

Elevated atmospheric CO₂ stimulates aboveground biomass in a fire-regenerated scrub-oak ecosystem

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Abstract

The effect of elevated atmospheric CO₂ concentration (C_a) on the aboveground biomass of three oak species, *Quercus myrtifolia*, *Q. geminata*, and *Q. chapmanii*, was estimated nondestructively using allometric relationships between stem diameter and aboveground biomass after four years of experimental treatment in a naturally fire-regenerated scrub-oak ecosystem. After burning a stand of scrub-oak vegetation, re-growing plants were exposed to either current ambient (379 $\mu\text{L L}^{-1}$ CO₂) or elevated (704 $\mu\text{L L}^{-1}$ CO₂) C_a in 16 open-top chambers over a four-year period, and measurements of stem diameter were carried out annually on all oak shoots within each chamber. Elevated C_a significantly increased aboveground biomass, expressed either per unit ground area or per shoot; elevated C_a had no effect on shoot density. The relative effect of elevated C_a on aboveground biomass increased each year of the study from 44% (May 96–Jan 97), to 55% (Jan 97–Jan 98), 66% (Jan 98–Jan 99), and 75% (Jan 99–Jan 00). The effect of elevated C_a was species specific: elevated C_a significantly increased aboveground biomass of the dominant species, *Q. myrtifolia*, and tended to increase aboveground biomass of *Q. chapmanii*, but had no effect on aboveground biomass of the subdominant, *Q. geminata*. These results show that rising atmospheric CO₂ has the potential to stimulate aboveground biomass production in ecosystems dominated by woody species, and that species-specific growth responses could, in the long term, alter the composition of the scrub-oak community.

Keywords: elevated CO₂, biomass, Florida scrub, *Quercus myrtifolia*, *Q. chapmanii*, *Q. geminata*, natural forest

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Introduction

The rise of atmospheric CO₂ concentration (C_a) is less than expected from the differential between the known emissions through fossil fuel burning and land-use change and the uptake of CO₂ in the oceans, suggesting that some of the CO₂ emitted through human activities is taken up by the terrestrial biosphere (Keeling *et al.* 1996; Fan *et al.* 1998). Field experiments examining the res-

ponses of managed and unmanaged ecosystems to elevated C_a help assess the capacity of terrestrial ecosystems for carbon sequestration now and in the future. Unmanaged forest and grassland ecosystems are especially important because they contain the bulk of the terrestrial carbon (Goudriaan 1993). Elevated C_a increases leaf photosynthesis (Drake *et al.* 1997), but whether or not this enhanced C-fixation rate will be maintained over the long term is not known. Plants grown in artificial conditions such as greenhouses for

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weeks to months probably will not exhibit the same response to increasing C_a as those growing in a natural ecosystem over several years. For example, artificial or reconstituted ecosystems lack mature nutrient cycles (Johnson & Ball 1996) that are important regulators of the ecosystem response to C_a. Although there is a great need for *in situ* studies, only a few experiments have measured the effects of elevated C_a on plant biomass in unmanaged ecosystems. Increased plant biomass in response to elevated C_a may result in long-term carbon storage in wood or soil organic matter.

Most field studies of the impacts of elevated C_a have been carried out in ecosystems dominated by herbaceous species. An arctic ecosystem showed no increase in aboveground biomass in response to elevated C_a (Tissue & Oechel 1987). A marsh ecosystem showed a nonsignificant 16% increase in aboveground biomass for the C3 species (Curtis *et al.* 1989; Arp *et al.* 1993). A C4 prairie grassland ecosystem in Kansas showed increased aboveground biomass productivity and leaf area index in dry years, but not in wet years (Owensby *et al.* 1999). A California C3 mixed grassland showed increased aboveground litter production under elevated CO₂ (Chiarello & Field 1996), resulting from the water-saving effect of elevated C_a on plants growing during the drier part of the year. A similar result was reported for a Mediterranean old field community (Navas *et al.* 1995; Roy *et al.* 1996), while a Swiss high-altitude alpine grassland showed no significant response of aboveground biomass, although elevated C_a increased the average shoot weight of one subdominant species, *Poa alpina*, by 47% (Schäppi & Körner 1996). Biomass in a low-altitude, highly diverse calcareous grassland ecosystem did not respond significantly to elevated C_a (Stocker *et al.* 1999).

In contrast to the relatively small stimulation of shoot growth in native herbaceous species discussed above, *Quercus ilex* in an Italian natural 'Macchia' scrub-oak ecosystem increased shoot length (200%), shoot diameter (38%) and number of leaves per shoot (36%) when exposed to elevated C_a (Scarascia-Mugnozza *et al.* 1996). Loblolly pine (*Pinus taeda*) stem basal area was increased 24% for a 50% increase in C_a (DeLucia *et al.* 1999). Studies of effects of elevated C_a on tree seedlings or juvenile trees generally showed an increase in aboveground biomass and leaf weight (Ceulemans & Mousseau 1994; Saxe *et al.* 1998; Norby *et al.* 1999). Modelling of fire-regenerated ecosystems on sandy soils (similar to the scrub-oak ecosystem studied here) show that a substantial response to elevated C_a can be expected, as faster growing plants in elevated C_a increase nutrient uptake, and thereby reduce nutrient losses (leaching and volatilization) in the first years following fire (Kirschbaum *et al.* 1998). The present paper reports the effect of elevated atmospheric

CO₂ concentration on aboveground biomass of a naturally fire-regenerated woody ecosystem.

Materials and methods

Ecosystem description

The Florida scrub-oak ecosystem is a xerophytic fire-regenerated, low-stature shrub community with a relatively short disturbance cycle of 7–10 y occupying well-drained infertile sandy soils (Schmalzer & Hinkle 1992a). The ecosystem, located on a 10–15 kyr-old barrier island, is dominated by vegetation that rapidly resprouts after fire, including *Quercus myrtifolia* Willd, *Q. geminata* Small, *Q. chapmani* Sargent, and *Serenoa repens* Small. Species of lesser abundance include ericaceous shrubs (*Lyonia fruticosa*, *L. lucida*), a blueberry (*Vaccinium myrsinites*), and a leguminous vine (*Galactia eliottia*). In total, 27 species of plants have been described (Schmalzer & Hinkle 1992a).

The experimental site was located on Merritt Island National Wildlife Refuge on Merritt Island, FL, USA (28°38'N, 80°42'W). The study site was an oak-dominated tract of the oak saw-palmetto scrub, which was distinct from the palmetto-dominated tracts by having a lower water table and lower soil organic matter content (Schmalzer & Hinkle 1992b). The soil was Pomello (Arenic Haplhumod) and Poala sands (Spodic Quartzipsamment), both moderately well drained sandy soils with low nutrients and pH (3.9–4.1). The soil had a marked organic layer at the top, and sometimes a B_h horizon at the depth of the water table. Organic matter content was 7% from 0 to 15 cm depth, 2% for 15–30 cm depth, and negligible below 30 cm (Schmalzer & Hinkle 1996); roots were also concentrated in the top 30 cm of soil (Day *et al.* 1996). The water table was at about 1.5–2.5 m depth, but occasionally rose close to the surface.

Climate

The 100-y average annual precipitation was 1310 mm with high variation from year to year, as illustrated by the exceptionally dry year of 1998 (Mailander 1990; Table 1). Most of the rain fell in intense short-duration thunderstorms during the wet season from June to October. The rainfall in 1996, 1997 and 1999 was somewhat above average, while in 1998 it was below average, especially for the main growth period between April and August (Table 1).

