevated CO_2 had no effect on slope of intercept.

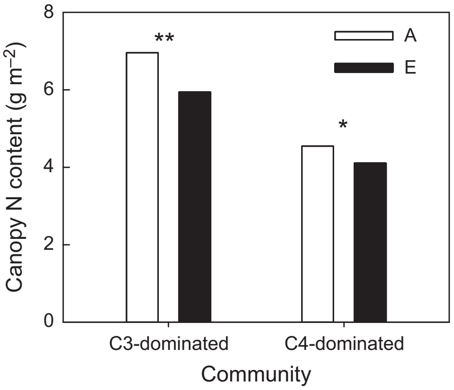

Fig. 6 Mean canopy N content (g N m^{-2}) at peak biomass in the C_3-dominated (*S. olneyi*) and C_4-dominated (*S. patens*) communities from 1987 to 2004 where data were available. Asterisks indicate that canopy N at elevated C_a is significantly less than at ambient C_a within community at the $P < 0.05$ (*) and $P < 0.01$ (**) levels.

low in 1995 and 1999 during years of relatively low precipitation and high PAR. Moreover, we found a significant CO_2 × year interaction ($P = 0.01$), which showed that the CO_2 effect varied from year to year.

Similar to the C_3-dominated community, elevated C_a significantly ($P < 0.01$) increased carbon uptake in the C_4-dominated community (Table 1), but the magnitude of the effect was greatly reduced: NEE_{net} averaged 1.5 kg C m^{-2} y^{-1} in ambient C_a and 1.7 kg C m^{-2} y^{-1} in elevated C_a or an average CO_2 stimulation of 13% throughout the study. In the C_4-dominated community NEE_{net} varied significantly ($P < 0.01$) from year to year ranging from 1.1 to 2.4 kg C m^{-2} y^{-1} in ambient C_a and from 1.2 to 2.5 kg C m^{-2} y^{-1} in elevated C_a. In contrast to the C_3-dominated community, however, no significant CO_2 × year interaction ($P = 0.69$) was seen in the C_4-dominated community, indicating that the CO_2 effect on NEE_{net} was consistent across interannual variability in environmental conditions.

Discussion

The objective of this study was to examine the effects of elevated C_a on CO_2 assimilation over a 19-year period in C_3-dominated and C_4-dominated tidal wetland communities. We tested the hypothesis that elevated C_a would enhance NEE_{net} in the C_3-dominated community, but not the C_4-dominated community. The data supported our hypothesis for the C_3-dominated community, but interestingly, we also found a lower but significant enhancement of NEE_{net} in the C_4-dominated community (ca. 31% in C_3 compared to 13% in C_4). In addition, we tested the hypothesis that elevated C_a would reduce ecosystem respiration at night in the C_3-dominated community and that this reduction in NEE_{net} would be correlated with indirect effects of elevated C_a on canopy nitrogen content. Although the data were quite variable, we found support for this hypothesis as NEE_{night} was associated with canopy N content (i.e. greater respiration occurred in canopies with greater N content) in both the C_3-dominated and C4-dominated community and no significant CO_2 effect on the slope of this relationship was observed, indicating no apparent direct effect of elevated C_a on NEE_{night}.

NEE$_{day}$

Data on diurnal NEE illustrated the high rates of carbon assimilation found in this ecosystem, even under ambient C_a conditions. The midseason mean maximum rate of midday NEE in the C_3-dominated community of about 35 μmol m^{-2} s^{-1} (Table 2; Rasse *et al.*, 2005) under ambient conditions was greater than most forested ecosystems. For example, 7 μmol m^{-2} s^{-1} was reported for a boreal woodland (Fan *et al.*, 1995), about 14 μmol m^{-2} s^{-1} for Florida slash pine and scrub oak ecosystems (Clark *et al.*, 1999; Hymus *et al.*, 2003; Powell *et al.*, 2006), 15 μmol m^{-2} s^{-1} in Amazonian rain forest and riparian wetlands (Grace *et al.*, 1996; Scott *et al.*, 2003), 22 μmol m^{-2} s^{-1} in northern hardwood stands (Wofsy *et al.*, 1993), and 28 μmol m^{-2} s^{-1} in a southern hardwood forest (Greco & Baldocchi, 1996). In addition, our midday maximum NEE data were also considerably higher (approximately threefold) than that reported for a high marsh on the Texas Gulf Coast (Heinsch *et al.*, 2004), but their marsh ecosystem was considerably more saline than the marsh in this study. However, our midday maximum rates of NEE were comparable to a native tall grass prairie ecosystem, which reported a maximum NEE of about 32 μmol m^{-2} s^{-1} at peak growth (Suyker & Verma, 2001). Thus, this marsh ecosystem is clearly capable of high rates of daytime carbon assimilation, exceeding many ecosystems studied to date.

