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Disturbance, rainfall and contrasting species responses mediated aboveground biomass response to 11 years of CO_2 enrichment in a Florida scrub-oak ecosystem

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Abstract

This study reports the aboveground biomass response of a fire-regenerated Florida scrub-oak ecosystem exposed to elevated CO_2 (1996–2007), from emergence after fire through canopy closure. Eleven years exposure to elevated CO_2 caused a 67% increase in aboveground shoot biomass. Growth stimulation was sustained throughout the experiment; although there was significant variability between years. The absolute stimulation of aboveground biomass generally declined over time, reflecting increasing environmental limitations to long-term growth response. Extensive defoliation caused by hurricanes in September 2004 was followed by a strong increase in shoot density in 2005 that may have resulted from reopening the canopy and relocating nitrogen from leaves to the nutrient-poor soil. Biomass response to elevated CO_2 was driven primarily by stimulation of growth of the dominant species, *Quercus myrtifolia*, while *Quercus geminata*, the other co-dominant oak, displayed no significant CO_2 response. Aboveground growth also displayed interannual variation, which was correlated with total annual rainfall. The rainfall × CO_2 interaction was partially masked at the community level by species-specific responses: elevated CO_2 had an ameliorating effect on *Q. myrtifolia* growth under water stress. The results of this long-term study not only show that atmospheric CO_2 concentration had a consistent stimulating effect on aboveground biomass production, but also showed that available water is the primary driver of interannual variation in shoot growth and that the long-term response to elevated CO_2 may have been caused by other factors such as nutrient limitation and disturbance.

Keywords: aboveground biomass, canopy closure, elevated CO_2, long-term stimulation, *Quercus geminata*, *Quercus myrtifolia*, resource limitation, scrub-oak, species-specific response

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Introduction

Increased carbon (C) uptake by plants grown in elevated atmospheric carbon dioxide (CO_2) concentration suggests that terrestrial ecosystems will partially mitigate the anthropogenic rise in CO_2 (Cramer *et al.*, 2001; Schimel *et al.*, 2001; IPCC, 2007). Hundreds of studies demonstrate initial stimulation of photosynthesis and plant growth to elevated CO_2 (for reviews see Drake *et al.*, 1997; Curtis & Wang, 1998; Saxe *et al.*, 1998; Norby *et al.*, 1999; Long *et al.*, 2004). For example, in glasshouse and controlled growth chamber experiments, biomass increased an average of 37% in response to a doubling of ambient CO_2 (Poorter, 1993). In field studies, free air CO_2 enrichment (FACE) experiments at $\sim$ 1.5 times ambient CO_2 reported 20% stimulation of biomass (Ainsworth & Long, 2005). The question remains whether this positive biomass response to elevated CO_2 will be sustained during the entire growth

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cycle of perennial species. Norby *et al.* (2005) demonstrated that forest net primary production (NPP) response to elevated CO_2 is consistent across species and ecosystems, but responses of shoot growth are inconsistent. For example, in a closed-canopy sweet gum plantation, sustained stimulation of C uptake under elevated CO_2 induced faster C cycling via increased leaf and fine root production and turnover, but yielded no significant increase in standing shoot biomass (Norby *et al.*, 2002). On the other hand, several long-term field studies report sustained biomass stimulation under elevated CO_2 (Ainsworth *et al.*, 2003; Rasse *et al.*, 2005; Kimball *et al.*, 2007). In a recent review, Körner (2006) suggests that biomass response to elevated CO_2 will decline as resources are depleted in spatially-limited systems. Frequently cited environmental limitations to long-term CO_2 stimulation of plant growth are water stress, nitrogen deficiency, and access to light in closing canopies.

Water availability almost universally limits plant growth. Water stress is alleviated by elevated CO_2, by reducing stomatal conductance, thereby improving water-use efficiency (Drake *et al.*, 1997; Long *et al.*, 2004). For example, in sweet gum, reductions in water use under elevated CO_2 increased annual biomass increment by 4.1% (Wullschleger & Norby, 2001; Wullschleger *et al.*, 2002). Baker *et al.* (1997) reported a 5–10% reduction in water use in rice (*Oryza sativa* L.) under CO_2 enrichment, which allowed 1–2 days more growth during a 20-day drought cycle. Finally, aboveground biomass stimulation by elevated CO_2 was higher during years with more rainfall, while stimulation of root biomass was reduced in a Chesapeake Bay tidal wetland (Erickson *et al.*, 2007).

Nutrient deficiency, specifically nitrogen (N), commonly limits plant growth. Elevated CO_2 typically reduces N concentration in plant tissues (McGuire *et al.*, 1995), but growth stimulation can persist through increased nitrogen-use efficiency (Drake *et al.*, 1997). However, in natural ecosystems, plant responses to elevated CO_2 may decline over time due to progressive nitrogen limitation. With time, an increasing proportion of N becomes bound in organic form in plant tissues, litter, and soil organic matter (Luo *et al.*, 2004; Johnson, 2006). Nitrogen availability is closely linked to sink capacity, the ability of a plant to utilize photosynthate (Stitt & Krapp, 1999; Paul & Foyer, 2001). Rasse & Tocquin (2006) demonstrated that sink limitation leads to increased leaf respiration, effectively removing excess assimilates. A limited sink capacity and excess carbohydrates trigger photosynthetic down-regulation by reducing the carboxylation rate of Rubisco (V_{cmax}) and the regeneration rate of ribulose 1,5-bisphosphate ($J_{\max}$) (Ainsworth & Rogers, 2007).