Allometric relationships

A previous elevated C_a study – described in Day *et al.* (1996) and conducted on a site adjacent to the current

Table 1 Monthly and yearly precipitation (ppt., mm) and mean air temperature (Temp., °C) for 1996, 1997, 1998, and 1999 (NASA weather station within 2 miles of the experimental site)

Month	1996		1997		1998		1999	
	Ppt.	Temp.	Ppt.	Temp.	Ppt.	Temp.	Ppt.	Temp.
Jan	163	15.6	61	17.2	60	18.3	80	16.8
Feb	31	16.7	25	20.0	204	16.7	38	16.6
Mar	394	17.8	71	22.2	58	17.2	11	17.2
Apr	39	20.6	99	21.1	12	21.7	44	23.2
May	35	25.0	94	24.4	9	25.0	104	23.9
Jun	427	26.1	196	26.7	5	30.0	150	26.0
Jul	57	28.3	188	28.3	93	30.0	50	28.6
Aug	142	27.2	127	28.3	104	28.9	236	27.7
Sep	185	27.2	109	27.2	188	27.2	325	25.9
Oct	124	23.9	105	24.4	33	26.1	250	23.6
Nov	16	20.6	72	20.6	61	22.8	54	20.1
Dec	44	17.2	232	17.8	12	19.4	61	15.9
Year	1657	22.2	1380	23.2	839	23.6	1403	22.1

Table 2 Relationship between the stem diameter (diam, mm) and the aboveground shoot mass (g shoot⁻¹) for two oak (*Quercus*) species grown under ambient or elevated CO₂ concentration, or in the unchambered plots after three years treatment in the previous study

Species	Treatment	N	Regression equation	R ²	95% CI	
					intercept	slope
<i>Q. myrtifolia</i>	Unchambered	232	$\ln(\text{mass}) = -1.915 + 2.888[\ln(\text{diam})]$	0.92	±0.190	±0.113
	Ambient	326	$\ln(\text{mass}) = -2.063 + 2.977[\ln(\text{diam})]$	0.89	±0.172	±0.117
	Elevated	270	$\ln(\text{mass}) = -2.023 + 2.938[\ln(\text{diam})]$	0.94	±0.171	±0.097
<i>Q. geminata</i>	Unchambered	175	$\ln(\text{mass}) = -1.423 + 2.599[\ln(\text{diam})]$	0.91	±0.193	±0.121
	Ambient	176	$\ln(\text{mass}) = -1.691 + 2.757[\ln(\text{diam})]$	0.90	±0.210	±0.138
	Elevated	87	$\ln(\text{mass}) = -1.477 + 2.613[\ln(\text{diam})]$	0.91	±0.278	±0.183

elevated C_a study yet within the same stand of scrub-oak vegetation – to generate relationships between aboveground biomass per individual shoot and basal diameter for the dominant oak species. In this previous study, the vegetation was cut back to ground level and removed from the plots at the beginning of the experiment. Octagonal open-top chambers were used to maintain either ambient C_a or elevated (ambient plus 350 μL L⁻¹) C_a; unchambered plots were also included, with three replicates of each treatment. The chambers were 2.3 m across by 2.3 m high and were made of a PVC pipe structure wrapped with a clear polyester film ('Mylar', Melinex 071; Courtaulds Performance Films, VA). CO₂ fumigation began on 4 April 1992. At the end of the experiment (June 1995) all shoots were cut off at ground level. Stem basal diameter 2–5 cm above ground level was measured with a digital caliper (Mitotoyu NTD13-6, Mitotoyu Corp, Japan) and shoots were dried to constant weight at 70 °C.

The relationship between stem basal diameter and individual shoot mass (leaves + stems) was determined for *Q. myrtifolia* and *Q. geminata* separately in both C_a treatments and for the unchambered plots. The relationship between biomass (g) and stem diameter (mm) was given by:

$$\ln(\text{mass}) = a + b * \ln(\text{diameter}),$$

as shown in Table 2 and Fig. 1. There were no significant differences in the allometric relationships between the ambient and elevated C_a treatments, but there was a small significant difference between the allometric relationship of stem diameter to shoot biomass in the unchambered plots and the ambient chambers for *Q. geminata* (Table 2). Small significant differences between the two *Quercus* species were also found. Because of these differences between treatments and species, all equations were used as calculated per treatment–species combination (Table 2). The allometric relationships for

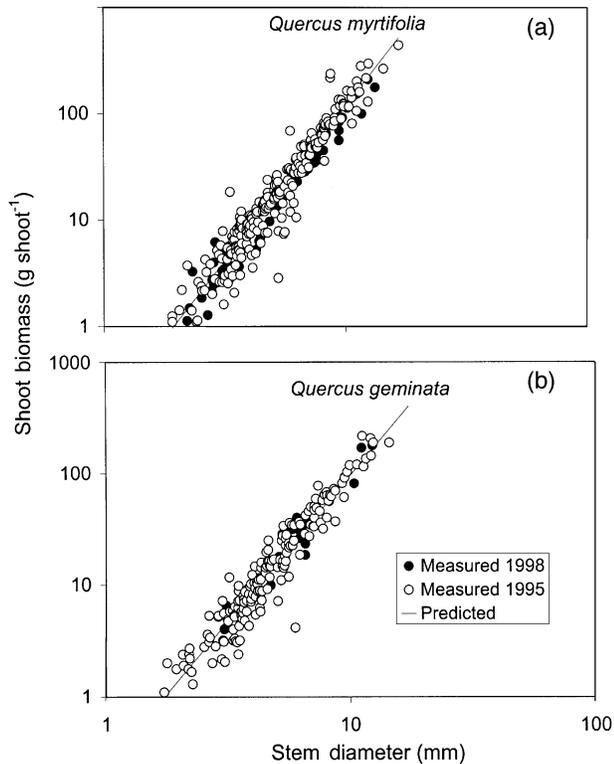


Fig. 1 The relationships between the stem basal diameter (mm) and the aboveground biomass (g shoot^{-1}) for individual shoots of (a) *Quercus myrtifolia* and (b) *Q. geminata*. Data are from (○) the unchambered plots from the previous elevated C_a study, and (●) independent measurements conducted during 1998 from sites adjacent to the current CO₂ experiment.

the third oak species, *Q. chapmanii*, could not be determined from the pilot study because of the low number of observations in the small plots. However, as *Q. chapmanii* is very similar to *Q. myrtifolia* in growth form, allometric relationships for *Q. myrtifolia* were used to estimate *Q. chapmanii* biomass.

In order to verify that the allometric relationships derived from the previous study would be applicable to the current study, 33 *Q. geminata* shoots and 84 *Q. myrtifolia* shoots were collected in July 1998 from two sites adjacent to the experimental area which were burned in May 1997. The ranges of stem diameters and shoot biomasses were similar for the 1995 and 1998 measurements, and relationships between stem diameter and total aboveground biomass in the 1998 collections were indistinguishable from those based on the previous study data (Fig. 1), showing that the equations were repeatable for cut (1995) and burned (1998) vegetation. Because of the destructive nature of these measurements, no attempt has been made to determine allometric relationships within the experimental plots themselves.

Table 3 Number of shoots (m^{-2} , mean \pm SE, $n = 8$) in the preburn vegetation for the three oak (*Quercus*) species averaged over the plots that were later assigned to ambient or elevated CO₂ treatments

	Ambient	Elevated	<i>P</i>
<i>Q. myrtifolia</i> total	13.12 \pm 1.52	11.59 \pm 1.80	0.53
>3 mm	10.82 \pm 1.45	9.84 \pm 1.41	0.64
>5 mm	7.60 \pm 0.92	7.27 \pm 0.85	0.80
>10 mm	2.81 \pm 0.28	3.26 \pm 0.42	0.38
<i>Q. geminata</i> total	4.23 \pm 0.64	4.46 \pm 1.34	0.88
>3 mm	3.81 \pm 0.64	3.90 \pm 1.10	0.97
>5 mm	3.10 \pm 0.64	2.89 \pm 0.81	0.84
>10 mm	0.95 \pm 0.35	0.76 \pm 0.28	0.71
<i>Q. chapmanii</i> total	1.38 \pm 0.46	1.80 \pm 0.46	0.52
>3 mm	0.97 \pm 0.21	1.54 \pm 0.42	0.25
>5 mm	0.45 \pm 0.11	1.15 \pm 0.32	0.04
>10 mm	0.12 \pm 0.07	0.35 \pm 0.14	0.15

A destructive biomass harvest will be reserved for the conclusion of the current experiment.

Pre-treatment biomass and species composition

Before the start of the experiment reported here, 19 plots were selected for representative species composition with the size of the footprint of the intended chambers. Aboveground fresh biomass was determined in the field and converted to dry mass, using relationships between fresh and dry shoot weight generated from 5 to 7 shoots per plot per oak species. The study site was dominated by *Q. myrtifolia*, whose shoots were four to seven times more numerous than those of *Q. geminata* (Table 3) and which accounted for more than 70% of the total preburn biomass (Table 4). *Quercus chapmanii* was the least abundant of the three oak species, but present in all the plots. The three oak species together accounted for about 96% of the total aboveground biomass before the burn. Total aboveground biomass was 1.68 kg m^{-2} for the plots later assigned to the ambient treatment and 1.83 kg m^{-2} for the plots later assigned to the elevated treatment. This difference in biomass was not significant (Tables 3 and 4). Although densities of *Q. chapmanii* stems with a stem diameter between 5 and 10 mm were higher in the plots later assigned to the elevated treatment, this accounted for a small proportion of the total oak densities, and densities of all other categories considered were indistinguishable between the plots later assigned to the two C_a treatments (Table 3).

