

Carbon dioxide assimilation by a wetland sedge canopy exposed to ambient and elevated CO₂: measurements and model analysis

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Summary

1. The wetland sedge *Scirpus olneyi* Gray displays fast rates of CO₂ assimilation and responds positively to increased atmospheric CO₂ concentration. The present study was aimed at identifying the ecophysiological traits specific to *S. olneyi* that drive these CO₂-assimilation patterns under ambient and elevated CO₂ conditions.
2. The net ecosystem exchange (NEE) of CO₂ between *S. olneyi* communities and the atmosphere was measured in open-top chambers.
3. We developed a new mechanistic model for *S. olneyi* communities based on published ecophysiological data and additional measurements of photosynthetic parameters.
4. Our NEE measurements confirmed that *S. olneyi* communities have a high rate of summertime CO₂ assimilation, with noontime peaks reaching 40 μmol CO₂ m⁻² ground s⁻¹ on productive summer days, and that elevated CO₂ increased *S. olneyi* CO₂ assimilation by *c.* 35–40%.
5. Using *S. olneyi*-specific ecophysiological parameters, comparison with measured NEE showed that the model accurately simulated these high rates of CO₂ uptake under ambient or elevated CO₂.
6. The model pointed to the Rubisco capacity of *Scirpus* leaves associated with their high total nitrogen content as the primary explanation for the high rates of CO₂ assimilation, and indicated that the vertical-leaf canopy structure of *S. olneyi* had comparatively little influence on CO₂ assimilation.

Key-words: Canopy structure, global change, leaf nitrogen, open-top chamber, *Scirpus*

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Introduction

Quantifying and understanding the CO₂-assimilation potential of plant communities and its evolution under increased atmospheric CO₂ concentrations is a critical component of carbon sequestration studies in terrestrial ecosystems. During summer daytime periods, the net ecosystem exchange (NEE) of CO₂ between terrestrial ecosystems and the atmosphere mostly reflects the net CO₂ assimilation by plants, as the heterotrophic respiration becomes comparatively small. Therefore summer daytime NEE measurements are a powerful tool to analyse *in situ* the responses of plant CO₂ assimilation to environmental conditions (Drake & Leadley 1991). In the present study, we modelled NEE and compared these results to field measurements as a way to identify which ecophysiological traits specific to

Scirpus olneyi drive CO₂-assimilation patterns under ambient and elevated CO₂ conditions.

Studies conducted on a few days of measurements suggest that the CO₂-assimilation potential of *S. olneyi* is high, whether measured at the leaf (Dejong, Drake & Pearcy 1982; Long & Drake 1991; Jacob, Greitner & Drake 1995) or canopy level (Drake & Leadley 1991; Drake *et al.* 1996a). High rates of CO₂ assimilation have been measured in at least one other *Scirpus* species (Pearcy & Ustin 1984). In addition, *S. olneyi* productivity responds vigorously to elevated CO₂ (Drake & Leadley 1991; Jacob *et al.* 1995; Drake *et al.* 1996a). Therefore *Scirpus* communities appear to have a strong potential for continued high rates of CO₂ assimilation throughout the 21st century.

Mechanistic modelling is a powerful tool to analyse the response of ecosystem CO₂ fluxes to environmental and ecological conditions such as species composition (Rasse *et al.* 2001a), forest harvest cycle (Rasse, Nemry & Ceulemans 2001b), nitrogen deposition (Rasse 2002), drought (Baldocchi 1997), air temperature and

canopy–air vapour pressure deficit (Kellomäki & Wang 2000). Accurate mechanistic modelling of an ecosystem demands that the simulated ecosystem functions be constrained by numerous ecophysiological measurements (de Pury & Farquhar 1997; Rasse *et al.* 2001a). Many such measurements have been conducted on *S. olneyi* communities during the past 25 years at a brackish wetland site on Chesapeake Bay, Maryland USA, creating a rich database and an excellent opportunity for accurate modelling of this ecosystem.

Materials and methods

MEASUREMENTS

Net ecosystem exchange of CO₂ was measured in 1989 for a *Scirpus olneyi* Gray community belonging to a brackish wetland at Chesapeake Bay. These measurements are part of an ongoing 15-year experiment, started in 1987, on the effects of elevated CO₂ on marsh-plant communities. The 1989 measurement campaign was chosen for the present study because, on the one hand, we wanted a year when the measurement technique was well established and routinely conducted; and, on the other hand, we wanted a year early in the 15-year series so that the model developed in the present study could be applied independently to other growing seasons in future interannual variability studies. *Scirpus olneyi* plants were exposed to ambient and elevated CO₂: ambient + 350 µmol CO₂ mol⁻¹ in open-top chambers (Curtis *et al.* 1989a; Leadley & Drake 1993). The experimental site was described in detail by Curtis *et al.* (1989a); Curtis, Drake & Whigham (1989b). Measurements were conducted in the open-top chambers for continuous periods shorter than a week, separated by approximately 2-week intervals, in order to minimize the impact of chamber closure on plant growth (Leadley & Drake 1993).

Measurements of *S. olneyi* leaf photosynthesis were conducted in the field on 20–24 August 2001 from 9:00 to 15:00 h using two LI-COR 6400 photosynthesis systems (LI-COR, Lincoln, Nebraska, USA). Although the photosynthetic organ of *S. olneyi* is a stem, not a leaf, we use the word ‘leaf’ in this article to avoid confusion when using widely accepted terms such as leaf area index (LAI) and specific leaf area (SLA). Fourteen plants chosen randomly from each treatment were measured on the consecutive days. Photosynthetic parameters were calculated according to McMurtrie & Wang (1993) based on the biochemical model of photosynthesis by Farquhar, von Caemmerer & Berry (1980) and von Caemmerer & Farquhar (1981). Dark respiration in the light (R_d , µmol m⁻² s⁻¹) and maximum rate of carboxylation ($V_{c_{max}}$, µmol m⁻² s⁻¹) were estimated from regression on measured photosynthetic rate for CO₂ of 60–350 µmol mol⁻¹ for individual leaves. Maximum rate of potential electron transport

(J_{max} , µmol m⁻² s⁻¹) was estimated from regression on measured photosynthetic rates for the whole *A-C*₁ curve (Harley *et al.* 1992).