While the canopy is relatively open, elevated CO_2 stimulates biomass production through its direct effect on photosynthesis, and indirectly through stimulating light interception through increased leaf area. This results in the so-called compound interest effect whereby CO_2 stimulates growth through a self-perpetuating cycle of increased leaf area production and carbon uptake (Ceulemans & Mousseau, 1994; Norby *et al.*, 1996). After canopy closure, further leaf area expansion is restricted. In this way, long-term canopy development will cause a reduction of the community growth response to elevated CO_2 over time, while for individual species, growth response may become limited due to reduced access to light.

Here we report on the response of the aboveground biomass to 11 years (1996–2007) of CO_2 enrichment in a Florida scrub-oak ecosystem. The Florida scrub-oak ecosystem is an ideal system for investigating long-term biomass responses to elevated CO_2 for three main reasons. First, because of a short fire-return period (10–15 years), we were able to analyze the effects of elevated CO_2 concentration on a natural scrub-oak community through an entire growth cycle from emergence through canopy closure. Canopy closure was reached in 2000 (Ainsworth *et al.*, 2002; Li *et al.*, 2007b), 4 years since fire, indicating a transition from leaf area expansion to a spatially-limited system (Körner, 2006). Root closure, whereby root production and turnover reach a dynamic equilibrium, coincided with canopy closure (Day *et al.*, 2006). These observations suggest that the oak species became increasingly light limited and potentially sink limited as well. Second, the soils are N poor, therefore any long-term nutrient limitation can be easily detected. For example, after initial CO_2 stimulation of the biomass of a leguminous vine *Galactia elliottii*, Hungate *et al.* (2004) observed long-term decline of this important nitrogen fixer. Elevated CO_2 initially increased plant N uptake (Hungate *et al.*, 1999), but after 4 years, Hungate *et al.* (2006) observed decreased soil N availability, suggesting progressive N limitation. Third, this system is subject to water stress (Powell *et al.*, 2006), thereby evaluate the importance of rainfall on the biomass responses. We previously reported reductions in stomatal conductance and transpiration under elevated CO_2 (Lodge *et al.*, 2001; Hymus *et al.*, 2002; Li *et al.*, 2003) and increased relative photosynthetic stimulation under drought conditions (Li *et al.*, 2007a).

The objective of the present research is to test whether a nutrient- and water-limited natural ecosystem can maintain a long-term biomass response to elevated CO_2 concentration after canopy closure. A second objective is to quantify the potential links between growth responses to elevated CO_2 on the one hand, and water stress and canopy-closure, on the other.

Materials and methods

Ecosystem description

The study site was located on the John F. Kennedy Space Center within Merritt Island National Wildlife Refuge, coastal central Florida (28°38′N, 80°42′W), USA. Climate is subtropical, characterized by mild, dry winters and hot, humid summers. Annual precipitation displays high variability around a 100-year mean of 131 cm yr^{-1}. Typically, a dry period occurs from April through early June, followed by the wet season from late June to October. Mean daily maximum and minimum temperatures are 22.3 and 9.6 °C for January and 33.3 and 21.9 °C for July. Soils are Pomello Sands (Arenic Haplahumod) which are acidic, well-drained, and nutrient-poor. A Bh horizon was found at different locations at approximately 1 m depth. The water table typically fluctuates between 1.5 and 2.5 m, but rising close to the surface following extreme rain events. Vegetation is typical of a fire-regenerated coastal Florida scrub-oak saw palmetto community (Schmalzer & Hinkle, 1992a). This ecosystem is dominated by three species of evergreen scrub-oaks which rapidly resprout after fire: *Quercus myrtifolia* Willd, *Quercus geminata* Small, and *Quercus chapmanii* Sargenti, together typically comprising 85–90% of aboveground biomass (Schmalzer & Hinkle, 1996). Less abundant species include: saw palmetto (*Serenoa repens*), rusty Lyonia (*Lyonia ferruginea*), tarflower (*Befaria racemosa*), shiny blueberry (*Vaccinium myrsinites*), wax myrtle (*Myrica cerifera*), and a leguminous vine (*G. elliottii*). At our site, *Q. myrtifolia* and *Q. geminata* are co-dominant. Over time, *Q. myrtifolia* remains low and bushy and *Q. geminata* continues to grow vertically, exceeding maximum *Q. myrtifolia* height by as much as 5 m (Guerin, 1993). Both oaks utilize groundwater at the study site, but xylem deuterium measurements show that *Q. geminata* uses the water table to a greater extent than does *Q. myrtifolia* (Hungate *et al*., 2002).

Experimental design

CO_2 was manipulated using open-top chambers (OTCs) consisting of 4 in PVC frames wrapped in a clear polyester film ('Mylar'; Melinex 071; Courtaulds Performance Films, Martinsville, VA, USA). Chambers were octagonal, 2.5 m tall, 3.45 m diameter at parallel sides, 3.66 m diameter diagonally, and enclosing 9.42 m^2 ground area. To minimize effects of wind intrusion on CO_2 treatment, a frustum was constructed atop each chamber, reducing the opening to 5.9 m^2, or about 60% of the chamber footprint. Before starting the experiment, 19 plots were selected for representative species composition. Within these plots, aboveground standing biomass was estimated, followed by a controlled burn of the entire site in August 1995 and January 1996. Immediately following the second burn, OTCs were constructed on 16 of the 19 plots. Treatments were randomly assigned to plots using a random block design. Blocks were selected based on preburn aboveground oak species composition. Eight additional plots were established postburn as unchambered controls (C). Fumigation with CO_2 commenced in May 1996 after all vegetation that had resprouted was cut back to ground level. CO_2 concentrations in the chambers were maintained at ambient (A) (~ 350 ppm in 1996 to ~ 380 ppm in 2007) and elevated (E) (ambient + 350 ppm) levels throughout the experiment except for periods between 13 September and 11 October 1999 and 13 August and 18 October 2004 during repairs following extreme wind events. See Dijkstra *et al*. (2002) for further details of experimental setup, chamber design and operation, and plot selection.

