Effects of elevated atmospheric CO₂ on net ecosystem CO₂ exchange of a scrub–oak ecosystem

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Abstract

We report the results of a 2-year study of effects of the elevated (current ambient plus 350 μmol CO₂ mol⁻¹) atmospheric CO₂ concentration (Cₐ) on net ecosystem CO₂ exchange (NEE) of a scrub–oak ecosystem. The measurements were made in open-top chambers (OTCs) modified to function as open gas-exchange systems. The OTCs enclosed samples of the ecosystem (ca. 10 m² surface area) that had regenerated after a fire, 5 years before, in either current ambient or elevated Cₐ. Throughout the study, elevated Cₐ increased maximum NEE (NEE_max) and the apparent quantum yield of the NEE (φₚₒₚₑₚₑₚₑ) during the photoperiod. The magnitude of the stimulation of NEE_max expressed per unit ground area, was seasonal, rising from 50% in the winter to 180% in the summer. The key to this stimulation was effects of elevated Cₐ and their interaction with the seasonal changes in the environment, on ecosystem leaf area index, photosynthesis and respiration. The separation of these factors was difficult. When expressed per unit leaf area the stimulation of NEE_max ranged from 7% to 60%, with the increase being dependent on increasing soil water content (W_soil). At night, the CO₂ effluxes from the ecosystem (NEE_night) were on an average 39% higher in elevated Cₐ. However, the increase varied between 6% and 64%, and had no clear seasonality. The partitioning of NEE_night into its belowground (R_below) and aboveground (R_above) components was carried out in the winter only. A 35% and 27% stimulation of NEE_night in December 1999 and 2000, respectively, was largely due to a 26% and 28% stimulation of R_below in the respective periods, because R_below constituted ca. 87% of NEE_night. The 37% and 42% stimulation of R_above in December 1999 and 2000, respectively, was less than the 65% and 80% stimulation of the aboveground biomass by elevated Cₐ at these times. An increase in the relative amount of the aboveground biomass in woody tissue, combined with a decrease in the specific rate of stem respiration of the dominant species Quercus myrtifolia in elevated Cₐ, was responsible for this effect. Throughout this study, elevated Cₐ had a greater effect on carbon uptake than on carbon loss, in terms of both the absolute flux and relative stimulation. Consequently, for this scrub–oak ecosystem carbon sequestration was greater in the elevated Cₐ during this 2-year study period.

Keywords: elevated CO₂, NEE, open-top chambers, respiration, scrub–oak ecosystem

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Introduction

Major research initiatives into the biological effects of global climate change are currently focused on increasing the understanding of the environmental controls on ecosystem carbon cycling, particularly those factors affected by increasing atmospheric CO₂ concentration (Cₐ). It is likely that increasing Cₐ will result in an increase in the net exchange of CO₂ between the biosphere and the atmosphere (NEE), through a stimulation of photosynthesis, increased water and nitrogen use efficiency and growth. (Recent reviews. Leaf physiology: Drake et al., 1997; Jarvis et al., 1999; Growth and phenology: Norby et al., 1999; Pritchard et al., 1999; Water relations: Wullschleger et al., 2002; Soil...
The results from field experiments have reported that a step increase in $C_a$ to the elevated levels predicted within the next hundred years results in increased carbon sequestration in aboveground (DeLucia et al., 1999; Norby et al., 2001; Oren et al., 2001; Dijkstra et al., 2002) and belowground biomass (DeLucia et al., 1999; Schlesinger & Lichter, 2001; Dilustro et al., 2002). A net increase in ecosystem carbon uptake in elevated $C_a$, would be expected to underlie these changes in biomass accumulation.

Currently, the number of studies that have measured NEE at both current ambient and elevated $C_a$ is limited, both with respect to the ecosystems in which they have been made and also the duration of the data sets generated. This is unfortunate for two key reasons. First, regular NEE measurements are ideally suited to the establishment of causative relationships between ecosystem carbon cycling, biotic and abiotic factors and their interaction with elevated $C_a$. Second, long-term measurements of NEE at elevated $C_a$ will yield data sets against which ecosystem models, which are typically parameterized using leaf level data (McMurtrie & Wang, 1993; Medlyn & Dewar, 1996; Rasse et al., 2001), can be tested.

Enclosure methods remain the only way that NEE measurements can currently be made at elevated $C_a$. Consequently, field experiments have been limited to low stature ecosystems. Studies in a C3 grassland (Stocker et al., 1999; Niklaus et al., 2000) and a marsh (Drake et al., 1996) demonstrated the potential for increased NEE during the photoperiod in elevated $C_a$. In contrast, the stimulation of NEE in elevated $C_a$ was transient in both the Arctic tundra (Oechel et al., 1994) and a C3 alpine grassland (Diemer & Körner, 1998), while for a C4 grassland the stimulation of NEE in elevated $C_a$ was only observed late in a 34-day measurement period, due to delayed senescence (Ham et al., 1995). With the exception of Drake et al., 1996, who observed a decrease in marsh ecosystem respiration in elevated $C_a$, effects on ecosystem respiration have not been typically observed (Diemer, 1994; Ham et al., 1995; Stocker et al., 1997). Currently, field studies on woody ecosystems are missing from the literature.