Leaf area index (LAI) of *S. olneyi* communities in the ambient and elevated CO₂ treatments was estimated by nondestructive censuses of shoot number, shoot height, base shoot width, and apex shoot width, as described by Curtis *et al.* (1989a). In the autumn of 1989, leaves were destructively sampled in the ambient and elevated CO₂ treatments, and divided into four equal-length segments. Total N analyses were conducted with a carbon–hydrogen–nitrogen analyser (Control Equipment Corp., Lowell, MA, USA) at the Horn Point Laboratory of the University of Maryland.

MODEL DEVELOPMENT AND PARAMETER ESTIMATION

Net ecosystem exchange was simulated with a new model specific to *S. olneyi*. The overall mathematical structure of the model was based on the ASPECTS model, which computes the evolution of carbon, nitrogen and water reservoirs by solving all differential equations defined between incoming and outgoing fluxes, as described by Rasse *et al.* (2001a) and Rasse (2002).

The model computes rates of photosynthesis according to a modified version of the theoretical model of de Pury & Farquhar (1997), which is a big-leaf model with a separate integration of sunlit- and shaded-leaf photosynthesis. Model parameters are summarized in Table 1. Canopy photosynthetic capacity results from the integration of the leaf photosynthetic capacity over the entire canopy. Within the photosynthesis submodel, stomatal conductance is computed by the semi-empirical model of Leuning (1995), which relates stomatal conductance to the net assimilation, CO₂ concentration at the leaf surface, and water vapour pressure deficit. In the model of de Pury & Farquhar (1997), the canopy photosynthetic Rubisco capacity (V_c) results from the integration of the leaf photosynthetic Rubisco capacity over the entire canopy, and is computed according to:

$$V_c = \text{LAI } \chi_n (N_0 - N_b) [1 - \exp(-k_n)] / k_n \quad (\text{eqn 1})$$

where χ_n is the ratio of photosynthetic capacity to leaf N, N_0 is the leaf N concentration (mmol m⁻² leaf) at the top of the canopy, N_b is the concentration of leaf N not associated with photosynthesis, and k_n is the coefficient of leaf-nitrogen allocation in the canopy. Therefore relationships between leaf N and canopy depth (k_n), and between the maximum canopy photosynthetic Rubisco capacity ($V_{c_{max}}$) and leaf N (χ_n), are needed to define the photosynthetic capacity.

The relationship between leaf N concentration and canopy depth was defined by de Pury & Farquhar (1997):

Table 1. List of photosynthesis model parameters

Model parameters	Value	Units	Source
Values obtained specifically for <i>Scirpus olneyi</i>			
V_{cmax} at 25 °C: max. photosynthesis Rubisco capacity	120	$\mu\text{mol m}^{-2} \text{s}^{-1}$	Measured, this study
J_{max} at 25 °C: max. rate of electron transport	238	$\mu\text{mol m}^{-2} \text{s}^{-1}$	Measured, this study
$J_{\text{max}}/V_{\text{cmax}}$	1.98	–	Measured, this study
Γ^* : CO ₂ compensation point without dark respiration	5.00	Pa	Measured, this study
k_n : Coefficient of N allocation in the canopy	0.425	–	Measured, this study
χ_n : Ratio of V_{cmax} to leaf N	0.54	$\text{mmol mol}^{-1} \text{s}^{-1}$	Computed from measurements (this study), and Curtis <i>et al.</i> (1989a); Curtis <i>et al.</i> (1989b)
Maximum LAI at ambient CO ₂ in 1989	2.6	–	Measured, this study
Maximum LAI at elevated CO ₂ in 1989	2.8	–	Measured, this study
Leaf N concentration	0.8–2.2	%	Curtis <i>et al.</i> (1989b); equation 4
Ratio of elevated-CO ₂ /ambient-CO ₂ leaf N	0.85	–	Curtis <i>et al.</i> (1989b), Drake <i>et al.</i> (1996b)
SLA: specific leaf area	0.0038	$\text{m}^2 \text{g}^{-1} \text{DW}$	Curtis <i>et al.</i> (1989a)
α : Empirical coefficient for maintenance respiration	3.5×10^{-4}	–	Computed from (Drake <i>et al.</i> 1996a)
Literature values for other species			
N_b : Leaf N not associated with photosynthesis	25	mmol m^{-2}	de Pury & Farquhar (1997)
K_c : Michaelis–Menten constant of Rubisco for CO ₂	40.4	Pa	de Pury & Farquhar (1997)
K_o : Michaelis–Menten constant of Rubisco for O ₂	24800	Pa	de Pury & Farquhar (1997)
Fraction of respiration to organ growth	0.20	–	Rasse <i>et al.</i> (2001a)
g_o : Stomatal conductance (g_s) at zero assimilation	0.01	$\text{mol m}^{-2} \text{s}^{-1}$	Leuning (1995)
a_i : Coefficient linking g_s to assimilation	8.5	–	Rasse <i>et al.</i> (2001a)
D_o : Coefficient linking g_s to vapour pressure deficit	1000	Pa	Leuning (1995)

$$(N_c - N_b)/(N_0 - N_b) = [1 - \exp(-k_n)]/k_n \quad (\text{eqn 2})$$

where N_c is the average canopy N concentration (mmol m^{-2} leaf). Because the *S. olneyi* canopy is erectophile, the distribution of N within the canopy is similar to that along the leaves. Our measurements on leaf N distribution indicated that $(N_c - N_b)$ was 81% of $(N_0 - N_b)$, which yielded a value of 0.425 for k_n .

