Effects of Elevated Atmospheric Carbon Dioxide on Biomass and Carbon Accumulation in a Model Regenerating Longleaf Pine Community

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ABSTRACT

Plant species vary in response to atmospheric CO_2 concentration due to differences in physiology, morphology, phenology, and symbiotic relationships. These differences make it very difficult to predict how plant communities will respond to elevated CO_2. Such information is critical to furthering our understanding of community and ecosystem responses to global climate change. To determine how a simple plant community might respond to elevated CO_2, a model regenerating longleaf pine community composed of five species was exposed to two CO_2 regimes (ambient, 365 μmol mol^{-1} and elevated, 720 μmol mol^{-1}) for 3 yr. Total above- and belowground biomass was 70 and 49% greater, respectively, in CO_2–enriched plots. Carbon (C) content followed a response pattern similar to biomass, resulting in a significant increase of 13.8 Mg C ha^{-1} under elevated CO_2. Responses of individual species, however, varied. Longleaf pine (*Pinus palustris* Mill.) was primarily responsible for the positive response to CO_2 enrichment. Wiregrass (*Aristida stricta* Michx.), rattlebox (*Crotalaria rotundifolia* Walt. Ex Gmel.), and butterfly weed (*Asclepias tuberosa* L.) exhibited negative above- and belowground biomass responses to elevated CO_2, while sand post oak (*Quercus margaretta* Ashe) did not differ significantly between CO_2 treatments. As with pine, C content followed patterns similar to biomass. Elevated CO_2 resulted in alterations in community structure. Longleaf pine comprised 88% of total biomass in CO_2–enriched plots, but only 76% in ambient plots. In contrast, wiregrass, rattlebox, and butterfly weed comprised 19% in ambient CO_2 plots, but only 8% under high CO_2. Therefore, while longleaf pine may perform well in a high CO_2 world, other members of this community may not compete as well, which could alter community function. Effects of elevated CO_2 on plant communities are complex, dynamic, and difficult to predict, clearly demonstrating the need for more research in this important area of global change science.

A TMOSPHERIC CO_2 concentration is rising, due primarily to fossil fuel combustion and deforestation, and is projected to double preindustrial levels within the next century (Keeling and Whorf, 1994). Experimentally doubling atmospheric CO_2 has been shown to increase plant biomass, on average, by almost 40% (Poorter, 1993). However, all species do not exhibit equivalent responses to CO_2 enrichment. Leaf morphology (Ceulemans and Mousseau, 1994; Saxe et al., 1998), physiology (Drake, 1992; Poorter, 1993), symbiotic relationships (Hartwig et al., 1996), and competition (Bazzaz and Carlson, 1984; Pritchard et al., 2001; Davis et al., 2002) all influence plant response to CO_2.

While individual plant response to elevated CO_2 may be predicted based on differences in the factors noted above, evidence from competition studies consistently suggests that response cannot be reliably predicted when species are grown in communities (Bazzaz and Carlson, 1984; Bazzaz, 1990; Bazzaz and McConnaughay, 1992; Ziska, 2003; Morgan et al., 2004). Given that CO_2–induced shifts in competitive advantages among species may alter species composition and community structure and function (Wray and Strain, 1987; Fajer, 1989; Bazzaz, 1990; Joel et al., 2001; Dijkstra et al., 2002), experiments which examine the effects of CO_2 enrichment on plant communities are critical for furthering our understanding of ecosystem response to global climate change.

Study of elevated CO_2 effects on plants under competition has been a topic for investigation for over two decades (see review by Bazzaz, 1990). Initial work tended to concentrate on annual plant species grown for short durations in containers placed in glasshouses or growth chambers (Bazzaz and Carlson, 1984; Reekie and Bazzaz, 1989; Körner and Arnone, 1992). This work was expanded to open-top chambers, but continued to be conducted using containers and for relatively short durations. More recent work has focused on field-grown plants utilizing open-top chambers and FACE (free-air CO_2 enrichment). However, an extreme paucity of information still exists for forest ecosystems, particularly tropical seasonal forests and dry tropical communities such as savannas and scrub vegetation ecosystems (Arnone, 1996), and the need for studies of forests and other long-lived plant species exposed for longer durations continues to be noted (Norby et al., 1999; Ward and Strain, 1999).