After weighing, the plant material was returned to the original plots and left to burn. A first, incomplete burn occurred in August 1995, and a second burn in January 1996 was required to completely burn all sites.

Immediately after the second burn, the field facility was built, access walkways were constructed to minimize damage to the vegetation, an instrument shelter was erected close to the chambers where the CO₂ control and the data-acquisition systems were housed, and a weather station was placed on top of the shelter (3 m height). Chambers were erected on 16 of the 19 selected sites, and eight more plots in the burned area were selected and assigned to the unchambered treatment.

New shoots emerging between the time of the burn and the start of the experiment (14 May 1996) were cut off at ground level just before the CO₂ fumigation began. *Quercus myrtifolia* and *Q. chapmanii* were the more productive resprouters during this short regrowth period, forming dense clumps of shoots. The numbers of shoots regrowing during this short period did not differ significantly among plots later assigned to unchambered, ambient, and elevated treatments (Table 5). However, significantly more biomass after this short regrowth period was found for *Q. myrtifolia* and *Q. chapmanii* in the unchambered plots as compared to the plots later assigned to the ambient C_a treatment, while there tended to be 50% less biomass of *Q. geminata* (Table 6). The plots later assigned to either ambient or elevated C_a treatments did not differ significantly in

growth characteristics during this period (Table 6).

Open-top chamber design and CO₂ control

The main frame of the octagonal open-top chambers used in this study was constructed from 4' PVC pipe. The height of the chamber was 2.5 m (including the frustum, see below), and the width was 3.45 m across the chamber between parallel sides (3.66 m from corner to corner), which enclosed 9.47 m² of ground area. The chamber was covered by panels made of a frame of PVC and covered with clear polyester film ('Mylar', Melinex 071), locked in place on the chamber frame with PVC clips. A first row of panels was about 0.3 m above ground level. To facilitate entrance to the chamber, the panels also served as doors, allowing access from all sides to the chamber. The gap between the panel and the ground was covered with Plexiglas, which was buried about 3 cm into the soil, avoiding severing major roots and plant structures. A frustum was placed at the top of the chamber, which left an opening of 5.9 m² or about 60% of the ground area footprint.

Air was blown into the open-top chamber through a main duct (45.7 cm diameter), divided between four smaller ducts (20.5 cm diameter), and dispersed inside the chamber through 2.5 cm openings at a rate of 24–30 m³ min⁻¹. With a chamber volume of 18.9 m³, air replacement rate was 1.3–1.6 chamber volumes min⁻¹. Pure CO₂ was mixed with ambient air just before the blower inlet. Blower speed and CO₂ injection were automatically reduced at night to 1/3 of the daytime values.

C_a was maintained over the full duration except for the period between 13 September and 11 October 1999, when repair work was carried out after two hurricanes. C_a was sampled at canopy height with multiple inlets across the chamber and measured with a LICOR 6262 IRGA (LICOR Inc, Lincoln, NB). The average daytime ambient C_a in the chambers was 381 µL L⁻¹ for 1997, 376 µL L⁻¹

Table 4 Dry weights of aboveground biomass for the three oaks (*Quercus*) and other species (kg m⁻², mean ± SE, *n* = 8) in the preburn vegetation averaged over plots that were later assigned to the ambient or elevated CO₂ treatments

	Ambient	Elevated	<i>P</i>
<i>Q. myrtifolia</i>	1.21 ± 0.12	1.38 ± 0.20	0.44
<i>Q. geminata</i>	0.37 ± 0.17	0.22 ± 0.08	0.45
<i>Q. chapmanii</i>	0.04 ± 0.02	0.14 ± 0.05	0.08
Other species	0.07 ± 0.02	0.10 ± 0.05	0.53
Total aboveground	1.68 ± 0.16	1.83 ± 0.13	0.31

Table 5 Number of shoots (m⁻², mean ± SE, *n* = 8) for the three oak (*Quercus*) species in the pre-experiment re-growth period (January – May 1996) for the plots that were later assigned to ambient, elevated, or unchambered treatments. P(chamber) refers to the statistical difference between the ambient and unchambered plots, and P(CO₂) to the difference between the ambient and elevated treatments

	Unchambered	Ambient	Elevated	<i>P</i>	
				chamber	CO ₂
<i>Q. myrtifolia</i>	23.0 ± 2.9	17.1 ± 3.3	19.8 ± 3.9	0.17	0.52
<i>Q. geminata</i>	2.5 ± 0.5	4.4 ± 1.0	4.2 ± 1.4	0.18	0.87
<i>Q. chapmanii</i>	5.0 ± 0.6	2.8 ± 0.5	3.0 ± 1.4	0.16	0.89
Total oak	30.2 ± 3.0	24.2 ± 3.9	27.0 ± 4.2	0.21	0.57

Table 6 Dry weights of aboveground biomass for the three oak (*Quercus*) species (g m⁻², mean ± SE, *n* = 8) in the pre-experiment re-growth period (January–May 1996) for the plots that were later assigned to ambient, elevated, or unchambered treatments. P(chamber) refers to the statistical difference between the ambient and unchambered plots, and P(CO₂) to the difference between the ambient and elevated treatments

	Unchambered	Ambient	Elevated	<i>P</i>	
				chamber	CO ₂
<i>Q. myrtifolia</i>	238 ± 22	156 ± 20	213 ± 29	0.03	0.12
<i>Q. geminata</i>	28 ± 5	67 ± 17	63 ± 22	0.11	0.87
<i>Q. chapmanii</i>	57 ± 10	28 ± 5	31 ± 15	0.10	0.84
Total oak	323 ± 20	250 ± 27	307 ± 31	0.01	0.14

for 1998, and 381 μL L⁻¹ for 1999. Average daytime C_a in the elevated chambers was 722 μL L⁻¹ for 1997, 700 μL L⁻¹ for 1998, and 691 μL L⁻¹ for 1999. A tipping bucket rain gauge (model 100508; Climatronics, Bohemia, NY) and a cup anemometer (model 3002 wind sentry anemometer; Young Co., MI) were installed on an instrument shelter in the field, close to the chambers. Open-top chambers were dependent on natural rainfall only.

Measurements of basal diameter and shoot density

Stem basal diameter at ground level was measured once a year in 1996, 1997, 1998, and 1999 between November and January on all oak shoots in each plot using an electronic caliper calibrated to an accuracy of 0.1 mm. At the same time, all shoots were counted and identified to species. Each chamber was divided into six triangular segments of equal area. To avoid any bias introduced by changes during the measurement period, stem diameters of shoots were measured in one segment in all the plots in order of unchambered, ambient and elevated plots and from blocks 1 to block 8, before the next segment was measured. Total aboveground biomass per shoot was calculated based on each individual measurement of stem diameter using the allometric relationships presented in Table 2. Based on these values, both the average mass per shoot for each oak species and aboveground biomass per m² ground area for each oak species and for the entire oak community were calculated. The annual increment in aboveground oak biomass (g m⁻² y⁻¹) was also calculated by subtracting aboveground biomass from the end of the previous year from that measured at the end of a given year. For example, the annual increment for 1998 was determined as biomass at the end of 1998 minus biomass at the end of 1997. Annual increment per chamber was calculated for

each species individually and for the entire oak community considered together.