Here, we report NEE measurements made during a 2-year period between July 1999 and 2001 at current ambient and elevated $C_a$ in a fire-dependent scrub-oak ecosystem of central Florida. The key findings at the site have been a sustained stimulation of photosynthesis for the main species (Li et al., 1999; 2000; Hymus et al., 2001; Ainsworth et al., 2002; Hymus et al., 2002a), little effect of elevated $C_a$ on leaf or soil respiration (Johnson et al., 2001; Hymus et al., 2002a) and a strong stimulation of aboveground biomass and ecosystem leaf area index (LAI) by elevated $C_a$ (Dijkstra et al., 2002; Hymus et al., 2002b). These findings provide the basis for testing the hypothesis that elevated $C_a$ will increase carbon uptake during the photoperiod, primarily due to the increased photosynthesis and leaf area, and increase carbon loss at night, due to increased biomass.

Materials and methods

Site description

The open-top chamber (OTC) project was sited in the fire-dependent, scrub-oak ecosystem of coastal central Florida on Merritt Island (28°38'N, 80°42'W), within NASA’s Kennedy Space Center. The substrates were well-drained Pomello (Arenic Haplahumod) and Poala Sands (Spodic quartzipsamment). Both were acidic and low in nutrients, most of which were locked up in the standing biomass and a soil organic layer approximately 30 cm in depth (Schmaltzer & Hinkle, 1992). The experimental site was representative of a fire-maintained scrub-oak palmetto community (Breininger & Schmalzer, 1990). The shrub layer was comprised of rhizomatous sclerophyllous evergreen oaks, which resprouted from belowground after fire (Breininger & Schmalzer, 1990). Three oak species, Quercus myrtifolia, Quercus geminata and Quercus chapmanii, typically comprise up to 85-90% of the aboveground biomass in this ecosystem (Schmaltzer & Hinkle, 1992). The climate was subtropical, warm and humid, with an average annual precipitation of 131 cm masking high year-to-year variability. The mean maximum and minimum temperatures in July, the hottest month, were 33.3 °C and 21.8 °C, respectively, and 22.3 °C and 9.5 °C in January, the coldest month (Schmaltzer & Hinkle, 1992). The combination of frequent fires, seasonal water stress and nutrient poor soil conditions maintains the composition and structure of the ecosystem.

Sixteen OTCs, each 2.5 m high with an octagonal surface area of 9.42 m², were established during spring 1996 on a site that had been partially burnt in July of 1995, and then completely burnt in a second fire in January 1996. Eight of the OTCs were maintained at the current ambient $C_a$ and eight at elevated $C_a$ (current ambient + 350 μmol CO₂ mol⁻¹). Here, we present the data of 2 years collected between June 1999, 3 years into the fire regeneration cycle, and July 2001, 5 years into the regeneration cycle. Within the context of a natural fire regeneration cycle that maybe between 7 and 40 years in length, the data presented here come from an early stage of ecosystem regeneration after fire.

Measurement of NEE

With the addition of custom-designed Lexan lids (Commercial Plastics, Orlando, FL, USA), the OTCs
functioned as an open gas-exchange system. Lids were added and NEE measured monthly for periods of 5–10 days. Air was blown through the OTCs at a rate of ca. 27 m:\textsuperscript{2} min\textsuperscript{-1}, entering through four circular ducts each of 20.3 cm diameter, total surface area 0.123 m\textsuperscript{2}, and exiting through exhaust ports in the lids with a total exit surface area of 0.096 m\textsuperscript{2}. The difference in the entrance and exit area increased the chamber air pressure, which provided protection against leaks of outside air into the OTCs. However, the increased pressure also suppressed soil CO\textsubscript{2} efflux (R\textsubscript{soil}, see the artifacts below). The ventilation rate was sufficient such that the chamber air was replaced 1.5 times a minute. An IRGA (LI 6262; LI-COR, Lincoln, NEB, USA) operated in the differential mode, measuring the difference between a reference CO\textsubscript{2} mol fraction, from one of four chamber inlet ducts, and a sample CO\textsubscript{2} mol fraction inside the chambers, at the canopy height. Midway through each OTC sampling, a switching valve reversed the cells of the IRGA through which the two air streams flowed. A differential was measured in each configuration with the final differential used being the mean of these two measurements. This protocol accounted for the problems associated with the contamination or aging of the IRGA cells. A second IRGA continuously measured the reference CO\textsubscript{2} mol fraction (chamber inlet) and fed this value into the differential analyzer, which then used an internal algorithm to correct the measured differential for changes in the reference C\textsubscript{a}. Both the reference and sample air streams were drawn from the OTCs at a flow rate of 5 L min\textsuperscript{-1}. After exhausting, the sample was fed to the IRGAs at a rate of 1 L min\textsuperscript{-1} after being individually mixed in flask volumes of 1.9 L. All 16 OTCs were sampled once every 26 min until August 1999; Niklaus et al. (2003), who showed that at night, when the OTC has a negligible effect on the microclimate, the NEE\textsubscript{night} measured inside the OTCs was not different from which we developed protocols to account for both these artifacts in this system. Leaks of outside air into the OTCs were investigated using N\textsubscript{2}O as an inert tracer, and found to occur only when wind speed exceeded 5 m s\textsuperscript{-1}. By excluding any data collected when the wind speeds exceeded 4 m s\textsuperscript{-1}, we minimized the possibility of the contaminated data entering our analysis. At night, the data collected at low wind speeds (<2 m s\textsuperscript{-1}) were also excluded. This was because at night, a wind speed greater than 2 m s\textsuperscript{-1} was necessary to mix air in and around the canopy to provide a stable reference C\textsubscript{a} of the air drawn into the OTCs. In the most extreme cases, the requirement of wind speeds greater than 2 m s\textsuperscript{-1} resulted in the exclusion of 80% of the night data collected in any given measurement period. Turbulent atmospheric conditions during the day resulted in good mixing of the air around the canopy, even at wind speeds below 2 m s\textsuperscript{-1}, and exclusion of the data was not required.