Biomass and shoots

Each year, between late December and early February, a comprehensive, nondestructive census of oaks was conducted within the plots. At each census, shoots of the individual species were counted and stem basal diameters measured at 2–5 cm above soil surface. A destructive harvest was conducted in June 2007 to determine final aboveground biomass in each plot. To estimate aboveground biomass from census data, allometric relationships were developed between aboveground biomass per shoot and shoot basal diameter for each oak species (Table 1). To compute allometric relationships, data from three destructive harvests were combined: (1) a pilot study conducted at an adjacent site between April 1992 and July 1995 (Day *et al*., 1996; Dijkstra *et al*., 2002), (2) an adjacent, unmanipulated site in 1998, and (3) final harvest in 2007. At final harvest, no

Table 1 Allometric relationships between stem diameter (diam, mm) and shoot biomass (mass, g) for three oak (*Quercus*) species using data from a pilot study in 1995, plants harvested at adjacent sites in 1998, and plants harvested from within experimental plots at the conclusion of this study in June 2007

Species	*N*	Regression equation	r^2	*P*
Quercus myrtifolia	375	ln(mass) = −1.8420 + ln(diam) 2.8307	0.945	<0.001
Quercus geminata	265	ln(mass) = −1.4289 + ln(diam) 2.6133	0.956	<0.001
Quercus chapmanii	71	ln(mass) = −1.4387 + ln(diam) 2.5742	0.967	<0.001

significant effects of CO_2 concentration on allometric relationships were observed (GLM procedure with treatment as a categorical variable; $P = 0.44$, 0.50, 0.58 for *Q. myrtifolia*, *Q. geminata*, and *Q. chapmanii*, respectively). Hence, allometric relationships were calculated by species, but not separately by treatment, in contrast to Dijkstra *et al*. (2002). Because of the presence of only a few individuals of *Q. chapmanii* in the pilot study, the relationship between stem diameter and biomass for this species was calculated from the 1998 and final harvest data. Allometry was then applied to all census data from the start of the experiment. To estimate annual accumulation, biomass increment was calculated from census biomass estimates of the current year minus the previous year; for example, biomass increment for 2002 represents growth that occurred between December 2001 and December 2002. For analysis, CO_2 stimulation was calculated as an effect relative to ambient treatment [Rel. stim. $(\%) = [(E-A)/A] \times 100$]. Absolute stimulation is calculated as elevated minus ambient (Abs. stim. $= E-A$).

Statistical analyses

To test for treatment differences in aboveground biomass and shoot density, repeated measures analysis of variance (ANOVA) was used to test between E and A (CO_2 effect) and between A and C (chamber effect) using the mixed model procedure of the SAS statistical system (Littell *et al*., 1998). An unstructured covariance model was used for evenly distributed observations in time with year treated as a repeated categorical variable. Degrees of freedom were determined using the Satterthwaite approximation. Differences in final harvest data were tested using one-way ANOVA between subject treatments. Linear regressions were conducted using SIGMAPLOT v8.0 (SPSS Inc., Chicago, IL, USA). Where applicable, means are displayed with calculated standard error (SE) values.

Results

Biomass

At harvest in 2007, aboveground biomass (including standing dead biomass) in the elevated CO_2 treatment (E) significantly exceeded biomass in the ambient treatment (A) ($P<0.01$) (Table 2). Oak aboveground biomass increased substantially throughout the experiment, displaying markedly linear growth (Fig. 1a). Significant differences were observed between E and A within the first year of fumigation. The relative effects of CO_2 concentration on community biomass increased steeply during the first 3 years, reaching 67.3% in 1999, and were stable for the remainder of the experiment. Repeated measures analysis showed significant differences between ambient and elevated chambers ($P = 0.01$) and treatment × time interaction ($P = 0.01$). At final harvest, the CO_2 effect on biomass was 67.5%. No significant difference was observed between A and C total biomass ($P = 0.65$), although a significant treatment × time interaction was observed (Table 3).