Statistical design

Sixteen plots were assigned to eight blocks of two plots each. This selection was based on similarity of the initial aboveground biomass, proximity, and considerations of infrastructure. CO₂ treatment (ambient or elevated) was randomly assigned to plots within the blocks. Eight unchambered plots were selected after the burn and one assigned to each of the eight selected blocks. For comparing aboveground biomass at the plot level, the statistical design of the experiment was a randomized block, with plots as the experimental units and time as a repeated measure. Response variables – total aboveground biomass, annual aboveground biomass increment, biomass per shoot and shoot density – were examined for each of the oak species individually as well as for the whole oak community considered together. For each response variable/species combination, two tests were conducted: ambient vs. elevated to determine the effect of C_a through time, and ambient vs. unchambered to determine the effect of the chambers through time. Statistical significance was accepted at *P* < 0.05. Because the unchambered plots were selected after the burn, information on preburn biomass was not available from these plots, limiting the ability to assign them to blocks with similar biomass and species composition with the ambient and elevated treatments. As noted above, significant differences between unchambered and ambient plots in biomass accumulation were observed during the brief re-sprouting period after the burn and before treatments were initiated (Jan–May 1996, see above). Thus, pre-existing differences between plots assigned to the unchambered and ambient treatments could influence the assessment of the chamber effect after the experiment began. For this reason, the comparison of ambient and elevated treatments is

emphasized in this paper, although data from the unchambered treatment are included to show the degree to which differences in biomass developed over time, indicating possible effects of the open-top chamber itself on the vegetation growth.

Results

Total aboveground biomass

Total aboveground oak biomass per unit ground area (summed for the three oak species) increased substantially throughout the experiment for all treatments (Fig. 2a, Table 7). Elevated C_a significantly increased total aboveground oak biomass over the 4-y period (Fig. 2a, Table 7). Increased aboveground biomass in elevated C_a was apparent after eight months (44%), and the relative stimulation increased over time, from 55% at the end of 1997, 66% at the end of 1998, to 75% at the end of 1999 (C_a -time interaction, Table 7). Total aboveground biomass in the ambient treatment was statistically indistinguishable from that in the unchambered plots (Fig. 2a, Table 7).

The three species did not respond in the same manner to C_a . Aboveground biomass of *Q. myrtifolia* showed an increasing response to elevated C_a through time (Fig. 2b, Table 7), similar to that observed for the total aboveground biomass (Fig. 2a). Elevated C_a increased *Q. myrtifolia* aboveground biomass by 35% at the end of 1996, by 52% at the end of 1997, by 71% at the end of 1998, and by 73% at the end of 1999. By contrast, elevated C_a caused very small changes in *Q. geminata* aboveground biomass (Fig. 2c) – a 27% increase in end of 1996, 4% increase end of 1997, 5% increase end of 1998, and 23% increase end of 1999 – that were not statistically significant (Table 7). This same pattern of species-specific responses to elevated C_a was also observed in the previous study, with large and significant responses of *Q. myrtifolia* but small and nonsignificant responses of *Q. geminata* (BG Drake *et al.* unpubl. data). Total aboveground biomass of *Q. chapmanii* showed a large (>150%) response to C_a , but this effect was not significant due to high variability (Fig. 2d, Table 7).

The effects of the open-top chambers on aboveground biomass were species-specific. Aboveground biomass of the dominant species *Q. myrtifolia* was similar in the ambient and unchambered treatments (Fig. 2b, Table 7), consistent with the absence of a chamber effect on total aboveground biomass (Fig. 2a, Table 7). However, *Q. geminata* had significantly more aboveground biomass in the ambient chambers compared to the unchambered plots (Fig. 2c, Table 7), while *Q. chapmanii* had significantly less aboveground biomass in the ambient chambers compared to the unchambered plots (Fig. 2d,

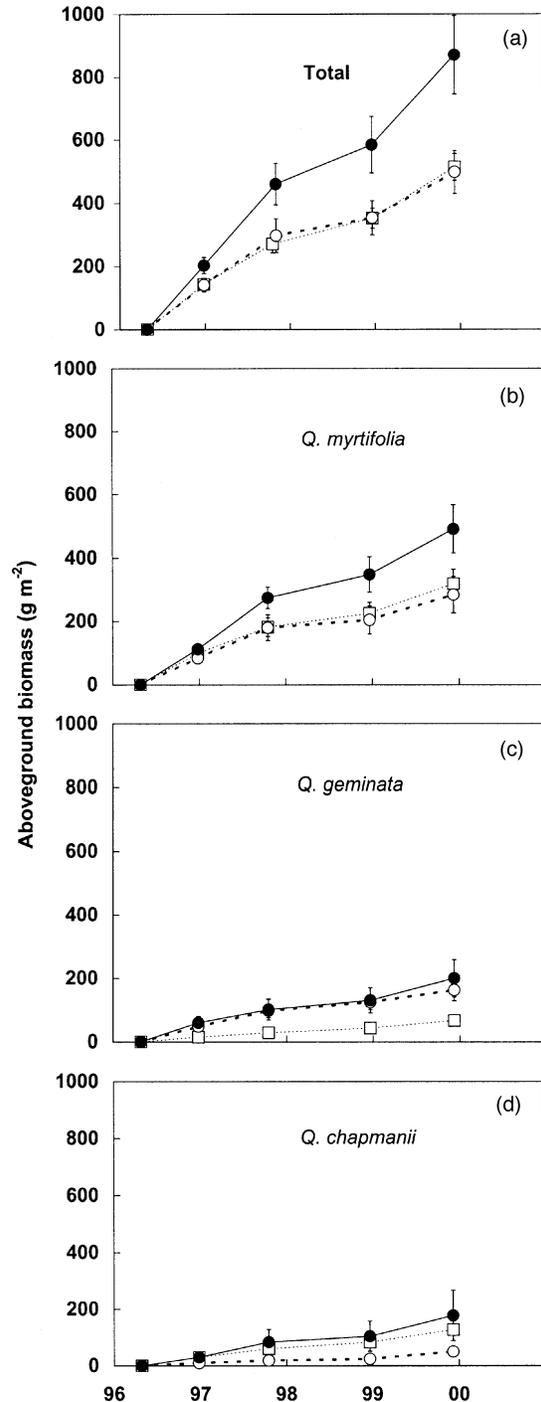


Fig. 2 The effect of elevated C_a on total aboveground biomass per unit ground area (g m^{-2}) of (a) total oaks, (b) *Quercus myrtifolia*, (c) *Q. geminata* and (d) *Q. chapmanii*. Symbols for treatments are: ambient (\circ), elevated (\bullet) and unchambered (\square).

Table 7). These differences in *Q. geminata* and *Q. chapmanii* biomass, however, may have reflected pre-existing differences in biomass between the sites later

Table 7 *P*-values from repeated measures analyses of variance for aboveground biomass for the three oak (*Quercus*) species separate and combined over the four-year experimental period (kg m⁻², main effects of treatment (either C_a or chamber), time and interaction between treatment and time). Means and SE for shoot density are presented in Fig. 2. 'A vs. E' refers to tests for differences between the ambient and elevated treatments through time, whereas 'U vs. A' refers to tests for differences between ambient and unchambered treatments through time

	Total aboveground biomass (g m ⁻²)		
	Treatment	Time	Trt × Time
Total			
A vs. E	0.022	<0.001	0.004
U vs. A	0.979	<0.001	0.579
<i>Q. myrtifolia</i>			
A vs. E	0.064	<0.001	0.004
U vs. A	0.569	<0.001	0.514
<i>Q. geminata</i>			
A vs. E	0.726	<0.001	0.660
U vs. A	0.006	<0.001	0.340
<i>Q. chapmanii</i>			
A vs. E	0.143	0.016	0.043
U vs. A	0.024	<0.001	0.022

assigned to the unchambered and ambient treatments (Table 6), rather than a true chamber effect.

Annual aboveground biomass increment

The annual increment in total aboveground oak biomass was positive for each year of the experiment (Table 8), though the extreme drought during the summer of 1998 (Table 1) substantially reduced annual increment in 1998. The increment in total aboveground oak biomass during the drought year was 51% lower than during 1997 and 54% lower than in 1999 (Tables 8 and 9, effect of Time), years during which precipitation was closer to the 100-y mean for the site. However, notwithstanding the reduction in the absolute growth rates, elevated C_a significantly increased annual increment in aboveground biomass by 122% during the drought year 1998, compared to a 65% increase in 1997 and a 116% increase in 1999. Total annual biomass increment in the unchambered plots was similar to and statistically indistinguishable from that observed in the ambient chambers. Annual increment in the unchambered plots was also reduced severely by the drought year of 1998.