Accounting for the suppression of R\textsubscript{soil} by increases in the air pressure inside the OTC was essentially a modeling exercise performed in two steps. First, we parameterized the model of Hanson et al. (1993) using concurrent measurements of R\textsubscript{soil}, soil temperature (T\textsubscript{soil}) and soil water content (W\textsubscript{soil}) collected at the site throughout the study period (Dore et al., 2003). The linear relationship between the modeled and measured fluxes was highly significant (t\textsubscript{1,15} = 7.6; P < 0.01; r\textsuperscript{2} = 0.80; Dore et al., 2003). Second, on nine occasions between March 2000 and July 2001, we measured the R\textsubscript{soil} in all the OTCs both before and after the addition of the lids. The percentage suppression of the R\textsubscript{soil} (g), due to pressurization of the OTC after the addition of the lids, varied from 32% to 63% on these occasions and was found to be significantly dependent on increases in W\textsubscript{soil} from 1.9% to 6.3% (g = 0.43 × ln (W\textsubscript{soil}) – 0.24; P < 0.01; r\textsuperscript{2} = 0.84; D. P. Johnson, unpublished results). From a modeled estimate of the R\textsubscript{soil} (mR\textsubscript{soil}) and an estimate of the percentage of R\textsubscript{soil} that was suppressed (g), we could correct each measurement in each chamber for the suppressed R\textsubscript{soil} (z). This procedure resulted in the NEE being

\[ NEE = NEE\ (1) + z, \quad (2) \]

where NEE\ (1) is the NEE calculated as described in Eqn (1), and

\[ z = mR_{soil} \times g. \]

The confidence in the effectiveness of these protocols to account for the experimental artifacts was provided by Dore et al. (2003), who showed that at night, when the OTC has a negligible effect on the microclimate, the NEE\textsubscript{night} measured inside the OTCs was not different.
from the NEE measured in the same stand using an eddy covariance system.

**Derivation of NEE parameters**

For each measurement period, data were divided into those collected during the photoperiod (PPFD > 50 μmol m⁻² s⁻¹; wind speed < 4 m s⁻¹) and those collected at night (PPFD < 1 μmol m⁻² s⁻¹; wind speed > 2 < 4 m s⁻¹). For the data collected in each OTC during the photoperiod, the response of NEE to PPFD was plotted and a non-rectangular hyperbola was fitted (Long & Hallgren, 1993). From each curve fit, NEE at the maximum PPFD measured during the measurement period (NEE_max), and the apparent quantum yield of NEE (φ_NEE), were obtained. Ecosystem respiration (NEE_night) was calculated as the average of all the individual NEE measurements made at night in each measurement period. The parameters NEE_max, φ_NEE, and NEE_night were all determined for individual OTCs during each measurement period. In this study NEE_max per unit leaf area was also expressed. This was possible in 11 periods when the NEE measurements coincided with measurements of LAI. Previously published data revealed LAI to be higher in elevated Cₐ rising from 20% higher in the winter to a maximum of 55% higher during the summer months. In ambient Cₐ, LAI increased from 0.8 to 1.2 from 0.9 to 1.6 and from 0.7 to 1.7 in 1999, 2000 and 2001, respectively. In elevated Cₐ, LAI increased from 1.1 to 1.5 from 1.1 to 2.3 and from 0.8 to 2.3 in 1999, 2000 and 2001, respectively. The ecosystem LAI was determined from measurements of light penetration through the canopy using Beer’s law, and is described in detail in Hymus et al. (2002b).