Biomass responses were species specific. *Q. myrtifolia* displayed a strong CO_2 response throughout the study (Fig. 1d), resulting in a 128% greater biomass at final harvest in 2007 (Table 2). In contrast to *Q. myrtifolia*, *Q. geminata* displayed no significant effect of CO_2 concentration (Fig. 1g, Table 3). Therefore, we conclude that the community biomass response was driven primarily by *Q. myrtifolia* (Fig. 1d, Table 3). However, *Q. geminata* displayed a significant CO_2 × time interaction, associated with a shift in species composition under ambient CO_2, while species composition remained constant under elevated CO_2 concentrations. (Table 4). At harvest, *Q. chapmanii* revealed a marginally significant CO_2 effect ($P = 0.07$). However, this species comprised only 3% and 6% of aboveground biomass in A and E, respectively, and thus did not influence the overall community response to CO_2. The three oak species combined comprised 89% and 90% of total A and E

Table 2 Total aboveground biomass ($g\,m^{-2}$, dry weight) by treatment and species in experimental plots at final harvest (June 2007)

	Biomass ($g\,m^{-2}$)			*P*-values	
Species	Ambient (A)	Elevated (E)	Control (C)	E vs. A	A vs. C
Quercus myrtifolia	519.7 ± 155.7	1186.2 ± 263.9	607.9 ± 116.0	**<0.05**	0.66
Quercus geminata	613.7 ± 96.1	651.6 ± 171.6	173.4 ± 45.7	0.85	**<0.01**
Quercus chapmanii	40.4 ± 10.0	128.1 ± 43.7	109.1 ± 30.2	0.07	**<0.05**
Other species	83.2 ± 23.6	136.6 ± 22.2	437.9 ± 91.8	0.12	**<0.01**
Standing dead	74.7 ± 14.5	83.7 ± 29.2	70.0 ± 16.7	0.81	0.85
Total	1313.1 ± 110.7	2186.2 ± 161.0	1398.4 ± 143.7	**<0.01**	0.65

P-values from one-way ANOVA tests for significant biomass differences in elevated vs. ambient chambers (E vs. A) and ambient chambers vs. unchambered control plots (A vs. C). Bold values indicate $P \leq 0.05$.

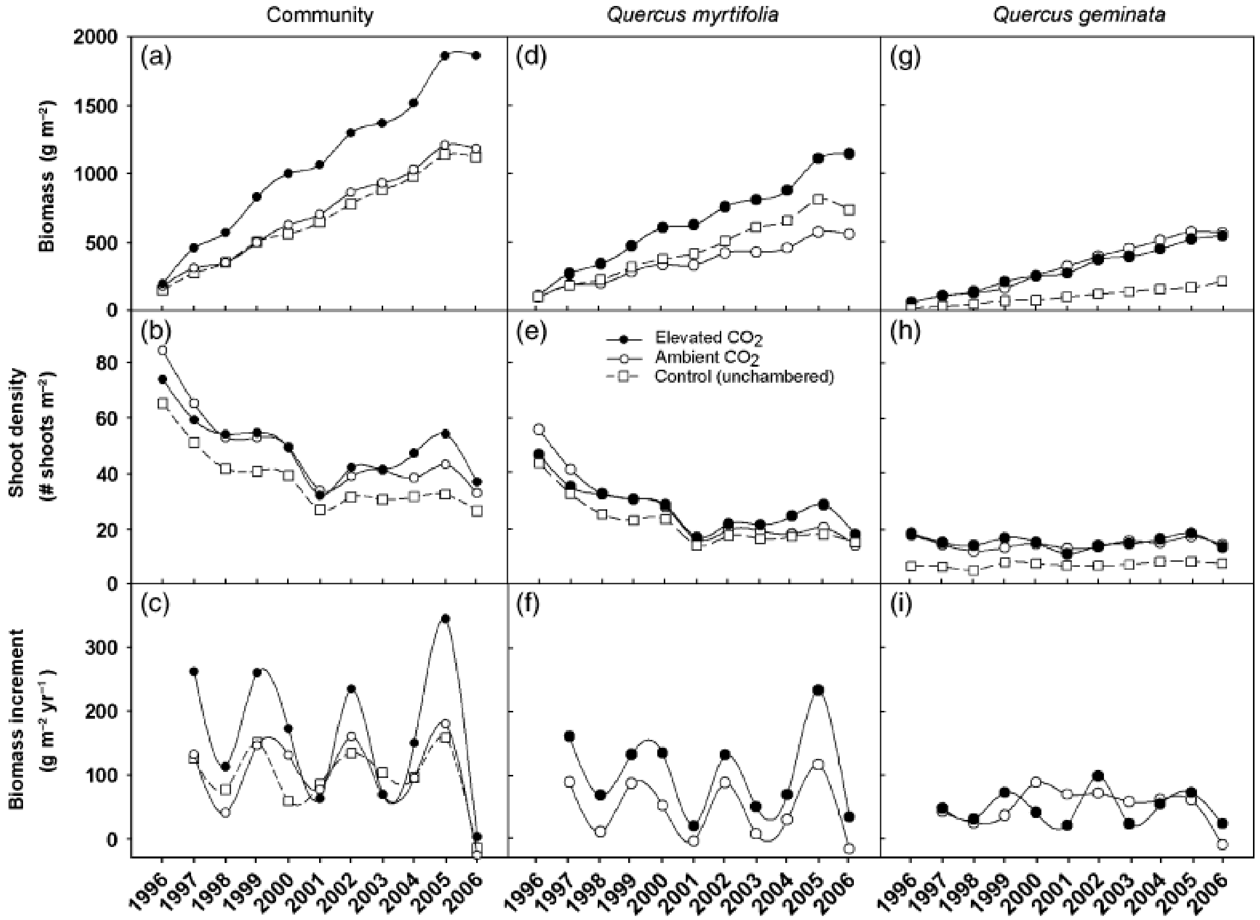

Fig. 1 Aboveground biomass, shoot density, and aboveground biomass increment by open-top chamber (OTC) treatments (ambient and elevated CO$_2$) and unchambered control for a scrub-oak community (a–c) and separately for two co-dominant scrub-oak species, *Quercus myrtifolia* (d–f) and *Quercus geminata* (g–i) over time. Data were collected at annual census conducted between late December and early February each year. Biomass values were estimated using allometric relationships (Table 1).

aboveground biomass, respectively, but only 64% of biomass in C plots in 2007. The low proportion of oak biomass in C plots was already present at the start of the experiment. No significant effects of CO$_2$ were detected for nonoak species biomass ($P = 0.12$) (Table 2).