Estimating χ_n requires that we know V_{cmax} and the leaf N concentration associated with photosynthesis. Our measurements indicate that V_{cmax} at 25 °C averages $120 \mu\text{mol CO}_2 \text{m}^{-2} \text{leaf s}^{-1}$ in late August. Although leaf N concentration was not measured simultaneously with V_{cmax} , we estimated that 221mmol N m^{-2} leaf was associated with photosynthesis in the upper section of the leaf where V_{cmax} was measured. This estimate was based on: (1) 1.1% leaf N of *Scirpus olneyi* in late August (Curtis *et al.* 1989b); (2) a specific leaf weight of 260g DW m^{-2} (Curtis *et al.* 1989a); (3) 25mmol N m^{-2} leaf not associated with photosynthesis (de Pury & Farquhar 1997); and (4) a k_n of 0.425 (this study). The resulting value of χ_n , based on the ratio of V_{cmax} at 25 °C and the N concentration associated with photosynthesis was $0.54 \text{mmol CO}_2 \text{mol}^{-1} \text{N s}^{-1}$.

Once k_n and χ_n have been determined, knowledge of the foliage N content is sufficient to estimate the distribution of V_{cmax} throughout the canopy. The foliage N content is the product of the foliage N concentration and the amount of foliage. The foliage N concentration fluctuates during the growing season. Curtis *et al.* (1989b) reported that foliage N concentration varied from about 2.2% in mid-May to about 0.8% in the end of October. Although the decrease in foliage N con-

centration with time is not linear, the data of Curtis *et al.* (1989b) indicate that it can be approximated by the following linear functions:

$$N_i = 2.2, \text{DOY} < 135$$

$$N_i = 2.2 - (\text{DOY} - 135) \times (2.2 - 1.4)/(180 - 135), \\ 135 \leq \text{DOY} \leq 180$$

$$N_i = 1.4 - (\text{DOY} - 180) \times (1.4 - 0.8)/(300 - 180), \\ 180 < \text{DOY} \leq 300$$

$$N_i = 0.8, \text{DOY} > 300 \quad (\text{eqn 3})$$

where DOY is the day of the year. The amount of foliage for a given LAI is determined by the SLA, which approximates $0.0038 \text{m}^2 \text{g}^{-1} \text{DW}$ for *S. olneyi* (Curtis *et al.* 1989a).

The maximum rate of photosynthesis is controlled by V_{cmax} in light-saturated conditions, and by J_{max} in light-limited conditions (de Pury & Farquhar 1997; von Caemmerer & Farquhar 1981). We measured J_{max} at 25 °C of $238 \mu\text{mol m}^{-2} \text{s}^{-1}$. Consequently, our measured $J_{\text{max}}/V_{\text{cmax}}$ ratio for *S. olneyi* was 1.98, which is close to the 2.1 reported by Watanabe, Evans & Chow (1994) for wheat.

The canopy of *S. olneyi*, which controls its light interception, is characterized by two important features: (1) a fairly small LAI; and (2) a structure composed of almost vertical leaves. In this study, the maximum LAI was obtained from the study of Curtis *et al.* (1989a). The erectophile nature of *S. olneyi* implies that light penetration in the canopy is different

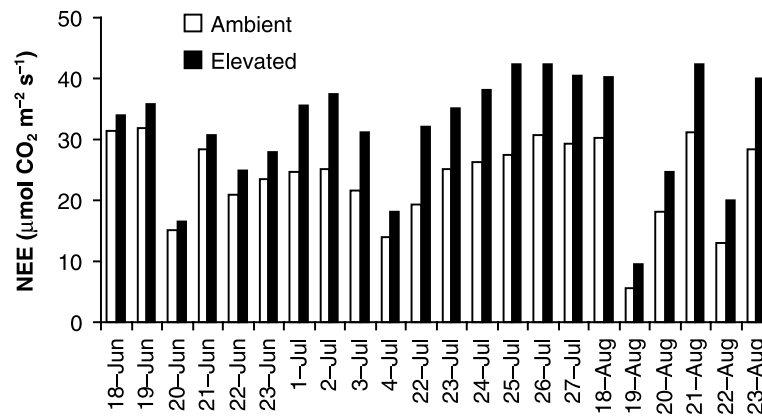


Fig. 1. Averaged 09:00–15:00 h net ecosystem exchange (NEE) of a *Scirpus olneyi* community measured under ambient and elevated CO₂ conditions in 1989.

from other nonvertical leaf plants, and that the light extinction coefficient (K_b) will be specific to this type of canopy. In the original de Pury & Farquhar (1997) model, the assumption was made that the canopy followed a hemispherical leaf distribution. For this study we have used the K_b equation reported by Campbell & Norman (1998) for vertical-leaf canopies:

$$K_b = (\pi/2) \tan[(\pi/2) - \alpha] \quad (\text{eqn 4})$$

In the model, α , the solar elevation angle, is computed according to the latitude and longitude of the study site, the day of the year, and the time of day, according to an algorithm reported by de Pury & Farquhar (1997).

The canopy reflection coefficient (ρ_c) used in the *S. olneyi* model was obtained from the measurements published by Drake (1976):

$$\rho_c = 27.03/(2\text{FIC} + 113.5) \quad (\text{eqn 5})$$

where FIC is the total amount of foliage carbon in g C m^{-2} .