Before European settlement, longleaf pine savannahs occupied 37.2 million ha of the southeastern United States (Landers et al., 1995). Since the early 1600s, timber harvesting, fire suppression, and conversion of forests to farmland have reduced the land area of these ecosystems to less than 4% of their original range (Peet and Allard, 1993; Landers et al., 1995). This loss is comparable to that of many endangered communities including the North American tallgrass prairie, the moist tropical coastal forest of Brazil, and the dry forests along the Pacific coast of Central America (Noss, 1989). Longleaf pine ecosystems are also very diverse,

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with some specific types having the highest reported values for species richness, including many threatened and endangered species, in the temperate Western Hemisphere (e.g., 140 species ha^{-1} for Mesic Longleaf Woodlands; Peet and Allard, 1993). To protect and maintain these important longleaf pine ecosystems it is necessary to understand the impacts of global change, including response to CO_2 enrichment, on their structure and function.

Davis et al. (2002) reported results from a model regenerating longleaf pine community, composed of species representing different structural and functional guilds, following 2 yr of exposure to ambient and elevated levels of atmospheric CO_2. They reported that total biomass for this community increased by 109% due primarily to increases in longleaf pine (117%) and in wiregrass (24%), the other keystone species of this community. The three other species in this study (sand post oak, rattlebox, and butterfly weed) showed either no effect or a decline in biomass (directly and as a percentage of total community biomass) when grown under high CO_2. It should be noted that the aboveground results of Davis et al. (2002) were derived primarily from allometric equations. Similarly, belowground results from this study (Pritchard et al., 2001) were also derived using nondestructive minirhizotron technology.

Here we report above- and belowground biomass and carbon content determined following a complete destructive harvest and following an additional year of exposure to ambient and elevated atmospheric CO_2 for this model regenerating longleaf pine community. Specific hypotheses addressed by this study were similar to those reported by Davis et al. (2002) and were as follows: (i) C_3 plants would increase growth to a greater extent than C_4 plants due to their greater photosynthetic response to elevated CO_2 (Bowes, 1993; Amthor, 1995); (ii) broadleaf C_3 plants would respond more favorably to elevated CO_2 than conifers due to being anatomically and morphologically better adapted to assimilate extra carbon (Ceulemans and Mousseau, 1994; Pritchard et al., 1998); (iii) N-fixing plant response to elevated CO_2 would exceed that of non-fixers; and (iv) the influence of elevated CO_2 on competitive relationships, acting through the mechanisms elucidated above, would alter structure of this forest community and its capacity for storing atmospheric carbon.

MATERIALS AND METHODS

Study Site

A model regenerating longleaf pine–wiregrass community was constructed in spring 1998 at the soil bin facilities of the National Soil Dynamics Laboratory in Auburn, AL. This model community was used to examine effects of CO_2 enrichment on plants at multiple scales, including leaf, whole-plant, and community. Descriptions of the study site and model community have been previously reported (Pritchard et al., 2001; Davis et al., 2002). Briefly, an assemblage of five early successional forest species representing major functional guilds within a typical longleaf pine–wiregrass community were chosen for study: longleaf pine, a C_3 evergreen conifer; wiregrass, a C_4 bunch grass; sand post oak, a C_3 broadleaf tree;

rattlebox, a C_3 perennial, herbaceous, N-fixing legume; and butterfly weed, a C_3, non-leguminous, herbaceous perennial. These species are common associates in early successional longleaf pine savannahs throughout the southeastern United States (Abrahamson and Hartnett, 1990). Before transplanting into the model community, all plants were grown in 15-cm³ containers from seed collected from natural sources.

This forest community was assembled in April 1998 on an outdoor soil bin (2 m deep, 6 m wide, and 76 m long) containing a Blanton loamy sand (loamy, siliceous, thermic Grossarenic Paleudults) taken from a longleaf pine area (Sandhills or Subxeric Gulf Coastal Plain type; *sensu* Peet and Allard, 1993) typical of the Southeastern Coastal Plains. Before planting, the soil bin was divided into 0.75-m² quadrats each possessing 16 equally spaced planting positions. The community was constructed by randomly assigning individuals of each species (three longleaf pine, three wiregrass, two sand post oak, one rattlebox, and one butterfly weed) into positions within each quadrat; six planting spaces per quadrat were left empty. This regime achieved planting densities reflective of naturally regenerating longleaf pine–wiregrass ecosystems (Hainds, 1995; Jacqmain, 1996). Plants were regularly irrigated during summer 1998 to facilitate community establishment using a metered drip irrigation system to deliver exact and consistent watering throughout the bin; thereafter, plants received only ambient rainfall. During the first 2 mo dead plants were replaced; thereafter, mortality was attributed to causes other than transplanting, and gaps were not refilled.