**Partitioning of Ecosystem Respiration**

Partitioning of NEE_night into its above- (R_above) and below (R_below) ground components was carried out by subtracting R_above from NEE_night in December 1999 and 2000 only. Aboveground respiration (R_above) was estimated at the same temperature as NEE_night by applying the temperature dependencies of leaf and stem respiration, determined for both Q. myrtifolia and Q. geminata in December 2000, to the biomass measurements of the aboveground stem biomass determined from the allometric relationships (Dijkstra et al., 2002) and leaf area (Hymus et al., 2002b) made in both December 1999 and 2000. The aboveground stem dry weight (SDW) of Q. myrtifolia and Q. geminata grown in the ambient and elevated Cₐ was determined from the measurements of stem basal diameter (SBD) using the following allometric relationships: ln(SDW) = -3.005 + 3.231(ln(SBD)) (r² = 0.91) and ln(SDW) = -2.913 + 3.196(ln(SBD)) (r² = 0.95) for Q. myrtifolia and Q. chapmanii growing in the elevated and ambient Cₐ, respectively. And ln(SDW) = -3.059 + 3.154(ln(SBD)) (r² = 0.92) and ln(SDW) = -2.962 + 3.094(ln(SBD)) (r² = 0.93) for Q. geminata growing in the elevated and ambient Cₐ, respectively. The stem biomass was 303 and 572 g C m⁻² in the ambient and elevated treatments, respectively, in December 1999, and 402 and 727 g C m⁻² in the ambient and elevated treatments, respectively, in December 2000. The temperature dependence of the leaf (R_leaf) and stem (R_stem) respiration for both Q. myrtifolia and Q. geminata was measured using the experimental setup described in detail in Hymus et al. (2002a). The selection of the current year foliage was as described in Hymus et al. (2002a). The samples of current year woody stem tissue (at least 1.5 g), of ca. nine months age, were removed by a razor within an hour of sunrise from both Q. myrtifolia and Q. geminata in each OTC. For each species in each OTC, a sample consisted of stem sections of up to 15 cm in length taken from at least five plants. Both the leaf and stem respiration rates were measured at 16 °C, 20 °C, 23 °C, 26 °C and 30 °C at their respective growth Cₐ. The measurements were made at least 30 min after each step change in the temperature of the air flowing through the cuvettes. This time was found to be sufficient for respiration rates to stabilize at the new temperature.

**Micrometeorological measurements**

Continuous measurements of T_soil (°C) measured at 10 cm depth, W_soil (%vol) measured between 0 and 15 cm depth and wind speed (m s⁻¹) and PPFD (μmol m⁻² s⁻¹) both measured at a height of 3 m were recorded with a datalogger (CR7, Campbell Scientific, Logan, UT, USA). The soil temperature and W_soil were measured in each plot using copper–constantan thermocouples (Omega Engineering, Stanford, CT, USA) and water content reflectometers (CS615, Campbell Scientific, Logan, UT, USA), respectively. The wind speed was measured with a cup-anemometer (R.M. Young Wind Sentry Set, Campbell Scientific, Logan, UT, USA) and PPFD using a quantum sensor (LI 190, LICOR, Lincoln, NB, USA).

**Statistical analysis**

The non-rectangular hyperbola, from which NEE_max and φ_NEE were derived, was fitted to plots of PPFD and NEE using graphical software (Sigma plot 2001, SPSS, Chicago, IL, USA). Repeated-measures analysis of variance was used to test for an effect of Cₐ and time on NEE_max and φ_NEE and NEE_night. Two-way ANOVA was used to test (i) the effect of Cₐ and temperature on leaf
and stem respiration of Q. myrtifolia and Q. geminata in December 2000, and (ii) the effect of the C\textsubscript{a} and year, on \( R_{\text{above}} \), \( R_{\text{below}} \), and total ecosystem respiration in December 1999 and 2000. For all the analyses, individual OTCs were used as replicates. For all the repeated measures and two-way ANOVAs carried out in this study, none of the interactions between the factors were significant (\( P > 0.05 \)). Consequently, the results of the interactions have not been reported in the text. All analysis was carried out using statistical software (Systat 7.0, Systat, Evanstone, IL, USA).

**Results**

Throughout this study, the summer months were characteristically warm and wet, the winter months were cooler and dryer (Fig. 1). The trends in \( T_{\text{air}} \) exhibited patterns typical of the geographic location, ranging from 19 °C in January 2001 to 35 °C in May 2001 during the photoperiod, and from 8°C in December 2001 to 26 °C in August 2000 during the night (Fig. 1b). The monthly rainfall totals followed general long-term precipitation patterns. However, the specific months often differed substantially from long-term averages. In particular, July 1999 and August 2000 were very dry for summer months, while September 1999 and March 2001 were much wetter than average (Fig. 1c).