Annual aboveground biomass increment for each of the three oak species was positive for each year of the study (Tables 8 and 9). The effects of elevated C_a on

Table 8 Annual increment in aboveground biomass (g m⁻² y⁻¹, means ± SE, *n* = 8) for each of the three oak (*Quercus*) species and total oak biomass combined. Increment is the difference in biomass between consecutive measurement periods (e.g. increment for 1997 is the difference in biomass measured end of 1997 and end of 1996). Relative effects of CO₂ and chamber treatment are shown as percentage differences: (E-A)/A × 100% and (A-U)/U × 100%. Statistical tests of these comparisons are summarized in Table 9

	1997	1998	1999
<i>Q. myrtifolia</i>	99.3 ± 27.5	24.6 ± 12.7	78.3 ± 20.2
Ambient			
Elevated	165.7 ± 23.6	76.1 ± 25.9	147.0 ± 23.8
Unchambered	85.3 ± 20.8	44.1 ± 9.6	96.0 ± 17.8
CO ₂ effect	66.8%	209.7%	87.7%
Chamber effect	16.5%	-44.3%	-18.4%
<i>Q. geminata</i>			
Ambient	51.7 ± 11.0	27.3 ± 4.6	33.8 ± 42.1
Elevated	42.3 ± 13.4	29.8 ± 8.6	70.9 ± 22.8
Unchambered	13.6 ± 4.8	14.9 ± 5.3	24.2 ± 7.2
CO ₂ effect	-18.2%	9.3%	110.0%
Chamber effect	280.1%	82.8%	39.8%
<i>Q. chapmanii</i>			
Ambient	9.0 ± 4.0	5.2 ± 3.1	24.1 ± 14.6
Elevated	55.4 ± 31.5	21.0 ± 8.7	75.5 ± 36.9
Unchambered	32.0 ± 4.9	23.7 ± 10.8	45.1 ± 9.1
CO ₂ effect	515.1%	302.6%	214.1%
Chamber effect	-71.8%	-78.0%	-46.7%
Total			
Ambient	160.0 ± 33.5	57.0 ± 14.0	136.1 ± 44.3
Elevated	263.3 ± 43.4	126.8 ± 28.8	293.4 ± 39.7
Unchambered	130.8 ± 22.0	82.7 ± 16.0	165.2 ± 22.5
CO ₂ effect	64.6%	122.4%	115.6%
Chamber effect	22.3%	-31.0%	-17.6%

annual aboveground biomass increment were also species specific: large and significant increases in *Q. myrtifolia*, no effect in *Q. geminata*, and large but nonsignificant (*P* = 0.113) trends in *Q. chapmanii* owing to high variability. Species also responded individually to the drought year of 1998. Drought strongly and significantly reduced annual aboveground biomass increment of *Q. myrtifolia* (Table 9, effect of Time for *Q. myrtifolia*), which was 59% lower in 1998 (the drought year) compared to 1997 and 56% lower compared to 1999 averaged over the ambient, elevated and unchambered plots. In *Q. chapmanii*, annual biomass increment was 43% lower during the drought year compared to 1997 and 66% lower compared to 1999, but this effect was only marginally significant. In *Q. geminata*, annual biomass increment tended to be lower during the drought year compared to 1997 and 1999, but the reduction was considerably smaller in this species and the effect was

Table 9 *P*-values from repeated measures analyses of variance for annual increment in aboveground biomass (main effects of treatment (either C_a or chamber), time and interaction between treatment and time). Means and SE for annual increment in aboveground biomass are presented in Table 8. 'A vs. E' refers to tests for differences between the ambient and elevated treatments through time, whereas 'U vs. A' refers to tests for differences between ambient and unchambered treatments through time

	P-values		
	Treatment	Time	Trt × Time
<i>Q. myrtifolia</i>			
A vs. E	0.037	< 0.001	0.850
U vs. A	0.563	0.015	0.243
<i>Q. geminata</i>			
A vs. E	0.570	0.539	0.438
U vs. A	0.242	0.814	0.742
<i>Q. chapmanii</i>			
A vs. E	0.113	0.092	0.079
U vs. A	0.070	0.091	0.963
Total			
A vs. E	0.040	0.001	0.167
U vs. A	0.626	0.019	0.449

not significant. For none of the three species was the interaction between C_a and time significant (Table 9). Nevertheless, the substantially larger increase in aboveground biomass increment of *Q. myrtifolia* caused by elevated C_a during the drought year (+210%) is remarkable, compared to the previous (+67%) and subsequent (+88%) years during which precipitation was closer to the 100-y average (Table 8).

Shoot density

The total number of oak shoots decreased over time (Table 10, Fig. 3a), from 75 m^{-2} in January 1997 to 47 m^{-2} in January 2000 for the ambient treatment (a 37% decrease), and from 76 m^{-2} in January 1997 to 56 m^{-2} in January 2000 for the elevated treatment (a 30% decrease). This reduction was likely the result of increasing canopy density and competition for light; the severe drought of 1998 did not appear to cause a larger reduction in shoot density than occurred during 1997 and 1999. Elevated C_a did not significantly affect shoot density of *Q. myrtifolia* and *Q. geminata* (Fig. 3b,c, Table 10). The nonsignificant tendency for higher densities of *Q. chapmanii* shoots in elevated C_a (Fig. 3c) was already established in the preburn vegetation (Table 3). Thus, the increase in total aboveground oak biomass in the elevated C_a treatment (Fig. 2) was not caused by a higher shoot density.

Table 10 *P*-values from repeated measures analyses of variance for shoot density (m^{-2} , main effects of treatment (either C_a or chamber), time and interaction between treatment and time). Means and SE for shoot density are presented in Fig. 3. 'A vs. E' refers to tests for differences between the ambient and elevated treatments through time, whereas 'U vs. A' refers to tests for differences between ambient and unchambered treatments through time

	Shoot density (m^{-2})		
	Treatment	Time	Trt × Time
<i>Q. myrtifolia</i>			
A vs. E	0.682	<0.001	0.109
U vs. A	0.212	<0.001	0.493
<i>Q. geminata</i>			
A vs. E	0.693	0.023	0.805
U vs. A	0.005	0.136	0.346
<i>Q. chapmanii</i>			
A vs. E	0.125	0.005	0.314
U vs. A	0.049	0.019	0.204
Total			
A vs. E	0.584	<0.001	0.020
U vs. A	0.157	<0.001	0.288

Compared to the unchambered plots, the ambient plots had similar densities of *Q. myrtifolia* shoots (Fig. 3b, Table 10), but had significantly higher densities of *Q. geminata* shoots (Fig. 3c, Table 10) and significantly lower densities of *Q. chapmanii* shoots (Fig. 3d, Table 10). In January 1997, the density of *Q. geminata* shoots was 142% higher in the ambient plots compared to the unchambered plots, a difference that declined to 68% by January 2000 (Fig. 3C). *Quercus chapmanii* densities were 41% lower in the ambient plots than in the unchambered plots in 1997, a difference that was maintained during each of the subsequent measurement periods. While these differences could indicate effects of the open-top chambers on the densities of these subdominant oaks, the pretreatment differences between ambient and unchambered plots for *Q. chapmanii* and *Q. geminata* densities (Table 5) were comparable in magnitude to those observed later (Fig. 3c,d, Table 10). Thus, these differences in shoot density may reflect pre-existing differences between the plots later assigned to unchambered and ambient C_a treatments rather than a true effect of the chambers.

Biomass per shoot

Biomass per shoot increased for all species over the four-year period, with somewhat smaller increases during the drought year of 1998 (Fig. 4, Table 11). Elevated C_a significantly increased biomass per shoot of *Q. myrtifolia*