Shoot density

Total shoot density displayed an exponential decay trend characteristic of self-thinning (Westoby, 1984) (Fig. 1b). An anomalous drop observed in 2001 coincided with the second year in a 2-year drought period (Li *et al*., 2007a), while the sudden increase in 2005 was associated with recovery after hurricane disturbance (Li *et al*., 2007b) (Fig. 1b). Repeated measures analysis showed no significant effects of CO$_2$ concentration on shoot density (Table 3). Thus, observed biomass stimulation reflected increased mass of individual shoots. Trends in shoot density were dominated by *Q. myrtifolia* (Fig. 1e), while *Q. geminata* displayed stable shoot densities throughout the experiment (Fig. 1h). Significant treatment differences between A and C shoot densities were observed at the time of the first census (Dijkstra *et al*., 2002) and persisted over time (Fig. 1b) associated with lower number of *Q. geminata* shoots (Table 3) and greater abundance of nonoak species in the control plots (Table 2).

Biomass increment and correlation with rainfall

Biomass increment showed large interannual variability in all treatments (Fig. 1c) and was positively correlated with annual rainfall across all treatments (Fig. 2). Repeated measures analysis showed significantly higher biomass increments in E and a marginally significant treatment × time interaction, but no significant differences between A and C (Table 3). Stimulation of biomass increment (g m^{-2} yr^{-1}) generally declined over the

Table 3 *P*-values resulting from repeated measures ANOVA between ambient and elevated chambers (E vs. A) and ambient and control plots (A vs. C) for aboveground biomass, biomass increment, and shoot density over time for all oaks and by species

			P-values		
Species	Test	Effect	Aboveground biomass	Biomass increment	Shoot density
All oaks	E vs. A	Treatment	**0.01**	**0.03**	0.47
		Treatment × Time	$<$**0.01**	0.09	$<$**0.01**
	A vs. C	Treatment	0.66	0.32	0.06
		Treatment × Time	$<$**0.01**	0.33	$<$**0.01**
Quercus myrtifolia	E vs. A	Treatment	**0.05**	0.09	0.85
		Treatment × Time	$<$**0.01**	0.82	$<$**0.01**
	A vs. C	Treatment	0.36	0.37	0.25
		Treatment × Time	**0.03**	$<$**0.01**	**0.03**
Quercus geminata	E vs. A	Treatment	0.83	0.90	0.89
		Treatment × Time	**0.03**	**0.02**	0.11
	A vs. C	Treatment	$<$**0.01**	$<$**0.01**	$<$**0.01**
		Treatment × Time	0.11	0.27	**0.05**

Bold values indicate $P \leq 0.05$.

Table 4 Percent species composition of total oak aboveground biomass by treatment in first year postburn (1996) and at harvest (2007)

		Treatment (%)		
Species	Year	Ambient	Elevated	Control
Quercus myrtifolia	1996	54	57	68
	2007	44	60	68
Quercus geminata	1996	33	30	10
	2007	52	33	20

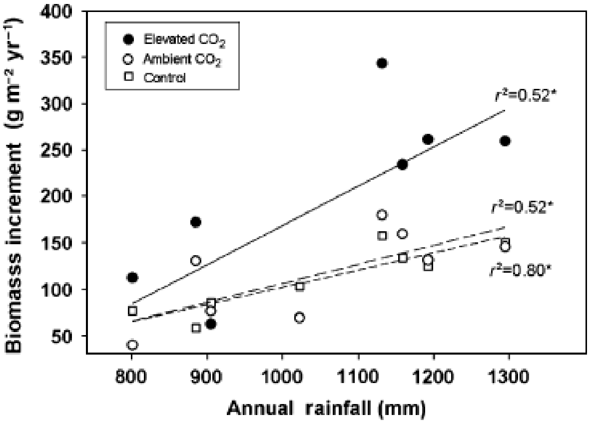

Fig. 2 Relationship between total oak biomass increment ($g\,m^{-2}\,yr^{-1}$) and annual rainfall (mm) for elevated, ambient and control treatments; * indicates significance at $P<0.05$. Outliers were excluded from the regression: data from 2004 based on atypical rainfall associated with hurricane events, and 2006 due to negative growth values.

course of the study (Fig. 3). When the biomass increment for 2005 was excluded from analysis, this decline over time was statistically significant. This suggests that ecosystem recovery after hurricane disturbance was able to make use of the combined effects of increased light and nitrogen made available by the decay of leaves dropped in the storm (Fig. 3).

Q. myrtifolia displayed a consistent and significant CO_2 response in biomass increment (Fig. 1f; Table 3). Biomass increment for *Q. geminata* did not show a significant CO_2 effect, although a significant treatment × time interaction was observed (Fig. 1i; Table 3). The relative effect of CO_2 on annual biomass increment exhibited a negative correlation with annual rainfall for *Q. myrtifolia*, but not for *Q. geminata* (Fig. 4), demonstrating that CO_2 provided a relative advantage for *Q. myrtifolia* under dry conditions; a trend consistent with observed leaf level gas exchange data under drought conditions (Li *et al*., 2007a). *Q. geminata* biomass increment displayed negligible interannual variability under ambient CO_2 concentrations between 2000 and 2005 and was higher than under elevated CO_2 concentration during several of the driest years (2000, 2001, and 2003) (Figs 1i and 4).