**Photoperiod**

The seasonal changes in \( NEE_{\text{max}} \) (expressed per m\(^2\) ground area) in the elevated \( C_{\text{a}} \) treatment tracked those in ambient \( C_{\text{a}} \). In both treatments, \( NEE_{\text{max}} \) rose sharply from winter minima during the spring, to reach summer maxima. This transition reflected increases in the temperature, rainfall and leaf area. The decline in \( NEE_{\text{max}} \) during the autumn and winter months reflected decreases in both the temperature and rainfall, in combination with decreased and senescing leaf area (Figs 1 and 2). The changes in \( NEE_{\text{max}} \) over time were statistically significant (\( F_{25,75} = 11.6; P < 0.01 \)). Throughout the measurement period, \( NEE_{\text{max}} \) was significantly higher in elevated \( C_{\text{a}} \) (\( F_{13} = 30.3; P = 0.01 \)). However, there was a marked seasonality to the degree of stimulation (Fig. 2b). During the spring, the stimulation of \( NEE_{\text{max}} \) increased, reaching a maximum during the summer months of ca. 180%. The stimulation then declined during the autumn and winter to a minimum of ca. 50%. When expressed per unit leaf area, minimizing the effect of the increased LAI in elevated \( C_{\text{a}} \), the stimulation of \( NNE_{\text{max}} \) was lower but still variable, and ranged from ca. 7% to ca. 60% (Fig. 2b). This variation was not dependent on the variation in \( T_{\text{air}} \) (\( P = 0.78; r^2 = 0.01 \)) or \( T_{\text{soil}} \) (\( P = 0.56; r^2 = 0.04 \)), but on \( W_{\text{soil}} \) (\( P = 0.01; r^2 = 0.54 \)), with the stimulation of \( NEE_{\text{max}} \) increasing as \( W_{\text{soil}} \) increased (Fig. 3). Importantly, the changes in \( W_{\text{soil}} \) were independent of changes in \( T_{\text{air}} \) (\( P = 0.31; r^2 = 0.04 \)), minimizing the possibility that the dependence of the stimulation of \( NEE_{\text{max}} \) in elevated \( C_{\text{a}} \) on \( W_{\text{soil}} \) was actually due to increases in \( T_{\text{air}} \).

At low light, elevated \( C_{\text{a}} \) significantly stimulated \( \phi_{\text{NEE}} \) (\( F_{13} = 31.3; P = 0.01 \); Fig. 4). While \( \phi_{\text{NEE}} \) was significantly dependent on time of the year (\( F_{25,75} = 6.2; \text{day length} \)).

Fig. 2 Trends in \( NEE_{\text{max}} \) measured monthly in both ambient (open circles) and elevated (closed circles) \( C_a \) between June 1999 and July 2001; each data point is the mean (±1 SE) of measurements made in ≥6 OTCs (a). For each month the percentage stimulation of \( NEE_{\text{max}} \) in elevated \( C_a \) is also shown, expressed both per m\(^2\) ground area (solid squares) and per m\(^2\) leaf area (open squares) (b).

Fig. 3 Plot of the percentage stimulation of \( NEE_{\text{max}} \) expressed per m\(^2\) leaf area, in elevated \( C_a \) against \( W_{\text{soil}} \) measured between 0 and 15 cm. A linear regression and 95% confidence intervals are shown.

Fig. 4 Trends in \( \phi_{\text{NEE}} \) measured monthly in both ambient (open circles) and elevated (closed circles) \( C_a \) between June 1999 and July 2001; each data point is the mean (±1 SE) of measurements made in ≥6 OTCs.

\( P<0.01 \) and the greatest stimulation of the \( \phi_{\text{NEE}} \) in elevated \( C_a \) was during the summer, a clear seasonality to the effect was not obvious.

Night

Both the \( C_a \) treatments exhibited the same significant changes in \( NEE_{\text{night}} \) throughout the study (F\( _{25,125}=28.9; \ P<0.01 \)). The increases from the winter minima to summer maxima followed increases in \( T_{\text{soil}} \) (Figs 5 and 6). Night respiration was significantly higher in elevated \( C_a \) averaging 39% over the study period, and varying between 6% and 64% in the elevated \( C_a \) (Fig. 5) (\( F_{1,8}=16.7; \ P=0.01 \)). However, there was no clear seasonality to the effect.