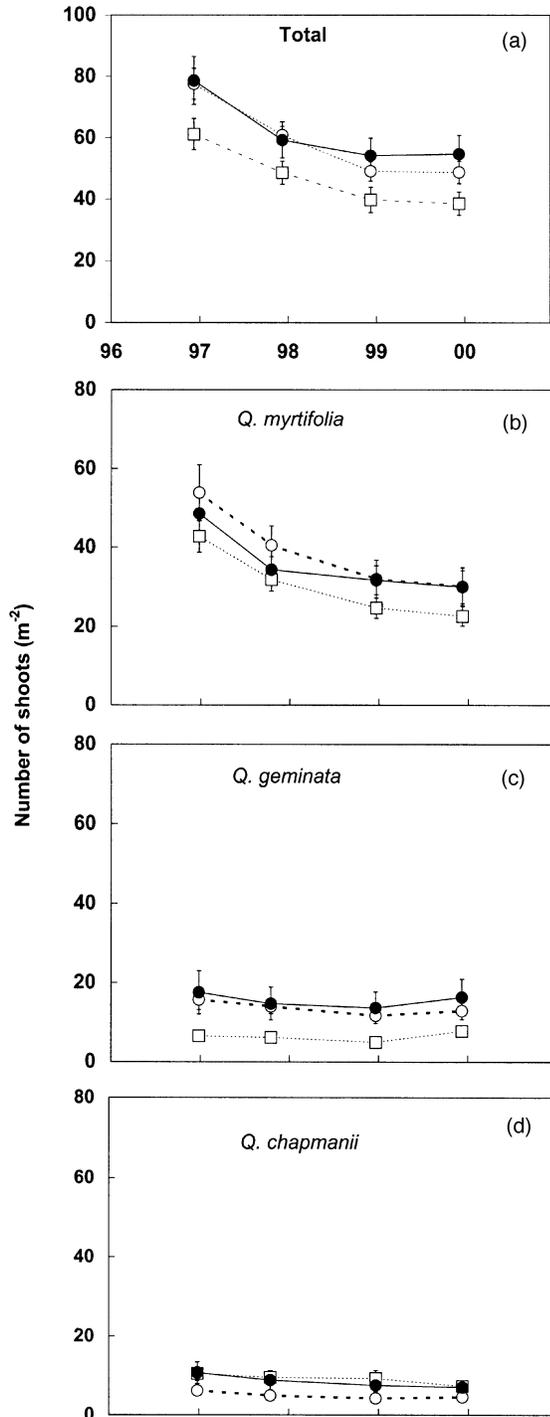


Fig. 3 The effect of elevated C_a on density of shoots (m^{-2}) for (a) total oaks, (b) *Quercus myrtifolia*, (c) *Q. geminata* and (d) *Q. chapmanii*. Symbols as in Fig. 2.

(Fig. 4a), an 81% stimulation by January 2000, and also significantly increased biomass per shoot of *Q. chapmanii*, a 98% stimulation by January 2000 (Fig. 4c). By contrast,

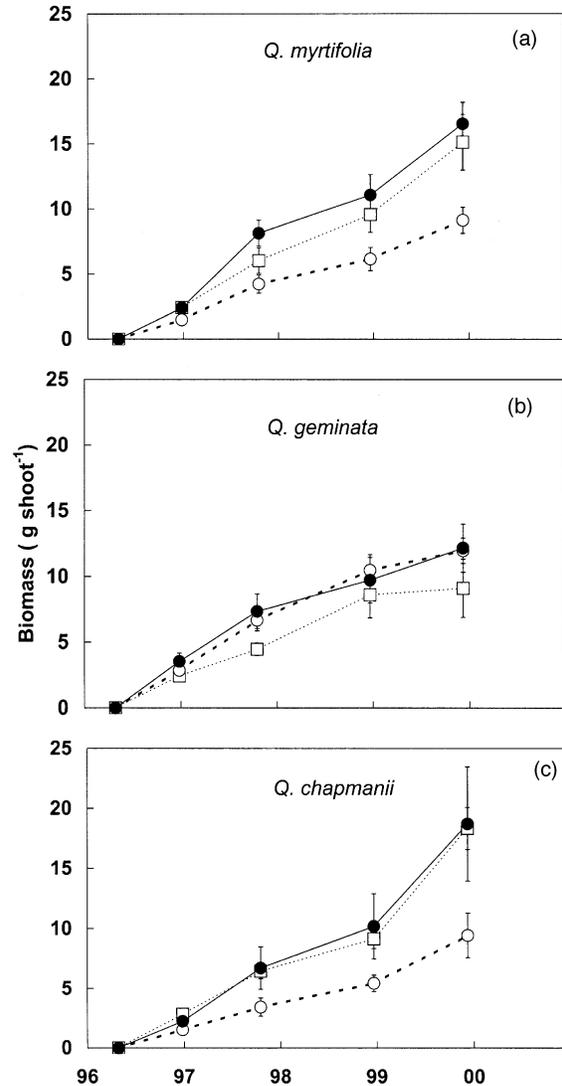


Fig. 4 The effect of elevated C_a on aboveground biomass ($g\ shoot^{-1}$) for (a) *Quercus myrtifolia*, (b) *Q. geminata* and (c) *Q. chapmanii*. Symbols as in Fig. 2.

elevated C_a had no effect on biomass per shoot of *Q. geminata* (Fig. 4b). Thus, the increase in biomass per ground area caused by elevated C_a (Fig. 2) was mainly the result of the difference in weight per shoot (Fig. 4) and not shoot density (Fig. 3).

The chambers caused species-specific changes in biomass per individual shoot. Biomass per shoot of *Q. myrtifolia* and *Q. chapmanii* in the ambient and unchambered treatments diverged through time, with increasingly higher biomass per shoot in the unchambered treatment compared to the ambient (Fig. 4a, Table 11, effect of Chamber, Chamber–Time interactions). By contrast, biomass per shoot of *Q. geminata* did not differ between ambient and unchambered treatments (Fig. 4b, Table 11). The chambers tended to reduce soil water

Table 11 *P*-values from repeated measures analyses of variance for biomass per shoot (g shoot⁻¹, main effects of treatment (either C_a or chamber), time, and interaction between treatment and time). Means and standard errors for shoot density are presented in Fig. 4. 'A vs. E' refers to tests for differences between the ambient and elevated treatments through time, whereas 'U vs. A' refers to tests for differences between ambient and unchambered treatments through time

	Biomass per shoot (g shoot ⁻¹)		
	Treatment	Time	Trt × Time
<i>Q. myrtifolia</i>			
A vs. E	0.012	<0.001	<0.001
U vs. A	0.151	<0.001	0.039
<i>Q. geminata</i>			
A vs. E	0.743	<0.001	0.496
U vs. A	0.698	<0.001	0.996
<i>Q. chapmanii</i>			
A vs. E	0.045	<0.001	0.001
U vs. A	0.040	<0.001	0.027

content (Hungate unpubl. data), possibly causing the reduction in growth of the less drought-tolerant species, *Q. myrtifolia* and *Q. chapmanii*, while not affecting growth of *Q. geminata*, the species with greater drought tolerance.

Discussion

In this study, elevated C_a substantially increased total aboveground oak biomass throughout four growing seasons in this Florida scrub-oak ecosystem (Fig. 2), primarily owing to increased biomass per shoot of the dominant oak species, *Q. myrtifolia*, and that of the subdominant, *Q. chapmanii* (Fig. 4). Elevated C_a did not significantly affect aboveground biomass per unit ground surface or per shoot of *Q. geminata*. The number of shoots per unit ground area was not affected by C_a for any of the three oak species (Fig. 3). The increased biomass and species-specific responses to elevated C_a observed here were similar to those found in a previous study conducted in this ecosystem (Drake *et al.* unpubl. data).

Many studies have examined responses of tree seedlings and saplings to elevated C_a, and most show a stimulation of aboveground growth. For example, averaging across 54 studies published between 1992 and 1997, Saxe *et al.* (1998) report a 49% stimulation of aboveground biomass for deciduous trees and a 130% stimulation for coniferous trees. However, many of these studies were conducted using greenhouses or growth chambers, and those that occurred in the field frequently used altered soils and/or only focused on the seedling

phase of growth. Thus, it has been questioned whether the fairly large growth stimulations observed in these studies have any bearing for the responses of 'intact' woody ecosystems to elevated C_a (Saxe *et al.* 1998). The results presented here show that elevated C_a can cause a stimulation of aboveground biomass in 'intact' ecosystems that is comparable (at least during the first four years following disturbance by fire) to stimulations observed for seedlings under less natural conditions. The biomass stimulation observed herein in response to elevated C_a was larger than that reported for a loblolly pine (*Pinus taeda*) plantation, in which a 25% stimulation of aboveground growth was observed after three years of exposure to elevated C_a (DeLucia *et al.* 1999). The elevated C_a treatment used in the Loblolly study (+ 200 μL L⁻¹) was less than in the present study (+ 325 μL L⁻¹). The present results were also similar to initial results obtained for *Quercus ilex* in a mediterranean 'Macchia' scrub ecosystem (Scarascia-Mugnozza *et al.* 1996), in which branch length increased by 66% and branch volume by 222% during the first three years of exposure to elevated C_a. Later measurements of litter fall suggested that the stimulation of growth by elevated C_a had ceased (De Angelis *et al.* 1999), although these measurements did not assess changes in the two main storage pools in trees, wood and roots.