Discussion

Long-term aboveground biomass response

CO_2 enrichment significantly increased aboveground biomass of the scrub-oak community. This response was driven primarily by the significant response to

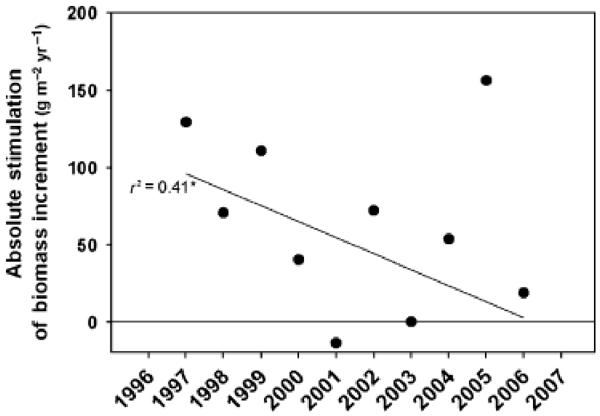

Fig. 3 Absolute stimulation (Abs. stim. = E−A) of biomass increment over time for all oaks combined. The linear regression excludes 2005 growth, an anomalous year, due to recovery from hurricane damage; * indicates $P < 0.05$.

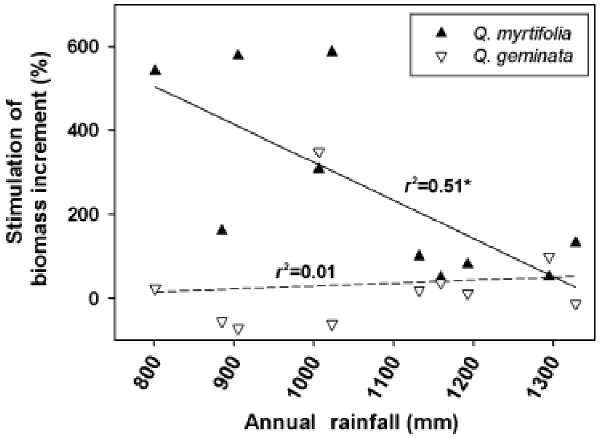

Fig. 4 Relationship between relative CO_2 stimulation of *Quercus geminata* and *Quercus myrtifolia* biomass increment and total annual rainfall; * indicates $P < 0.05$.

elevated CO_2 by the dominant oak species, *Q. myrtifolia*. Several other long-term field studies have reported sustained biomass stimulation (Rasse *et al.*, 2005; Wittig *et al.*, 2005; Erickson *et al.*, 2007; Kimball *et al.*, 2007). Our results are unique in which stimulation was sustained after the community reached canopy closure (Ainsworth *et al.*, 2002; Li *et al.*, 2007b), root closure (Day *et al.*, 2006), and displayed nitrogen limitation (Hungate *et al.*, 2006): three critical constraints predicted to limit CO_2 response (Norby *et al.*, 1999; Körner, 2006). Canopy closure was reached in 2000, after which leaf area index (LAI) reached stable values, except during recovery from hurricane damage sustained in 2004 (Li *et al.*, 2007b). Studies on forests have typically reported an absence of biomass stimulation for closed canopies (Norby *et al.*, 2004; Körner *et al.*, 2005). However, Oren *et al.* (2001) showed biomass stimulation after canopy closure to be sustainable in the absence of nutrient limitation (i.e. nitrogen). At our site, plant nitrogen uptake initially increased under elevated CO_2, reaching maximum uptake in 1999. Thereafter, N uptake declined and indications of progressive nitrogen limitation became apparent (Hungate *et al.*, 2006). Fine root response paralleled N uptake trends. Initial CO_2 stimulation hastened fine root closure by several months, after which the CO_2 effect on fine roots diminished, suggesting that the community reached dynamic equilibrium in terms of fine root production and mortality (Day *et al.*, 2006). Aboveground growth appeared linked to these trends, as cumulative biomass stimulation increased through 1999, but then stabilized for the remainder of the experiment. Similarly, NPP estimated from leaf litter production rates showed an initial increase (Hungate *et al.*, 2006). However, canopy damage incurred from two hurricanes in September 2004 temporally renewed the effect of CO_2 concentration on aboveground biomass production. At the site, 113 km h^{-1} winds caused extensive defoliation, producing a sharp decrease in LAI, but only minor structural damage (Li *et al.*, 2007b). Defoliation effectively opened the canopy, as evidenced by a surge of new shoots observed in 2005, a common trend among hurricane-disturbed ecosystems (Brokaw & Walker, 1991; Fernandez & Fetcher, 1991). This hurricane effect is clearly demonstrated as a spike in stimulation of incremental growth in 2005 (Fig. 3). Excluding 2005 data, the effects of CO_2 concentration on absolute annual biomass increment declined throughout the study (Fig. 3). Additionally, previous studies demonstrate that plant growth increases following hurricanes due to the pulse of nutrients from decomposing canopy leaves relocated to the forest floor (Lodge *et al.*, 1991; Herbert *et al.*, 1999). At our site, nitrogen from dropped leaves represented a substantial increase over typical annual rates of N uptake (Hungate *et al.*, 2006; Li *et al.*, 2007b). This extra nitrogen would not be immediately available, but would be gradually released through decomposition, resulting in a delayed effect on plant growth (Dilustro *et al.*, 2001). Thus, the reopening of the canopy and additional pulse of available nitrogen may have effectively removed previous light and nutrient limitations and contributed to a renewed biomass response to elevated CO_2. LAI and ecosystem CO_2 uptake, determined via eddy covariance measurements at an adjacent site, declined immediately after the hurricanes and did not return to stable, prehurricane levels until 2006 (Powell *et al.*, 2006; Li *et al.*, 2007b). Despite a 22% reduction in ecosystem C uptake following the hurricanes (Powell *et al.*, 2006), biomass increment values were higher across all treatments in 2005 than in any