Autotrophic maintenance respiration (R_m) is computed according to the equation used in ASPECTS, which uses a linear relationship with N content and an exponential relationship with temperature (Rasse *et al.* 2001a). The equation was adjusted to *S. olneyi* based on data presented by Drake *et al.* (1996a) which indicate that the maintenance respiration of the leaf tissue averages $0.015 \text{ g C (g leaf C)}^{-1} \text{ day}^{-1}$. Growth respiration was computed as 20% of growth assimilates allocated to each reservoir: leaves, fine roots and coarse roots, as in the ASPECTS model (Rasse *et al.* 2001a).

Increased atmospheric CO₂ concentration modifies the size and N concentration of the *Scirpus* plants, which affects their LAI and photosynthetic potential. Studies conducted at the research site indicate that leaf N concentration is decreased by approximately 15% under elevated CO₂ (Curtis *et al.* 1989b; Drake *et al.* 1996b). Measurements conducted in 1989 indicate that the LAI of the *S. olneyi* community averaged 2.6 and 2.8 in ambient and elevated CO₂ conditions, respec-

tively (B.G.D., unpublished data). The evolution of LAI throughout the growing season was obtained from Curtis *et al.* (1989a).

Results

MEASUREMENTS

Elevated CO₂ increased the 09:00–15:00 h NEE by an average of 36% as compared with the ambient CO₂ treatment (Fig. 1). It reached a maximum of about $30 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in the ambient treatment, and about $40 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in the elevated treatment. The highest hourly daytime NEE peaks were about 40 and $50 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in the ambient and elevated CO₂ treatments, respectively (Fig. 2a,b).

Out of the 22 days of measurement available in summer 1989, differences between ambient and elevated CO₂ treatments were smaller in June than in July and August. The small CO₂ effect on photosynthesis observed in June 1989 was not associated with low NEE values, which were actually close to their maximum for the entire summer period in the ambient treatment (Figs 1 and 2a,b). The measured PAR was lower between 18 and 23 June than during most of the July and August measuring periods (Fig. 3). For example, on 18 June NEE peaked at $36 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ with a hourly PAR peaking at about $1000 \mu\text{mol m}^{-2} \text{ s}^{-1}$, while a month later, on 26 July, the NEE peaked at $38 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ under a maximum PAR of about $2000 \mu\text{mol m}^{-2} \text{ s}^{-1}$. The temperature regime of these 2 days was similar (data not shown).

SIMULATION RESULTS

The model accurately simulated the NEE of the *S. olneyi* communities under ambient and elevated CO₂. The slope of the linear regression line between measured and simulated values was 0.89 and 0.98 for the ambient and elevated CO₂ treatments, respectively, $r^2 = 0.91$ and 0.94 (Fig. 4a,b). The diurnal pattern was described well by the model.

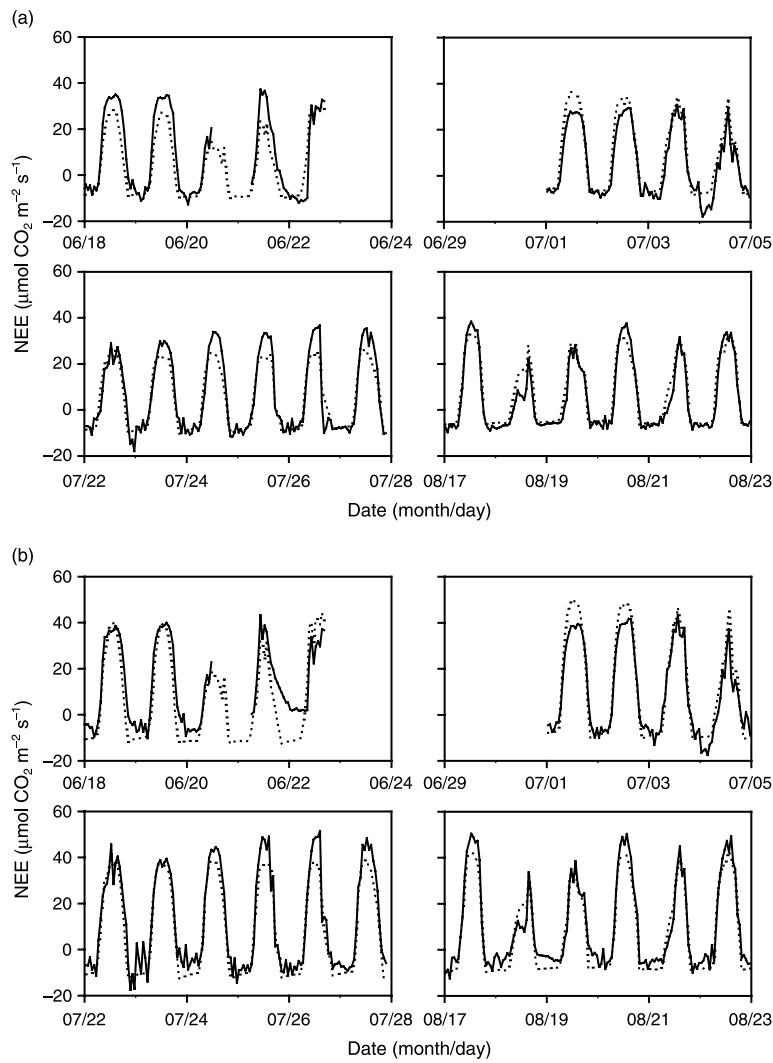


Fig. 2. Measured (solid lines) and simulated (dotted lines) hourly NEE under (a) ambient and (b) elevated CO_2 for four 4–6-day periods throughout summer 1989.