Open-top chambers (Rogers et al., 1983), encompassing 7.3 m² of ground surface area, were used to deliver target CO_2 concentrations of 365 μmol mol^{-1} (ambient) or 720 μmol mol^{-1} (elevated) beginning June 1998 using a delivery system described by Mitchell et al. (1995). Actual CO_2 concentrations over the 3-yr measurement period ($\pm$SE) were as follows: ambient daytime = 376.2 ($\pm$0.1); elevated daytime = 701.4 ($\pm$0.2); ambient nighttime = 407.6 ($\pm$0.01); and elevated nighttime = 758.6 ($\pm$0.2) (daytime was taken as 0700 to 1900 h CST; n was approximately 91 000 for each measurement). The bin was divided into six blocks and each CO_2 treatment was randomly assigned to one open top chamber within each block. The experimental design was a randomized complete block design, with blocks occurring along the length of the soil bin.

Aboveground Biomass

Aboveground portions of plants in experimental plots were destructively harvested in June 2001 after 3 yr of CO_2 exposure. All plants within a plot were harvested in the order of: longleaf pine, sand post oak, butterfly weed, rattlebox, and wiregrass. Following harvest, aboveground parameters (e.g., height, diameter, numbers of branches and/or leaves) were assessed using standard practices. Diameters were measured at ground line using high precision digital calipers. Individual plants were then subdivided into component organs depending on species: longleaf pine and sand post oak were separated by leaves, branches, and stems; butterfly weed plants were separated into leaves and stems (branches were included in stem biomass); the morphology of rattlebox and wiregrass did not facilitate the separation of leaves from stems. Plant component parts were placed in paper bags and dried to a constant weight at 55°C in a forced-air drying oven. Following removal of aboveground biomass, all litter was removed from plots, separated by species, oven-dried, and weighed. Following drying, biomass components and litter were ground separately to pass through a 0.2-mm mesh sieve. Carbon and nitrogen concentrations were determined using a LECO (St. Joseph, MI) 600-CHN analyzer.

Belowground Biomass

Immediately following harvest of aboveground biomass, fine root biomass was assessed using large soil cores (24.5 cm diameter $\times$ 60 cm deep) and an extraction method of our own design (Prior et al., 2004). Steel core tubes were driven into the ground using a hydraulic cylinder mounted on the front of a small tractor and an iron driving head which rested on the outer top edge of the steel core tube. Once the tube had been driven completely into the ground (i.e., so the top of the tube was even with the soil surface), the driving head was removed and the hydraulic cylinder was connected to a chain attached to a collar located just below a small outer lip of the core tube. The hydraulic cylinder was then used to remove the core tube with soil from the ground. Eight cores were extracted from each plot. Extracted core tubes were immediately placed into buckets (to prevent loss of soil from the bottom of the tube) and moved to a hydraulic device which pushed the soil out of the core tube to a set distance (i.e., 15 cm) and this quantity of soil was sliced from the main tube. This process was repeated four times for each core tube, giving core depth increments of 0 to 15, 15 to 30, 30 to 45, and 45 to 60 cm. All soil from each depth increment was sieved through a 2-mm mesh screen; roots were removed, bagged, and stored in a walk-in cold room (4°C) until processing. Fine roots were separated, based on color and morphology, into three classes (longleaf pine, sand post oak, and other). The latter class of fine roots was most likely dominated by wiregrass, which has a fibrous root system. Rattlebox and butterfly weed have tuberous root systems with limited lateral root spread and the vast majority of their roots were obtained during the spade extraction. Each class of roots was further segregated into three diameter classes (>2, 0.5–2, and <0.5 mm) before placement in a drying oven for dry weight determination, as previously described. As with aboveground biomass, all root samples were ground and carbon and nitrogen concentrations determined.