Table 5 Summary of photosynthetic acclimation to elevated CO$_2$ by species over time

		Was significant reduction observed under elevated CO$_2$?														
Species	Measure	Aug 1996	Jul 1997	Apr 1998	Aug 1998	Dec 1998	Mar 1999	Jun 1999	Jan 2000	Jul 2000	Aug 2000	Aug 2002	Oct 2003	Jul 2004	Dec 2004	Jun 2005
Quercus geminata	V_{cmax}	No	*	*	*	No	Yes	No	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
	J_{max}	No	*	*	*	Yes	Yes	No	No	Yes	Yes	Yes	Yes	No	No	No
Quercus myrtifolia	V_{cmax}	Yes	Yes	No	Yes	No	No	No	No	No	No	Yes	No	No	No	No
	J_{max}	No	No	No	No	No	No	No	No	No	No	No	No	No	No	No

Values indicate results of one-way ANOVA to test significant reductions ($P<0.05$) in leaf maximum carboxylation capacity (V_{cmax}) and maximum rate of RubP regeneration (J_{max}) under elevated and ambient CO$_2$ treatment (Li *et al*., 1999, 2007a, unpublished data; Hymus *et al*., 2001, 2002; Ainsworth *et al*., 2002). See references for measurement details.
*No data available.

other year of the experiment (Fig. 1). The discrepancy between reduced assimilation and increased growth suggests that storage carbohydrates may have been remobilized during recovery from hurricane damage. This high regrowth after the hurricane may also have been the result of high N availability (Fig. 3). This response to hurricane damage may be similar to ecosystem recovery after fire, when scrub-oaks remobilize belowground reserves for growth following fire disturbance (Schmalzer & Hinkle, 1992b; Langley *et al*., 2002). This comparison underscores the potential effects of disturbance on plant C allocation patterns which may alter the ecosystem carbon budget. In the absence of hurricane disturbance, biomass response may have continued to decline.

Species-specific response

Q. myrtifolia showed a strong biomass response to elevated CO$_2$ throughout the experiment, in contrast to *Q. geminata*. Variation in the growth responses to CO$_2$ enrichment is commonly observed among species (Poorter, 1993; Ainsworth & Long, 2005), and is typically attributed to differences in the response of photosynthesis (Nowak *et al*., 2004). Over the experiment, response of photosynthesis in the two oaks mirrored the effects of CO$_2$ on biomass increments (Li *et al*., 1999, 2007a, unpublished data; Hymus *et al*., 2001, 2002; Ainsworth *et al*., 2002). *Q. geminata* generally displayed photosynthetic acclimation to elevated CO$_2$, as reductions in V_{cmax} and J_{max} (Table 5). *Q. myrtifolia* initially displayed reduction in V_{cmax} (Li *et al*., 1999), but never displayed reduction in J_{max} (Table 5). Under growth conditions, both oak species consistently showed increased rates of leaf net photosynthesis (Li *et al*., 1999, 2007a, unpublished data; Hymus *et al*., 2001, 2002; Ainsworth *et al*., 2002). However, long-term mean stimulation of *Q. myrtifolia* net photosynthesis was approximately twice that of *Q. geminata* (63% and 35%, respectively). Although the mechanisms are not fully understood, it is believed that sink limitations trigger acclimation of the photosynthetic system (Ainsworth & Rogers, 2007). Contrasting photosynthetic responses observed between these species may thus have resulted from fundamental differences in how each species controls sink activity. By examining responses in *Arabidopsis thaliana* mutants unable to synthesize starch, Rasse & Tocquin (2006) demonstrated that starch production exerts strong control over photosynthesis and growth. Early in this study, Li *et al*. (1999) reported significant increases in leaf starch content in *Q. myrtifolia* under elevated CO$_2$, but not in *Q. geminata*, corresponding to the brief time period in which *Q. myrtifolia* displayed photosynthetic acclimation and *Q. geminata* did not (Table 5).

Although acclimation in *Q. geminata* reduced photosynthetic capacity in E (Table 5), net photosynthesis was consistently and significantly stimulated over the course of the study. Similarly, stimulation of *Q. myrtifolia* photosynthesis exceeded stimulation of aboveground biomass, reiterating a common observation that there is no 1 : 1 relationship between leaf photosynthesis and plant growth. This study reports only aboveground response but there is now evidence that additional carbon assimilated as a result of CO_2 stimulation of photosynthesis was allocated belowground. Plants may increase assimilate allocation to belowground structures under nutrient limitation (Ericsson, 1995) and water stress (Schenk & Jackson, 2002). At this site, from measurements using ground penetrating radar, Stover *et al*. (2007) showed that belowground biomass of coarse roots and storage structures in E exceeded A by approximately 2400 $g\,m^{-2}$ (37%) by December 2005, an increase of about 284 $g\,m^{-2}\,yr^{-1}$ or almost three times the average increment of biomass of shoots. Further investigation into the fate of assimilated carbon is needed to quantify the relationships between C uptake, allocation, and growth response to elevated CO_2.