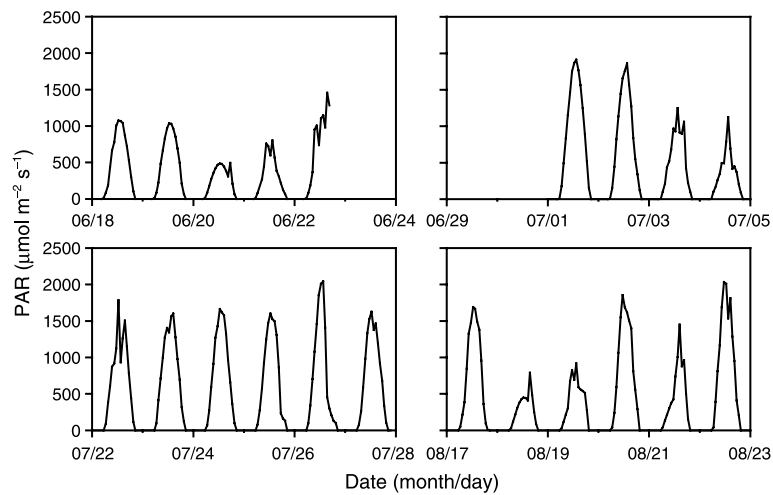


Fig. 3. Measured photosynthetic active radiation (PAR, in $\mu\text{mol}^{-2} \text{ s}^{-1}$) corresponding to the period of NEE measurements.

Predicted peaks of daily NEE under ambient conditions were of comparable magnitude to those measured in the open-top chambers, although some daily maxima were overestimated while others were under-

estimated. Model simulations were in good agreement with the measurements, indicating that the maximum NEE of an *S. olneyi* community under ambient CO_2 is between 35 and 40 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. This agreement

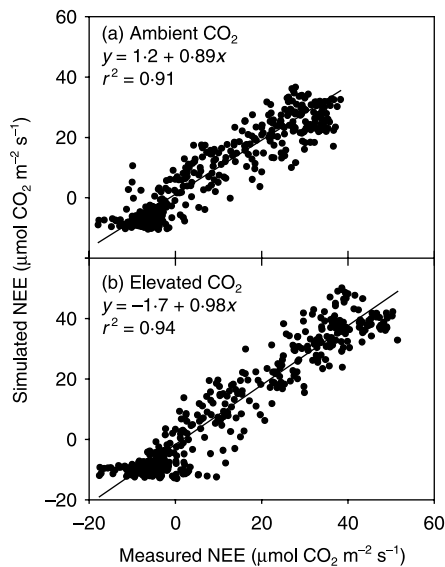


Fig. 4. Measured vs simulated NEE for *Scirpus olneyi* grown under either ambient (a) or elevated (b) CO₂ conditions. Symbols are data points; lines are linear regressions.

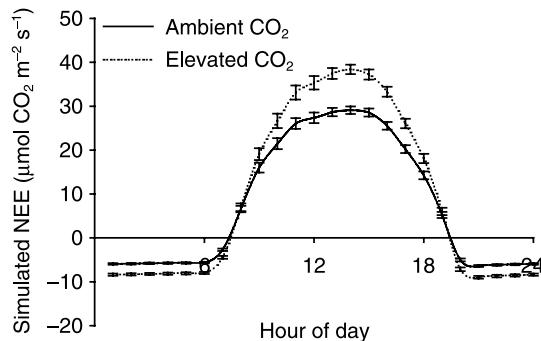


Fig. 5. Hourly simulated NEE of the *Scirpus* community, averaged over the month of July 1989. Error bars ± 1 SE for $n = 31$.

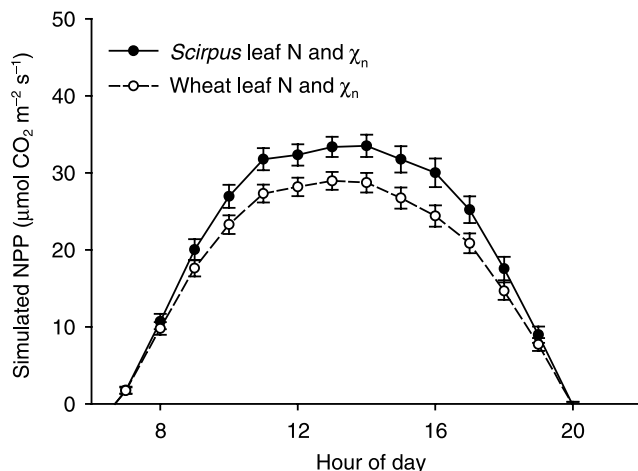


Fig. 6. Sensitivity analysis on the effect of leaf N and χ_n on the hourly simulated NPP averaged over the month of July 1989. Simulation run conducted for *Scirpus olneyi* compared to a run conducted with total leaf N and χ_n reported for wheat by de Pury & Farquhar (1997), all other parameters remaining identical to those of *S. olneyi*. Error bars ± 1 SE for $n = 30$.

did not result from a model calibration process because all model parameters were either measured specifically for *S. olneyi*, or kept unchanged as compared with ASPECTS (Rasse *et al.* 2001a). The model slightly underestimated the NEE during 18–23 June and 22–27 July, while it slightly overestimated it from 1 to 4 July.

The model accurately simulated the CO₂ fertilization effect on *Scirpus*. Under elevated CO₂, the model predicted that the maximum NEE of a *S. olneyi* community is about 50 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ – on 1 July maximum measured NEE was also about 50 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, although this was reached on different dates from that predicted by the model, i.e. 26 July and 17 August (Fig. 2b). The model predicted that the July average NEE peaks at noon were 27 and 38 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ under ambient and elevated CO₂, respectively (Fig. 5). Over the same month, the model estimated that the total CO₂ fixation by *Scirpus* was 157 and 226 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ under ambient and elevated CO₂, respectively, values obtained by integrating the curves presented in Fig. 5.