Despite high rates of ambient NEE, elevated C_a significantly enhanced NEE_{day} in both the C_3- and C_4-dominated communities (Table 1; Fig. 4). In contrast to early findings from the study that indicated the disappearance of a CO_2 effect on NEE in the C_4-dominated community, the findings from the long-term data indicated a sustained response in the C_4-dominated community. This difference in findings illustrates the importance of long-term data. Overall, the effects of elevated C_a on NEE_{day} were greater in the C_3-dominated community (approximately twofold). Stimulation of NEE_{day} by elevated C_a was mediated by significant increases in both ϕ_{NEE} and NEE_{2000} (Tables 2 and 3). While these parameters and NEE_{day} were stimulated in both communities, the mechanisms underlying these responses were likely different between the two communities.

In the C_3-dominated community, elevated C_a stimulation of NEE_{day} resulted not only from a direct stimulation of photosynthetic carbon assimilation under elevated C_a (Drake *et al.*, 1997) but also from increased C_3 photosynthetic shoot biomass production (Erickson *et al.*, 2007). Elevated C_a increased the efficiency with which light was used for net carbon uptake (ϕ_{NEE}; Table 2) by the ecosystem (Drake *et al.*, 1997). Similarly, the data showed sustained and increased efficiency in the use of nitrogen for net carbon assimilation (Fig. 3, Table 4). Thus, despite acclimation of photosynthesis in *S. olneyi* (Jacob *et al.*, 1995; Drake *et al.*, 1996b) and potentially other indirect effects of elevated C_a on carbon and nitrogen cycling (e.g., decomposition), our data indicated that elevated C_a sustained stimulation of annual carbon uptake throughout the 19-year duration of the study. We also saw a significant $CO_2 \times$ year interaction on NEE_{day} (Table 1) in the C_3-dominated community, likely indicating interactions with annual climate variability. For example, in three wet years (1996, 2000 & 2003), elevated C_a increased NEE_{day} on average by ca. 29%, while in three dry years (1995, 1999 & 2002) the average effect of elevated C_a was only ca. 4%. Rasse *et al.* (2005), who showed that stimulation of measured instantaneous NEE by elevated C_a was positively correlated with precipitation.

The significant stimulation of NEE_{day} under elevated C_a in the C_4-dominated community was harder to explain. No significant enhancement of photosynthetic biomass was found for the C_4-dominated community (Erickson *et al.*, 2007) and no significant stimulation of leaf-level photosynthetic capacity was seen for *S. patens* (Ziska *et al.*, 1990). Therefore, increased carbon uptake in the C_4-dominated community is consistent with either improved water relations, which was reported for *S. patens* (Arp *et al.*, 1993) and could have resulted in increased carbon uptake, especially during conditions that induce stomatal closure (e.g., high VPD, flooding, and/or high salinity) and/or decreased autotrophic respiration (Gonzalez-Meler *et al.*, 2004) associated with significantly reduced plant nitrogen content (Erickson *et al.*, 2007).

Nighttime ecosystem respiration

In contrast to relatively high assimilation of CO_2, loss of carbon through ecosystem respiration was comparatively low, about -7 μmol m^{-2} s^{-1} under ambient conditions. Tidal wetlands soils are anaerobic (Bridgham *et al.*, 2006) and they export significant amounts of dissolved organic and inorganic carbon (Jordan & Correll, 1991; and Marsh *et al.*, 2005). These facts suggest that soil respiration is relatively low (Jordan & Correll, 1991) and that NEE_{night} is therefore predominantly shoot respiration. In comparison, a tall grass native prairie with similar rates of daytime NEE and presumably little export of dissolved organic and inorganic carbon, showed much greater rates of nighttime NEE (around -11.4 μmol m^{-2} s^{-1} at peak growth, Suyker & Verma, 2001).