The partitioning of \( NEE_{\text{night}} \) into its above- and belowground components was attempted in the winter only. In December 1999 and 2000, \( R_{\text{below}} \) accounted for 86% and 89% of the ecosystem respiration, respectively (Table 1). The \( R_{\text{below}} \) was 26% and 28% higher in elevated \( C_a \) in December 1999 and 2000, respectively; neither effect was significant when testing at \( P<0.05 \), but both were significant at \( P<0.1 \). During both the months, \( R_{\text{above}} \) was significantly higher in elevated \( C_a \), by 35% (\( t_{1,14}=2.25; \ P=0.02 \)) and 42% (\( t_{1,14}=1.94; \ P=0.04 \)) in 1999 and 2000, respectively (Table 1). The partitioning of \( NEE_{\text{night}} \) between \( R_{\text{above}} \) and \( R_{\text{below}} \) was achieved by scaling up leaf and stem respiration measurements to the ecosystem using biomass inventories. The \( R_{\text{leaf}} \) and \( R_{\text{stem}} \) of \( Q. \) \( \text{geminata} \) and \( Q. \) \( \text{myrtifolia} \) were always significantly dependent on \( T_{\text{air}} \) (\( P<0.01 \)). The temperature dependence of \( R_{\text{leaf}} \) and \( R_{\text{stem}} \) of \( Q. \) \( \text{geminata} \) and \( R_{\text{leaf}} \) of \( Q. \) \( \text{myrtifolia} \) was unaffected by growth in elevated \( C_a \) (Fig. 7a, b and d).
Fig. 5 Trends in $\text{NEE}_{\text{night}}$ measured monthly in both ambient (open circles) and elevated (closed circles) $C_a$ between June 1999 and July 2001; each data point is the mean ($\pm$ 1 SE) of measurements made in $\geq 6$ OTCs (a). For each month the percentage stimulation of $\text{NEE}_{\text{night}}$ in elevated $C_a$ is also shown (b).

However, $R_{\text{stem}}$ of $Q. \text{myrtifolia}$ was significantly lower in elevated $C_a$ at all temperatures ($F_{1,61} = 14.4; P<0.01$; Fig. 7c). For both $Q. \text{geminata}$ and $Q. \text{myrtifolia}$, $R_{\text{leaf}}$ was higher than the $R_{\text{stem}}$.

Discussion
This study explored the effect of elevated $C_a$ on $\text{NEE}$ of a scrub-oak ecosystem. The study was performed over a 25-month period, beginning 3 years into a fire-regeneration cycle. We tested the hypothesis that elevated $C_a$ would stimulate ecosystem carbon uptake during the photoperiod, and carbon loss at night. This hypothesis was confirmed. However, at night the increase in aboveground respiration was less than the increase in the aboveground biomass.

Photoperiod
During the photoperiod maximum and light-limited $\text{NEE}$, both expressed per unit ground area, were significantly higher in elevated $C_a$ (Figs 2a and 4). For $\Phi_{\text{NEE}}$, there was a clear seasonality to this stimulation, rising to a summer maximum from a winter minimum. For $\Psi_{\text{NEE}}$, any seasonality was less obvious; however, the largest effect of the elevated $C_a$ was also observed in the summer months. The increase in the effect of the elevated $C_a$ on $\Phi_{\text{NEE}}$ during the spring and summer months was consistent with increases in LAI during

Table 1  Partitioning ecosystem respiration

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<th>$R_{\text{below}}$ (µmol m$^{-2}$ s$^{-1}$)</th>
<th>$R_{\text{above}}$ (µmol m$^{-2}$ s$^{-1}$)</th>
<th>$\text{NEE}_{\text{night}}$ (µmol m$^{-2}$ s$^{-1}$)</th>
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<tbody>
<tr>
<td></td>
<td>Ambient</td>
<td>Elevated</td>
<td>S (%)</td>
</tr>
<tr>
<td>Dec. 1999</td>
<td>2.98 ± 0.22</td>
<td>3.08 ± 0.50</td>
<td>28*</td>
</tr>
<tr>
<td>Dec. 2000</td>
<td>4.59 ± 0.49</td>
<td>5.78 ± 0.61</td>
<td>26*</td>
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The partitioning was achieved by subtracting $R_{\text{above}}$ from $\text{NEE}_{\text{night}}$ with the residual being $R_{\text{below}}$ in December 1999 and 2000. The stimulation of each component in elevated $C_a$ is also shown (S). All the data are expressed per m$^2$ ground area. Statistical significance of the differences between means is shown (**$P<0.05$; *$P<0.1$).
this period in elevated C\textsubscript{a} (Hymus et al., 2002b). During the winter months, the leaf-fall rates increase in elevated C\textsubscript{a}, relative to those in the ambient C\textsubscript{a}, and the stimulation of the LAI declines (Stiling et al., 2002; Hymus et al., 2002b). However, for both NEE\textsubscript{max} and \( \phi \text{NEE} \), when expressed per unit ground area, the changes in the leaf area would not have been solely responsible for the observed seasonality to the stimulation. The following three key factors should in theory have affected the stimulation of NEE in elevated C\textsubscript{a}.