Leaf N and χ_n effects on plant photosynthesis were tested through a sensitivity analysis that compared identical simulation runs conducted (1) with *S. olneyi* parameters only, as in Table 1; and (2) with total foliage N and χ_n values reported for wheat by de Pury & Farquhar (1997), all other parameters remaining at their *Scirpus* values. Using wheat foliage N and χ_n values reduced the average simulated net plant productivity (NPP) for June 1989 by 4.5 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ during midday hours, which represents a 14% decrease in NPP (Fig. 6).

Implementing a vertical leaf canopy structure in the model, as compared to the default hemispherical assumption, reduced simulated plant productivity from May to July, and increased it in September (Fig. 7). The largest difference was observed in June with a 3.7% reduction in simulated NPP, while a 0.8% increase was predicted for September.

Discussion

Scirpus olneyi responded favourably to elevated CO₂ conditions by increasing its CO₂ assimilation by about 35–40% (Fig. 1). The model accurately captured the magnitude of the response (Fig. 2b), which gives us confidence that this response resulted from the positive effects of high CO₂ and increased LAI, somewhat counterbalanced by a decrease in leaf N concentration, as described in the model. A vast amount of literature is now available on plant responses to elevated CO₂. Gielen & Ceulemans (2001), in a review of 28 experiments on poplar trees (*Populus*), reported that the average increase by elevated CO₂ of the net photosynthesis was 74%. In a more extensive review across tree species and ecosystems, Norby *et al.* (1999) reported an average photosynthesis increase under elevated CO₂ of 60%. Most studies measure direct photosynthetic

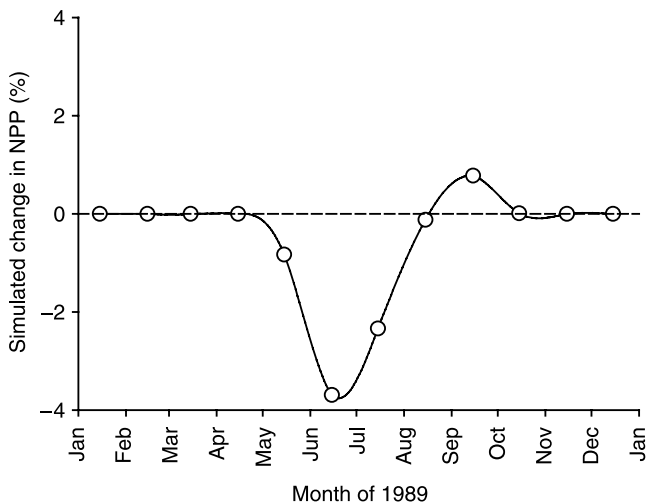


Fig. 7. Sensitivity analysis comparing the effects of vertical vs hemispherical leaf distribution on the monthly simulated NPP throughout 1989. Results are represented as a percentage: $100 \times (\text{vertical NPP} - \text{hemispherical NPP}) / \text{vertical NPP}$.

rates and biomass. We measured the NEE, which is driven mostly by photosynthesis during the daytime, but also incorporates ecosystem respiratory fluxes. Therefore we expect our NEE-response estimate to be less than that of photosynthesis alone. In a review across species and ecosystems, Poorter & Pérez-Soba (2001) indicate that a mild water stress increases the relative response to elevated CO_2 , probably due to associated stomatal closure. Although water stress may occur in the salt marsh, its occurrence is not as probable as in most forest ecosystems, which would explain the potentially smaller response of *S. olneyi* to elevated CO_2 compared with that of tree species. Because *Scirpus*-dominated ecosystems are extremely productive (Drake & Leadley 1991), a 35–40% productivity increase might represent a larger additional amount of carbon fixed as compared to a 60% increase in less productive forest ecosystems. Wetlands cover an estimated 6 million km^2 worldwide, with about 15% of this total located in temperate regions (Mitsch, Mitsch & Turner 1994). Our study suggests that temperate C_3 wetlands have a huge potential for increased plant productivity during the 21st century. The proportion of this photosynthetic carbon that will actually remain sequestered in the wetland ecosystem will depend on the balancing effect of elevated temperature on increased carbon losses from wetland litter and soils (Drake *et al.* 1996b), which is beyond the scope of the present study.

Scirpus olneyi has a great capacity for fixing atmospheric CO_2 , as indicated by the high daytime NEE measured in this study. Hence we regularly measured NEE peaks between 35 and 40 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ under ambient CO_2 concentration, and estimated an average daily maximum of 27 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ at noon over the entire month of July 1989 (Fig. 2a; Fig. 5). At comparable latitude, temperate forest ecosystems of north-

ern Europe and the USA have daytime NEE peaks ranging from 20 to 30 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (Baldochi 1997; Schmid *et al.* 2000; Rasse *et al.* 2001a). Mixed-grass prairies have a 2–4-week average peak daytime NEE of about 15 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in the southern plains (Sims & Bradford 2001). During summer daytime periods, the NEE of terrestrial ecosystems mostly reflects the net CO_2 assimilation by plants, as heterotrophic respiration becomes comparatively small. It appears that our CO_2 assimilation rates measured under ambient CO_2 concentration are in the upper range of reported values for other natural ecosystems. Nevertheless, our measured values remain well below the nearly 70 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ reported at midday for irrigated and fertilized rice fields in early to late reproductive stages (Campbell *et al.* 2001).