As reported in a previous article (Drake *et al.*, 1996b), elevated C_a significantly depressed absolute value of NEE_{night} in the C_3-dominated community. Reduced ecosystem respiration contributed to increased net carbon assimilation in this wetland (Table 4, Fig. 5). We found that elevated C_a significantly reduced NEE_{night} in both the C3-dominated Scirpus and C_4-dominated community (Tables 1 and 4). Throughout the 19-year study the depression of ecosystem respiration and standing crop of canopy N, averaged about −8% and −14.7% in the *Scripus* C3 and about −11.7% and −9.7% in the *Spartina* C4 dominated communities. A 7% reduction in annual ecosystem respiration annual caused by elevated C_a was reported in Scots pine (Wang, 1996).

The reduction in NEE_{night} under elevated C_a was strongly associated with reduction in total standing crop of canopy nitrogen (Fig. 5, Table 4). Jacob *et al.* (1995) report reduction in about 50% in soluble foliar protein of *S. olneyi*. The concentration of soluble leaf nitrogen has been related to plant respiration rates (Azcon-Bieto *et al.*, 1994; Ryan, 1995; Reich *et al.*, 1998; Tjoelker *et al.*, 1999). The indirect effect of reduced plant tissue nitrogen observed under elevated C_a (Erickson *et al.*, 2007) mediated by down-regulation of photosynthetic and other metabolic enzymes (Jacob *et al.*, 1995) likely explained why values of NEE_{night} were reduced under elevated C_a despite increased *S. olneyi* biomass production.

Seasonally integrated net ecosystem exchange

High rates of photosynthesis combined with low rates of respiration in largely anaerobic soils resulted in substantial net carbon uptake in this wetland ecosystem. For example, mean NEP (kg C m^{-2} y^{-1}) for ambient conditions was nearly double that of a slash pine stand in Florida (Clark *et al.*, 1999) and more than 20% greater than a southern hardwood forest (Greco & Baldocchi, 1996). Furthermore, data from this long-term study indicated that elevated C_a of ca. 700 μmol mol^{-1} is likely to stimulate net carbon uptake not only via increased net photosynthesis during the day but also via reduced carbon losses at night in both C_3- and C_4-dominated communities in this high marsh ecosystem (Tables 1 and 4; Fig. 5). Throughout the 19-year duration of the study elevated C_a increased NEE_{net} by 10.6 kg C m^{-2} in the C_3-dominated community, and by 3.9 kg C m^{-2} in the C_4-dominated community. In the C_3-dominated community about 9.8 kg C m^{-2} was from increased NEE_{day} and 0.8 kg C m^{-2} was from reduced NEE_{night}, while in the C_4-dominated community, 2.9 kg C m^{-2} was from increased NEE_{day} and 1.0 kg C m^{-2} was from reduced NEE_{night}.

The fate of much of the carbon assimilated in this marsh community is not well understood. Based on data collected during 2003, only ca. 10% of the increased carbon assimilated by the C_3-dominated community under elevated C_a could be accounted for in biomass (Erickson *et al.*, 2007). In fact, in some cases increased NEE_{net} was even associated with reduced carbon in biomass (e.g., C_4-dominated community). It is possible that our methods underestimate biomass: peak biomass may occur at different times each year depending on environmental conditions, new shoot production may occur into the fall, we may have underestimated root biomass production by sampling only once per year with root ingrowth cores that would miss fine root turnover (Neill, 1992). It also appears unlikely that the elevated C_a stimulation of carbon loss as methane is a significant factor in ecosystem carbon balance (Marsh *et al.*, 2005). Instead, the most likely fate of the excess carbon assimilated under elevated C_a is dissolved organic and inorganic carbon, some of which is exported from the marsh (Jordan & Correll, 1991; Marsh *et al.*, 2005), and some remains as new soil accretion as has been recently shown to occur in short-term elevated CO_2 studies (Langley *et al.*, 2009) on Kirkpatrick Marsh.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Data S1. Data on the model used to determine the coefficients for the light response curve, seasonal variation in the coefficients, and seasonal variation in measured and modeled total daily CO_2 assimilation.