(1) Higher summer temperatures. Long (1991) provided a physiological basis for increasing stimulation of both light-saturated and light-limited photosynthesis as leaf temperature increases in elevated C\textsubscript{a}. This is because elevated C\textsubscript{a} will inhibit the oxygenation of Rubisco, which becomes progressively favored relative to carboxylation at higher temperatures, due to a relatively greater decrease in both the solubility of CO\textsubscript{2} and specificity of Rubisco for CO\textsubscript{2} (Jordan & Ogren, 1984). Long (1991) extended this analysis to a hypothetical canopy with an LAI of three (a value being approached at this site), to show that at 35 °C, a temperature frequently experienced at this site, the canopy photosynthesis would double with an increase in C\textsubscript{a} from 350 to 650 \( \mu \text{mol mol}^{-1} \).

(2) Leaf photosynthetic capacity. Between June 1999 and August 2000, Ainsworth et al. (2002) showed that stimulation of light-saturated photosynthesis of sun leaves of the three oak species in elevated C\textsubscript{a} displayed seasonal and inter-annual variability. For Q. geminata, which exhibited varying degrees of acclimatory decreases in \( V_{\text{c,max}} \), the stimulation of A\textsubscript{sat} ranged from a maximum of ca. 40% in December 1999 to a complete loss of stimulation in August 1999. For Q. myrtifolia, which did not acclimate to the elevated C\textsubscript{a}, the stimulation of A\textsubscript{sat} ranged from a maximum of ca. 150% for young leaves in the spring, to ca. 40% for mature leaves in June 1999. For senescing Q. myrtifolia leaves in 1998 the stimulation of A\textsubscript{sat} in the elevated C\textsubscript{a} was 97% (Li et al., 2000).

(3) Respiratory fluxes. Because NEE during the photoperiod is the difference between carbon uptake by photosynthesis and carbon loss by both autotrophic and heterotrophic respiration, an effect of elevated C\textsubscript{a} on any component of ecosystem respiration would have affected the stimulation of the NEE in elevated C\textsubscript{a} during the photoperiod. While no statistically significant effects of elevated C\textsubscript{a} on soil respiration have yet been shown at this site (Johnson et al., 2001; Table 1), this should not hide the fact that on occasions soil respiration is higher in elevated C\textsubscript{a} (Table 1). Similarly, elevated C\textsubscript{a} was shown to have no direct effect on leaf respiration of two oak species in this study; however, the indirect effects of long-term growth in elevated C\textsubscript{a} have been observed. For Q. myrtifolia, leaf respiration was increased during the spring (Hymus et al., 2002a), while in this study the stem respiration was decreased during the winter (Fig. 7).

Separating the relative influence of the factors described above on increasing NEE in elevated C\textsubscript{a} is not easy. A start was to express NEE\textsubscript{max} on a unit leaf area basis, thereby accounting for the increase in LAI in the elevated C\textsubscript{a}. When expressed per unit leaf area the stimulation of \( NEE_{\text{max}} \) ranged from 7% to 60%. Contrary to expectations, the stimulation of NEE\textsubscript{max} expressed per unit leaf area, was not temperature dependent, but dependent on increases in \( W_{\text{sat}} \) (Fig. 3). This finding is novel and it suggests that as the water availability increases, the ecosystem carbon uptake may be increasingly stimulated in elevated C\textsubscript{a}. The fact that changes in \( W_{\text{sat}} \) were found to be independent of changes in temperature strengthens the finding. However, we are unable to discount the possibility that the periods of increased \( W_{\text{sat}} \) coincided with other factors that would have increased the stimulation of NEE in elevated C\textsubscript{a}, for example little or no acclimation of
photosynthetic capacity to elevated $C_a$. Alternatively, it is possible that the small range in what are very low $W_{soil}$ values, cannot really be thought of as representing a transition from low to high $W_{soil}$. This study has highlighted how difficult it is to separate the many processes responsible for changing $NEE$ in elevated $C_a$, which was one of the stated aims of this study. It is expected that future modeling studies at this site will provide insights into the relative importance of the multiple mechanisms by which $NEE$ is increased in elevated $C_a$.

Throughout this study, the stimulation of $NEE_{max}$ expressed per unit leaf area, averaged 29%. This was lower than the average 69% and 32% stimulation of $A_{sat}$ for sun leaves of Q. myrtifolia and Q. geminata, respectively, determined from multiple studies carried out at this site (Li et al., 2000; Hymus et al., 2001, 2002a; Ainsworth et al., 2002). Given that the stimulation of soil, leaf and woody tissue respiration is smaller than the stimulation of $A_{sat}$ in elevated $C_a$, at this site, we would have expected the stimulation of the leaf area-based $NEE_{max}$ to be greater than the stimulation of sun leaf $A_{sat}$. Clearly, there is a significant factor decreasing the effect of the elevated $C_a$ on $NEE_{max}$. Increased shade in the denser elevated $C_a$ canopy is most likely this factor. While photosynthesis of the light-limited leaves within the canopy will still be stimulated by elevated $C_a$, due to the competitive suppression of photorespiration, the stimulation will be much less than that of the sun leaves (Long & Drake, 1991; Osborne et al., 1997). The combination of this physiological response with the fact that light penetrating the denser canopy will be greatly reduced in elevated $C_a$ is important. It has been shown that through the combination of these two factors, photosynthesis of Q. myrtifolia leaves within the canopy was only 6% higher in elevated $C_a$ compared with a 34% stimulation of the sun leaf photosynthesis (J. H. Li unpublished results).