There are a number of ways in which fire disturbance before the start of the experiment reported here could have contributed to the relatively large and increasing C_a-stimulation of aboveground biomass observed (Sage 1996): (i) the sudden reduction of the shoot:root ratio by fire could have strongly favoured shoot allocation in elevated C_a; (ii) the pulse of available soil nutrients typically following fire could have released plants from nutrient competition favouring a large response to elevated C_a; and (iii) the opening of the canopy, by releasing plants from light competition, again, could have allowed a relatively large response to elevated C_a.

The disturbance of the shoot-root ratio by fire may have favoured a large aboveground biomass response to elevated C_a. The fire before the start of the experiment removed all aboveground biomass and litter. For both treatments, the decreased shoot:root ratio would have changed carbon allocation in the plant in favour of shoot growth. While elevated C_a does cause a large stimulation of belowground growth in this scrub-oak ecosystem, as shown by results from both the previous and current studies (Day *et al.* 1996; J. Dilustro, pers. comm.), the combination of increased photosynthesis in elevated C_a and a strong aboveground sink in both treatments may have allowed a strong CO₂ effect on aboveground biomass to be expressed as well. This is very different from the situation of a mature grass ecosystem under

extreme nutrient limitation, where the allocation pattern would favour root growth predominantly.

Nutrient availability is frequently greater immediately following disturbance by fire (Van Cleve *et al.* 1983; Blank *et al.* 1994), and previous studies on scrub-oak vegetation show a peak of both N and P availability 2–5 y after fire (Schmalzer & Hinkle 1996). Some studies show greater growth responses of plants to elevated C_a when nutrient availability is high (Poorter *et al.* 1996), raising the possibility that the large stimulation of aboveground biomass observed herein resulted partially from a pulse of nutrient availability following fire disturbance. In the present experiment, availability of ortho-P in the A horizon (as measured by resin lysimeters) was highest during 1997, lower in 1998, and lower still in 1999, reflecting a pulse of P availability following fire disturbance (Johnson *et al.* 2001). However, neither nitrate- nor ammonium-N showed this pattern; rather, availability of mineral N in the A horizon was strongly reduced during 1998 – the drought year – with 1999 values similar to those found for 1997 (Johnson *et al.* 2001). While elevated C_a reduced leaf and stem N concentrations in these oaks by 5–10% (Stiling *et al.* 1999 and B. Hungate, unpubl. data), this reduction is too small to completely explain the 75% stimulation of aboveground biomass by nutrient dilution. Elevated C_a increases root length density in this ecosystem (Day *et al.* 1996; J. Dilustro, pers. comm.), indicating increased exploration of the soil and, possibly, increased nutrient uptake, consistent with the reductions in soil N and P availability observed in the elevated CO₂ treatment (Johnson *et al.* 2001). Thus, the large growth response observed herein may have been supported by increased availability and greater nutrient uptake following fire disturbance. Consistent with these arguments, elevated C_a increased N-uptake in *Q. robur* (Vivian *et al.* 1996). In contrast, Norby *et al.* (1986) found that an 85% increase in biomass was not accompanied by any increase in N-uptake of the white oak.

While fire typically increases soil nutrient availability temporarily, nitrogen losses as particulate and volatile compounds in smoke, wind and water erosion, and leaching and trace gas fluxes are also typically high following fire (Raison *et al.* 1985); this lost N must be replaced from other sources. In the present experiment, elevated C_a increased the growth and aboveground N mass productivity of an N-fixing species, *Galactia elliotia*, thereby increasing the flux of nitrogen into the ecosystem (Hungate *et al.* 1999). Additionally, the increased growth of the canopy and growth below ground (Day *et al.* 1996; J. Dilustro, pers. comm.) could also have decreased the nitrogen losses through leaching and volatilization, as predicted through modelling studies (e.g. Kirschbaum *et al.* 1998). Increased nitrogen use efficiency, increased nitrogen uptake from the ecosystem through reduced

losses, and increased input through nitrogen fixation could all contribute to maintaining a strong biomass response to elevated C_a. Further research is needed to quantify the different nutrient sources for the vegetation growth, so predictions can be made whether future limitations can be expected.

Finally, high light intensities and low shoot densities and leaf area following fire mean that plants are not competing for light and may show relatively large growth responses to elevated C_a (Sage 1996). Thus, the open structure of the canopy following fire in the present experiment could also have contributed to the large stimulation of aboveground growth observed in response to elevated C_a. Additionally, possibly because of the open structure of the canopy during the first four years of the experiment, elevated C_a has increased leaf area index (LAI) by 22–63%, depending on time of year and method of determining LAI (Hymus *et al.* unpubl. data). The observed increase in LAI could explain the increasing biomass response through time shown here. As the canopy reaches closure in the next few years, one might expect to see the relative stimulation of aboveground biomass decline to a constant value, determined by the response of leaf photosynthetic characteristics and respiration, as was modelled for cereal grasses (Grashoff *et al.* 1995), and found by Idso (1999) for sour orange trees. Indeed, a sustained and constant stimulation of photosynthetic efficiency in trees has been reported (Norby *et al.* 1999). This would result in a declining relative biomass response, but at the same time, a continued accumulation of total biomass in wood and roots.

Physiological acclimation and species differences

Photosynthetic acclimation to long-term elevated C_a has been reported in many instances (Drake *et al.* 1997) and is expected to affect carbohydrate production and growth accordingly. However, acclimation of photosynthesis in plants in elevated C_a, when it occurs, is very rarely sufficient to remove completely the stimulation of photosynthesis in plants in elevated C_a compared to ambient C_a (Drake *et al.* 1997). In the present study, the aboveground biomass of the dominant *Q. myrtifolia* responded strongly to elevated C_a, while a subdominant species, *Q. geminata*, showed no increase (Figs 2,4). The responsive dominant species *Q. myrtifolia* also showed a large response to elevated C_a in photosynthetic rate during 1997 (Li *et al.* 1999). In this sense, in this early stage of the experiment at least, a large response of net photosynthesis was associated with large biomass increases in this species. However, increased photosynthesis was also observed in *Q. geminata* during 1997 (Li

et al. 1999), with smaller increases during 1998 and 1999 (Ainsworth and Long, pers. comm.). Because no stimulation of aboveground biomass was seen in *Q. geminata* in the same time periods, it is possible that the extra photosynthate produced in response to elevated C_a preferentially supports root growth (Day *et al.* 1996; J. Dilustro, pers. communication).

Interactions with water stress: the drought year of 1998

Elevated C_a stimulated aboveground biomass during each year of this study, including the drought year of 1998. A number of studies have found relatively larger photosynthetic and biomass responses to elevated C_a under drought stress (Idso & Idso 1994). For *Q. myrtifolia*, the species that showed significant aboveground response to elevated C_a , the relative effect of elevated C_a on biomass accumulation was higher during the drought year (210% for 1998) compared to the non-drought years (67% for 1997, 88% for 1999). While the interaction between C_a and year was not significant for annual increment in aboveground biomass for this species, drought did not preclude a large response to elevated C_a , and our results are not inconsistent with the notion that the response to CO_2 is larger under drought. *Q. geminata*, the subdominant species that showed no biomass response to elevated C_a , also showed very little response to the drought of 1998. Possibly, the properties that buffer this species from water stress are also related to its low potential to respond to elevated C_a .

Conclusions

During the first four years after fire disturbance, elevated C_a increased aboveground biomass in a scrub-oak ecosystem, estimated using allometric relationships. Biomass responses were species specific, with one subdominant species, *Q. geminata*, showing no response to elevated C_a , while the dominant species, *Q. myrtifolia*, showed a very large response, largely determining the overall response of the oak community. The third subdominant oak species, *Q. chapmanii*, showed large increases to elevated CO_2 , but owing to its large standard error, this effect was not statistically significant. Determining whether these biomass stimulations during the first four years following fire disturbance can be sustained after the canopy closes is critical for understanding the long-term responses of ecosystems dominated by woody vegetation to elevated C_a .