Our modelling analyses indicate that the measured high rates of CO_2 assimilation by *S. olneyi* communities are explained by the ecophysiological properties of the plant. Hence the potential rate of CO_2 fixation is controlled mainly by the amount of N associated with photosynthesis per unit ground area (de Pury & Farquhar 1997). Although the LAI of *S. olneyi* is fairly small (2.6–2.8 in this study), the specific leaf weight is high (260 g DW m^{-2} leaf), larger than that of temperate deciduous trees, which ranges between 60 and 170 g DW m^{-2} , and at the upper end of values observed for coniferous trees (Murray & Ceulemans 1998). The foliage N concentration of *S. olneyi* ranges between 0.8 and 2.2 depending on the time of year (Curtis *et al.* 1989b). Although the period of maximum leaf biomass does not correspond to the period of maximum N concentration, *S. olneyi* accumulates up to 10 g N m^{-2} of ground in its photosynthetic organs (Curtis *et al.* 1989b), much more than the 4 g N m^{-2} of ground reported by de Pury & Farquhar (1997) for a wheat canopy. In an extensive literature review, Wright & Westoby (2001) reported that the N content per unit leaf area is between 1 and 2 g N m^{-2} for most grass and woody species, which suggests that most canopies contain less N than *S. olneyi* canopies when reported per unit ground area.

The large amount of N per unit leaf area explains the high V_{cmax} and J_{max} at 25 °C measured in this study: 120 and 238 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, respectively. Hence these values are higher than those generally reported for other species. Dreyer *et al.* (2001) reported that V_{cmax} and J_{max} at 25 °C of seven temperate tree species average 77 and 139 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, respectively. In a literature review covering 109 species, Wullschlegel (1993) reported average V_{cmax} and J_{max} values across ecosystems of 64 and 134 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, respectively, with maxima of 194 and 372 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, respectively. Consequently, our measured values of V_{cmax} and J_{max} for *S. olneyi* are in the upper range of those measured across ecosystems, although they remain well below the maximum reported. Our sensitivity analysis confirms that the combination of total foliage N and χ_n of *S. olneyi*, associated with its

V_{cmax} and J_{max} , is more efficient for CO₂ assimilation than that of wheat (Fig. 6). The high rate of CO₂ assimilation in *S. olneyi* is driven by the large amount of N contained in its foliage: two to three times that of wheat. *Scirpus olneyi* outperforms wheat in terms of CO₂ assimilation despite a wheat χ_n of 1.16 (de Pury & Farquhar 1997), which is much larger than the 0.54 obtained for *S. olneyi*. This suggests that the proportion of Rubisco to total foliage N is smaller in *S. olneyi* than in wheat, although this difference is more than compensated for by the large amounts of N in the foliage of *S. olneyi*.

Our sensitivity analysis on canopy structure indicates that foliage verticality in *S. olneyi* does not explain its high rates of CO₂ assimilation. Simulated *Scirpus* productivity is slightly decreased during most of the growing season by the erect nature of its foliage (Fig. 7). The largest productivity reduction is predicted in June, when the sun is at its highest position in the sky and the light beams fall almost vertically on the canopy, resulting in less radiation being intercepted by the vertical-leaf canopy as compared with the hemispherical one. This reduction in radiation interception under high solar angles has been measured by Drake (1984), who reported that PAR absorption by *S. olneyi* canopies declined from a high of approximately 0.85 at dawn to a low of approximately 0.55 around noon. We therefore conclude that it is the high photosynthetic capacity of the leaf tissue, not the structure of the canopy, that drives the high rates of CO₂ assimilation in *S. olneyi*.

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References

- Baldocchi, D. (1997) Measuring and modeling carbon dioxide and water vapour exchange over a temperate broad-leaved forest during the 1995 summer drought. *Plant, Cell and Environment* **20**, 1108–1112.
- von Caemmerer, S. & Farquhar, G.D. (1981) Some relationships between the biochemistry of photosynthesis and the gas-exchange of leaves. *Planta* **153**, 376–387.
- Campbell, C.S., Heilman, J.L., McInnes, K.J., Wilson, L.T., Medley, J.C., Wu, G. & Cobos, D.R. (2001) Diel and seasonal variation in CO₂ flux on irrigated rice. *Agricultural and Forest Meteorology* **108**, 15–27.
- Campbell, G.S. & Norman, J.M. (1998) *An Introduction to Environmental Biophysics*, 2nd edn. Springer-Verlag, New York.
- Curtis, P.S., Drake, B.G., Leadly, P.W., Arp, W.J. & Whigham, D.F. (1989a) Growth and senescence in plant communities exposed to elevated CO₂ concentrations on an estuarine marsh. *Oecologia* **78**, 20–26.
- Curtis, P.S., Drake, B.G. & Whigham, D.F. (1989b) Nitrogen and carbon dynamics in C₃ and C₄ estuarine marsh plants grown under elevated CO₂ *in situ*. *Oecologia* **78**, 297–301.
- Dejong, T.M., Drake, B.G. & Pearcy, R.W. (1982) Gas