Night

In this system, changes in $NEE_{night}$ tracked changes in temperature in both the $C_a$ treatments (Figs 1, 5 and 6). Over the study period, elevated $C_a$ significantly increased $NEE_{night}$. This increase averaged 39%, but ranged from 6% to 64%. While the highest stimulation was during the winter months, this effect was far from consistent.

In this study we made two attempts to partition $NEE_{night}$. During December 1999 and 2000, the increase in $NEE_{night}$ in elevated $C_a$ was driven by increases in $R_{below}$, which accounted for up to ca. 87% of $NEE_{night}$ (Table 1). A high within-treatment variability meant that the increase in $R_{below}$ in elevated $C_a$ in both December 1999 and 2000 was not statistically significant ($P = 0.06$ and 0.08). These two isolated measurement periods, in which $R_{below}$ was increased in the elevated $C_a$, need to be placed within the context of long-term data sets in which there has been no statistically significant effect of elevated $C_a$ on either the soil [CO$_2$] (Johnson et al., 2001) or $R_{soil}$ (unpublished results), even though there are times (also winter months) when the $R_{soil}$ is higher in elevated $C_a$. It is conceivable that during the winter months when the respiratory fluxes from the soil are low, the increases in the $R_{soil}$ that are small in absolute terms will yield large relative stimulations.

Aboveground respiration was significantly increased by 35% and 42% in December 1999 and December 2000. However, $R_{above}$ accounted for only ca. 13% of $NEE_{night}$. The stimulation in $R_{above}$ in elevated $C_a$ was less than the increase in aboveground biomass of 66% and 79% in December 1999 and 2000, respectively, reported in Dijkstra et al. (2002). In the absence of any direct effect of elevated $C_a$ on mitochondrial respiration (Jahnke, 2001; Hymus et al., 2002a), two indirect effects were likely occurring. First, growth in elevated $C_a$ decreased stem respiration indirectly in Q. myrtifolia (Fig. 7), this may well have been due to a decrease in the ratio of respiring to non-respiring tissue in the larger stems in elevated $C_a$. This finding remains to be tested on stems of increasing age. Second, the ratio of leaf biomass to woody biomass was decreasing in elevated $C_a$. In December 1999 and 2000, the woody biomass was increased by 89% and 80%, respectively, in elevated $C_a$, while leaf biomass, which had higher specific respiration rates than the woody biomass (Fig. 7), was increased by only 40% and 22% in December 1999 and 2000, respectively.

In this study, we partitioned $NEE_{night}$ by subtracting $R_{above}$ from $NEE_{night}$ to yield $R_{below}$. An alternative was to have subtracted $R_{soil}$ modeled from soil chamber measurements, from $NEE_{night}$ to yield $R_{above}$. We chose the former method because of the comprehensive nature of our biomass sampling, in which the woody biomass of every oak in each chamber is determined. This removed the problems of trying to sample representatively on a smaller scale, as had to be carried out using the soil chamber to measure $R_{soil}$. Also, given the large proportion of the $NEE_{night}$ that was derived from the soil, even the small relative errors in measuring this flux would lead to large partitioning errors.

As far as we know, this study constitutes the largest data set showing the effects of the elevated $C_a$ on $NEE$ measured in situ, and is the first to be carried out in a woody ecosystem. In the context of previous field studies (Diemer, 1994; Oechel et al., 1994; Ham et al., 1997).
our finding of a sustained stimulation of both light-limited and maximum NEE during the photoperiod, which was still evident after 6 years regeneration in the elevated $C_a$ is novel (in the marsh ecosystem of the Chesapeake Bay, an increased ecosystem carbon uptake in the elevated $C_a$ has been observed for 16 years, B. G. Drake, unpublished results). As expected, this effect was due to the numerous interactions between elevated $C_a$, climate, ecosystem processes and physiology. The key factor among those responsible for the seasonal variability in the effect was increases in ecosystem leaf area in the elevated $C_a$ and changes in $W_{net}$. Also novel was the sustained increase in ecosystem respiration in elevated $C_a$, and the smaller stimulation than would have been expected from the increase in the above-ground biomass. Given that the night-time flux, and its stimulation by elevated $C_a$, was smaller than CO$_2$ uptake during the photoperiod and its stimulation by elevated $C_a$, we conclude that during this two-year period more carbon was sequestered at elevated $C_a$ in this ecosystem. Based on these findings, elevated $C_a$ would be expected to speed up the rate of postfire biomass accumulation, which would be expected to shorten the fire return cycle in this fire-dependent ecosystem.

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