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References

- Arp WJ, Drake BG, Pockman WT, Curtis PS, Whigham DF (1993) Interactions between C3 and C4 salt march plant species during four years of exposure to elevated atmospheric CO_2 . *Vegetatio*, **104/105**, 133–143.
- Blank RB, Allen F, Young JA (1994) Extractable soil anions in soils following wildfire in a sagebrush-grass community. *Soil Science Society of America Journal*, **58**, 564–570.
- Ceulemans R, Mousseau M (1994) Effect of elevated atmospheric CO_2 on woody plants. *New Phytologist*, **127**, 425–446.
- Chiarello NR, Field CR (1996) Annual grassland responses to elevated CO_2 in multiyear community microcosms. In: *Carbon Dioxide, Populations and Communities* (eds Körner C, Bazzaz FA), pp. 139–157. Academic Press, London.
- Curtis PS, Drake BG, Leadley PW, Arp WJ, Whigham DF (1989) Growth and senescence in plant communities exposed to elevated CO_2 concentrations on an estuarine marsh. *Oecologia*, **78**, 20–26.
- Day FP, Weber EP, Hinkle CR, Drake BG (1996) Effects of elevated CO_2 on fine root length and distribution in an oak-palmetto scrub ecosystem in central Florida. *Global Change Biology*, **2**, 101–106.
- De Angelis P, Scarascia-Mugnozza GE (1999) Contribution from the University of Viterbo. In: *Predicted impacts of rising Carbon dioxide and temperature on forests in Europe at stand scale: Final Report* (Coordinator Jarvis PG). Ecocraft Environment R & D, ENV4-CT95-0077 IC20-CT96-0028.
- DeLucia EH, Hamilton JG, Naidu SL *et al.* (1999) Net primary productivity of a forest ecosystem with experimental CO_2 enrichment. *Science*, **284**, 1177–1179.
- Drake BG, González-Meler MA, Long SP (1997) More efficient plants: a consequence of rising atmospheric CO_2 ? *Annual Review of Plant Physiology and Molecular Biology*, **48**, 607–637.
- Fan S, Gloor M, Mahlman J *et al.* (1998) A large terrestrial carbon sink in North America implied by atmospheric and oceanic carbon dioxide data and models. *Science*, **282**, 442–446.
- Goudriaan J (1993) Interaction of ocean and biosphere in their transient responses to increasing atmospheric CO_2 . *Vegetatio*, **104/105**, 329–337.
- Grashoff C, Dijkstra P, Nonhebel S, Schapendonk AHCM, Van de Geijn SC (1995) Effects of climate change on productivity of cereals and legumes; model evaluation of observed year-to-year variability of the CO_2 response. *Global Change Biology*, **1**, 417–428.
- Hungate BA, Dijkstra P, Johnson DW, Hinkle CR, Drake BG (1999) Elevated CO_2 increases nitrogen fixation and decreases soil nitrogen mineralization in Florida scrub oak. *Global Change Biology*, **5**, 781–789.

- Idso SB (1999) The long-term response of trees to atmospheric CO₂ enrichment. *Global Change Biology*, **5**, 493–495.
- Idso KE, Idso SB (1994) Plant responses to atmospheric CO₂ enrichment in the face of environmental constraints: a review of the past 10 years' research. *Agriculture and Forest Meteorology*, **69**, 153–203.
- Johnson DW, Ball JT (1996) Interactions between CO₂ and nitrogen in forests: can we extrapolate from the seedling to the stand level?. In: *Carbon Dioxide and Terrestrial Ecosystems* (eds Koch GW, Mooney HA.), pp. 283–297. Academic Press, London.
- Johnson DW, Hungate BA, Dijkstra P, Hymus G, Drake BG (2001) Effects of elevated carbon dioxide on soils in a Florida scrub oak ecosystem. *Journal of Environmental Quality*, **30**, 501–507.
- Keeling RF, Piper SC, Heimann M (1996) Global and hemispheric CO₂ sinks deduced from changes in the atmospheric CO₂. *Nature*, **381**, 218–221.
- Kirschbaum MUF, Medlyn BE, King DA *et al.* (1998) Modelling forest growth response to increasing CO₂ concentration in relation to various factors affecting nutrient supply. *Global Change Biology*, **4**, 23–41.
- Li J, Dijkstra P, Hinkle CR, Wheeler RM, Drake BG (1999) Photosynthetic acclimation to elevated CO₂ concentration in the Florida scrub-oak species, *Quercus geminata* and *Quercus myrtifolia*, growing in their native environment. *Tree Physiology*, **19**, 229–234.
- Mailander JL (1990) *Climate of the Kennedy Space Center and Vicinity*. NASA Technical Memo 103498. Kennedy Space Center, Cape Canaveral, FL.
- Navas M-L, Guillermin J-L, Fabreguettes J, Roy J (1995) The influence of elevated CO₂ on community structure, biomass and carbon balance of mediterranean old-field microcosms. *Global Change Biology*, **1**, 325–335.
- Norby RJ, Pastor J, Melillo JM (1986) Carbon–nitrogen interactions in CO₂ enriched white oak: physiological and long-term perspectives. *Tree Physiology*, **2**, 233–241.
- Norby RJ, Wullschlegel SD, Gunderson CA, Johnson DW, Ceulemans R (1999) Tree responses to rising CO₂ in field experiments: implications for the future forest. *Plant, Cell and Environment*, **22**, 683–714.
- Owensby CE, Ham JM, Knapp AK, Auen LM (1999) Biomass production and species composition change in a tallgrass prairie ecosystem after long-term exposure to elevated atmospheric CO₂. *Global Change Biology*, **5**, 497–506.
- Poorter H, Roumet C, Campbell BD (1996) Interspecific variation in the growth response of plants to elevated CO₂: a search for functional types. In: *Carbon Dioxide, Populations and Communities* (eds Körner C, Bazzaz FA), pp. 375–412. Academic Press, London.
- Raison RJ, Khanna PK, Woods PV (1985) Transfer of elements to the atmosphere during low-intensity prescribed fires in three Australian subalpine eucalypt forests. *Canadian Journal of Forest Research*, **15**, 657–664.
- Roy J, Guillermin J-L, Navas M-L, Dhillion S (1996) Responses to elevated CO₂ in Mediterranean old-field microcosms: species, community and ecosystem components. In: *Carbon Dioxide, Populations and Communities* (eds Körner C, Bazzaz FA), pp. 123–137. Academic Press, London.
- Sage RF (1996) Modification of fire disturbance by elevated CO₂. In: *Carbon Dioxide, Populations and Communities* (eds Körner C, Bazzaz FA), pp. 231–249. Academic Press, London.
- Saxe H, Ellsworth DS, Heath J (1998) Tree and forest functioning in an enriched CO₂ atmosphere. *New Phytologist*, **139**, 395–436.
- Scarascia-Mugnozza GE, De Angelis P, Matteucci G, Kuzminsky E (1996) Carbon metabolism and plant growth under elevated CO₂ in a natural *Quercus ilex* L. 'Macchia' stand. In: *Carbon Dioxide, Populations and Communities* (eds Körner C, Bazzaz FA), pp. 209–230. Academic Press, London.
- Schäppi B, Körner C (1996) Growth responses of an alpine grassland to elevated CO₂. *Oecologia*, **105**, 43–52.
- Schmalzer PA, Hinkle CR (1992a) Recovery of oak-saw palmetto scrub after fire. *Castanea*, **57**, 158–173.
- Schmalzer PA, Hinkle CR (1992b) Species composition and structure of oak-saw palmetto scrub vegetation. *Castanea*, **57**, 220–251.
- Schmalzer PA, Hinkle CR (1996) Biomass and nutrients in aboveground vegetation and soils of Florida oak-saw Palmetto scrub. *Castanea*, **61**, 168–193.
- Stiling P, Rossi AM, Hungate B, Dijkstra P, Hinkle CR, Knott WM, Drake BG (1999) Decreased leaf-miner abundance in elevated CO₂ reduced leaf quality and increased parasitoid attack. *Ecological Applications*, **9**, 240–244.
- Stocker R, Körner C, Schmid B, Niklaus PA, Leadley PW (1999) A field study of the effects of elevated CO₂ and plant species diversity on ecosystem-level gas exchange in a planted calcareous grassland. *Global Change Biology*, **5**, 95–105.
- Tissue D, Oechel WC (1987) Response of *Eriophorum vaginatum* to elevated CO₂ and temperature in the Alaskan tussock tundra. *Ecology*, **68**, 401–410.
- Van Cleve K, Dyrness CT, Viereck LA *et al.* (1983) Taiga ecosystems in interior Alaska. *Bioscience*, **33**, 39–44.
- Vivin P, Martin F, Guehl JM (1996) Acquisition and within plant allocation of C-13 and N-15 in CO₂ enriched *Quercus robur* plants. *Physiologia Plantarum*, **98**, 89–96.