- exchange responses of Chesapeake Bay tidal marsh species under field and laboratory conditions. *Oecologia* **52**, 5–11.
- Drake, B.G. (1976) Seasonal changes in reflectance and standing crop biomass in three salt marsh communities. *Plant Physiology* **58**, 696–699.
- Drake, B.G. (1984) Light response characteristics of net CO₂ exchange in brackish wetland plant community. *Oecologia* **63**, 263–270.
- Drake, B.G. & Leadley, P.W. (1991) Canopy photosynthesis of crops and native plant communities exposed to long-term elevated CO₂. *Plant, Cell and Environment* **14**, 853–860.
- Drake, B.G., Muehe, M.S., Peresta, G., González-Meler, M.A. & Matamala, R. (1996a) Acclimation of photosynthesis, respiration and ecosystem carbon flux of a wetland on Chesapeake Bay, Maryland to elevated atmospheric CO₂ concentration. *Plant and Soil* **187**, 111–118.
- Drake, B.G., Peresta, G., Beugeling, E. & Matamala, R. (1996b) Long-term elevated CO₂ exposure in a Chesapeake Bay wetland: ecosystem gas exchange, primary production, and tissue nitrogen. *Carbon Dioxide and Terrestrial Ecosystems* (eds G.W. Koch & H.A. Mooney), pp. 197–214. Academic Press, San Diego, CA.
- Dreyer, E., Le Roux, X., Montpied, P., Daudet, F.A. & Masson, F. (2001) Temperature response of leaf photosynthetic capacity in seedlings from seven temperate tree species. *Tree Physiology* **21**, 223–232.
- Farquhar, G.D., von Caemmerer, S. & Berry, J.A. (1980) A biochemical model of photosynthetic CO₂ assimilation in leaves of C₃ species. *Planta* **149**, 78–90.
- Gielen, B. & Ceulemans, R. (2001) The likely impact of rising atmospheric CO₂ on natural and managed *Populus*: a literature review. *Environmental Pollution* **115**, 335–358.
- Harley, P.C., Thomas, R.B., Reynolds, J.F. & Strain, B.R. (1992) Modelling photosynthesis of cotton grown in elevated CO₂. *Plant, Cell and Environment* **15**, 271–282.
- Jacob, J., Greitner, C. & Drake, B.G. (1995) Acclimation of photosynthesis in relation to rubisco and non-structural carbohydrate contents and *in situ* carboxylase activity in *Scirpus olneyi* grown at elevated CO₂ in the field. *Plant, Cell and Environment* **18**, 875–884.
- Kellomäki, S. & Wang, K.-Y. (2000) Short-term environmental controls on carbon dioxide flux in a boreal coniferous forest: model computation compared with measurements by eddy covariance. *Ecological Modelling* **128**, 63–68.
- Leadley, P.W. & Drake, B.G. (1993) Open top chambers for exposing plant canopies to elevated CO₂ concentration and for measuring net gas exchange. *Vegetatio* **104/105**, 3–15.
- Leuning, R. (1995) A critical appraisal of a combined stomatal-photosynthesis model for C₃ plants. *Plant, Cell and Environment* **18**, 339–355.
- Long, S.P. & Drake, B.G. (1991) Effect of the long-term elevation of CO₂ concentration in the field on the quantum yield of photosynthesis of the C₃ sedge, *Scirpus olneyi*. *Plant Physiology* **96**, 221–226.
- McMurtrie, R.E. & Wang, Y.-P. (1993) Mathematical models of the photosynthetic response of tree stands to rising CO₂ concentration and temperatures. *Plant, Cell and Environment* **16**, 1–3.
- Mitsch, W.J., Mitsch, R.H. & Turner, R.E. (1994) Wetlands of the Old and New Worlds: ecology and management. *Global Wetlands Old World and New* (ed. W.J. Mitsch), pp. 3–56. Elsevier, Amsterdam, the Netherlands.
- Murray, M.B. & Ceulemans, R. (1998) Will tree foliage be larger and live longer? *European Forests and Global Change: The Likely Impacts of Rising CO₂ and Temperature* (ed. P.J. Jarvis), pp. 94–125. Cambridge University Press, Cambridge, UK.
- Norby, R.J., Wullschlegel, S.D., Gunderson, C.A., Johnson, D.W. & Ceulemans, R. (1999) Tree responses to rising CO₂ in field experiments: implications for the future forest. *Plant, Cell and Environment* **22**, 683–714.

- Pearcy, R.W. & Ustin, S.L. (1984) Effects of salinity on growth and photosynthesis of three California tidal marsh species. *Oecologia* **62**, 68–73.
- Poorter, H. & Pérez-Soba, M. (2001) The growth response of plants to elevated CO₂ under non-optimal environmental conditions. *Oecologia* **129**, 1–20.
- de Pury, D.G.G. & Farquhar, G.D. (1997) Simple scaling of photosynthesis from leaves to canopies without the errors of big-leaf models. *Plant, Cell and Environment* **20**, 537–557.
- Rasse, D.P. (2002) Nitrogen deposition and atmospheric CO₂ interactions on fine root dynamics in temperate forests: a theoretical model analysis. *Global Change Biology* **8**, 486–503.
- Rasse, D.P., François, L., Aubinet, M., Kowalski, A.S., Vande Walle, I., Laitat, E. & Gérard, J.-C. (2001a) Modelling short-term CO₂ fluxes and long-term tree growth in temperate forests with ASPECTS. *Ecological Modelling* **141**, 35–52.
- Rasse, D.P., Nemry, B. & Ceulemans, R. (2001b) Stand-thinning effects on C fluxes in 20th and 21st century Scots pine forests: a sensitivity analysis with ASPECTS. *Models for the Sustainable Management of Temperate Plantation Forests – Proceedings 41* (eds J.-M. Carnus, R. Dewar, D. Loustau, M. Tomé & C. Orazio), pp. 18–30. European Forest Institute, Joensuu, Finland.
- Schmid, H.P., Grimon, C.S.B., Cropley, F., Offerle, B. & Su, H.-B. (2000) Measurements of CO₂ and energy fluxes over a mixed hardwood forest in the mid-western United States. *Agriculture and Forest Meteorology* **103**, 357–374.
- Sims, P.L. & Bradford, J.A. (2001) Carbon dioxide fluxes in a southern plains prairie. *Agriculture and Forest Meteorology* **109**, 117–134.
- Watanabe, N., Evans, J.R. & Chow, W.S. (1994) Changes of the photosynthetic properties of Australian wheat cultivars over the last century. *Australian Journal of Plant Physiology* **21**, 169–183.
- Wright, I.J. & Westoby, M. (2001) Understanding seedling growth relationships through specific leaf area and leaf nitrogen concentration: generalisations across growth forms and growth irradiance. *Oecologia* **127**, 21–29.
- Wullschlegel, S.D. (1993) Biochemical limitations to carbon assimilation in C₃ plants – a retrospective analysis of the A/C_i curves from 109 species. *Journal of Experimental Botany* **44**, 907–920.

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