Species-specific responses also contributed to a shift in species composition. Natural ecosystems often demonstrate a species shift in aboveground biomass under elevated CO_2. This is attributed to changes in competitive relationships (Niklaus *et al*., 2001; Ramseier *et al*., 2005), derived from species-specific responses to CO_2 and environmental factors such as nitrogen (Berendse *et al*., 2001; Joel *et al*., 2001) and water availability (Owensby *et al*., 1999; Belote *et al*., 2004; Morgan *et al*., 2004). In this study, a species composition shift was observed, but only in the chambers exposed to ambient CO_2 (Table 4). In terms of percent biomass composition, over the course of the study, *Q. geminata* steadily increased (+19%) and *Q. myrtifolia* steadily decreased (−10%) from 1996 values in A, while composition remained stable in E and C (Table 4). This composition shift may have been partially responsible for the disconnect between stimulation of *Q. geminata* net photosynthesis and the apparent lack of biomass response to elevated CO_2. This trend may also indicate that chamber effects on species composition were ameliorated by elevated CO_2. OTCs commonly alter microclimate, particularly temperature, light, and relative humidity (Drake *et al*., 1989; Van Oijen *et al*., 1999), and minor effects on plant growth may compound over time (Leadley & Drake, 1993). At our site, OTCs increased daytime air temperature by $4 \pm 0.2\,^{\circ}C$ and vapor pressure deficit (VPD) by 0.7 ± 0.05 kPa compared with unchambered control sites (Dore *et al*., 2003). Additionally, frustums reduced rainfall penetration into OTCs by 40%. These unintentional effects created a warmer, drier growth environment, consistent with predicted future climate scenarios (Weltzin *et al*., 2003; IPCC, 2007). Our study was not explicitly designed to quantify OTC microclimate effects on biomass; however, the observed shift in A biomass composition, not apparent in E, qualitatively demonstrates that the combination of warmer, drier conditions under ambient CO_2 favors *Q. geminata* growth relative to *Q. myrtifolia* and that elevated CO_2 may counteract this effect. The observed interactions between growth and water availability also suggest this interpretation, as discussed below.

Interactions with rainfall

Water availability limits ecosystem productivity (Huxman *et al*., 2004) and the scrub-oak ecosystem is no exception (Powell *et al*., 2006). Although these oaks are phreatophytic, hence use both soil- and groundwater sources, annual rainfall showed significant correlations with community growth response to elevated CO_2 (Fig. 2). Because of sandy, well-drained soils, groundwater provides a stable water source for scrub-oaks compared with soil moisture which is only a transient resource immediately following rain events (Hungate *et al*., 2002). In fact, Schmalzer & Hinkle (1992a) demonstrated that water table depth mediates scrub-oak ecosystem composition, suggesting that annual rainfall captured the general long-term trends of both soil water content and water table depth. This study observed significant positive correlations between annual rainfall and community biomass increment across treatments, with plants exposed to elevated CO_2 showing a steeper response to rainfall than those exposed to ambient CO_2 (Fig. 2). This trend is consistent with observations from our site of a positive correlation between CO_2 stimulation of NEE and water availability (Hymus *et al*., 2003). Similar results were reported for a Chesapeake Bay wetland (Rasse & Tocquin, 2006) and for Mojave Desert shrubs (Naumberg *et al*., 2003), where larger photosynthetic responses to CO_2 enrichment were observed during years with more rainfall. Our results also indicate that relative CO_2 stimulation of *Q. myrtifolia* biomass increment significantly decreased as rainfall increased, while no significant interaction was observed for *Q. geminata* (Fig. 4). This reflects a relative ameliorating effect of elevated CO_2 on *Q. myrtifolia* growth under water stress (Fig. 4), consistent with theoretical predictions based on reduced stomatal conductance (Drake *et al*., 1997) and consistent with a previous study from our site showing increased stimulation of net photosynthesis in *Q. myrtifolia* under drought conditions (Li *et al*., 2007a). The ability of *Q. geminata* to use groundwater may explain its competitive advantage over *Q. myrtifolia* under dry conditions at current CO_2 levels, resulting in the aboveground composition shift observed in A. Xylem deuterium measurements from our site show that *Q. geminata* uses groundwater more readily than *Q. myrtifolia* (Hungate *et al*., 2002). Under drier soil conditions in the OTCs, these competitive traits manifest as a species shift in A, without significant impact on total biomass production relative to C. The ameliorative effects of elevated CO_2 on *Q. myrtifolia* growth under water stress may have decoupled the ecosystem relationship with groundwater, thus preventing a similar shift from occurring in E. Over time and compounded by natural fire cycles, these competitive interactions could potentially yield significant changes in ecosystem composition and C cycling.

Conclusions

Our results suggest that future research should focus on determining the interactive processes and mechanisms linking photosynthesis, assimilate allocation, and sink development, as these relationships may be the key to understanding the species-specific responses observed in this study, as well as the progressive limitations on ecosystem growth response to rising CO_2.

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