Following coring, coarse root biomass was assessed using one of two methods. Coarse roots for wiregrass, rattlebox, and butterfly weed were dug from each plot using standard sharpshooter spades. Two spades (one on each side of the plant) were inserted into the soil about 25 cm away from the plant to a depth of about 30 cm, the soil was loosened, and the entire root system retrieved. Coarse roots for longleaf pine and sand post oak were extracted by: removing a small volume of soil from around each stump by hand; connecting a clamp to the stump just below the soil surface; connecting the clamp to a hydraulic cylinder mounted on the front of a small tractor; and raising the cylinder until the taproot and attached large lateral roots were loosened from the soil. After soaking in water, coarse roots were washed free of soil using a soft bristle brush, placed in paper bags, and dried to a constant weight at 55°C. Undoubtedly, the extraction of longleaf pine and sand post oak did not recover the entire coarse root biomass for each tree; however, as the same technique was employed for all trees in all plots, the relative amount of coarse roots removed should be comparable.

Data Analysis

Data analysis was conducted using the mixed model procedures (Proc Mixed) of the Statistical Analysis System (Littell et al., 1996). Error terms appropriate to the randomized block design were used to test the significance of CO_2 concentration. In all cases, differences were considered significant at the $\alpha \leq 0.05$ and trends were recognized at $0.05 \leq \alpha \leq 0.15$.

RESULTS

Species Response

Longleaf Pine

Percent mortality did not differ between CO_2 treatments. However, all anatomical measurements (i.e., height, diameter, and branch number, length, and density) were significantly greater for plants grown under elevated CO_2 (Table 1). Concomitant with this increase in growth, dry weight of all plant organs (i.e., needles, branches, stems, coarse roots, and fine roots) were significantly greater when grown under high CO_2 (Fig. 1A), resulting in an 88% increase in total plant dry weight. Dry weight of plant litter was also significantly higher for plants grown under high, compared with ambient, CO_2 (Table 1). Elevated atmospheric CO_2 resulted in changes in biomass allocation patterns (Fig. 2A). Allocation to branches and stems was increased under high CO_2, while allocation to needles and roots was decreased. This altered allocation resulted in a significantly lower root to shoot ratio for plants grown under elevated CO_2 (Fig. 3).

Sand Post Oak

No significant differences between CO_2 treatments were detected for any anatomical (Table 1) or biomass

Table 1. The response of growth and litter variables to ambient (365 μmol mol^{-1}) and elevated (720 μmol mol^{-1}) CO_2 for the five species following 3 yr of exposure. Means with associated separation statistics and percent change (ambient to elevated) are shown.

| Parameter	Ambient CO_2	Elevated CO_2	Percent change	P values
Longleaf pine				
Mortality, %	16.5	14.5	−12.1	0.604
Height, cm	109.3	159.1	45.6	<0.001
Diameter, cm	4.20	4.74	12.9	<0.001
Branch number	1.9	3.7	94.7	0.002
Branch density, no. m^{-1}	1.3	1.9	46.2	0.030
Average branch length, cm	4.9	10.4	112.2	0.001
Litter dry weight, g m^{-2}	387.6	684.2	76.5	<0.001
Sand post oak				
Mortality, %	10.8	7.8	−27.8	0.434
Height, cm	43.7	54.9	25.6	0.264
Leaf number	52.6	64.3	22.2	0.562
Leaf density, no. m^{-1}	89.4	83.1	−7.0	0.508
Litter dry weight, g m^{-2}	10.1	17.3	71.3	0.185
Wiregrass				
Mortality, %	9.7	19.1	96.9	0.009
Diameter, cm	5.23	5.02	−4.0	0.330
Total clump area, cm^2	913.0	692.4	−24.2	0.009
Litter dry weight, g m^{-2}	25.3	60.2	137.9	0.012
Butterfly weed				
Mortality, %	61.6	69.3	12.5	0.504
Height, cm	73.7	58.4	−20.8	0.261
Stem length, cm	179.8	95.8	−46.7	0.025
Reproductive plants, %	53.1	33.1	−37.7	0.245
Litter dry weight, g m^{-2}	22.2	20.2	−9.0	0.783
Rattlebox				
Mortality, %	−4.4	13.1	–	0.514
Reproductive plants, %	30.2	22.1	−26.8	0.242
Litter dry weight, g m^{-2}	11.5	23.3	102.6	0.269
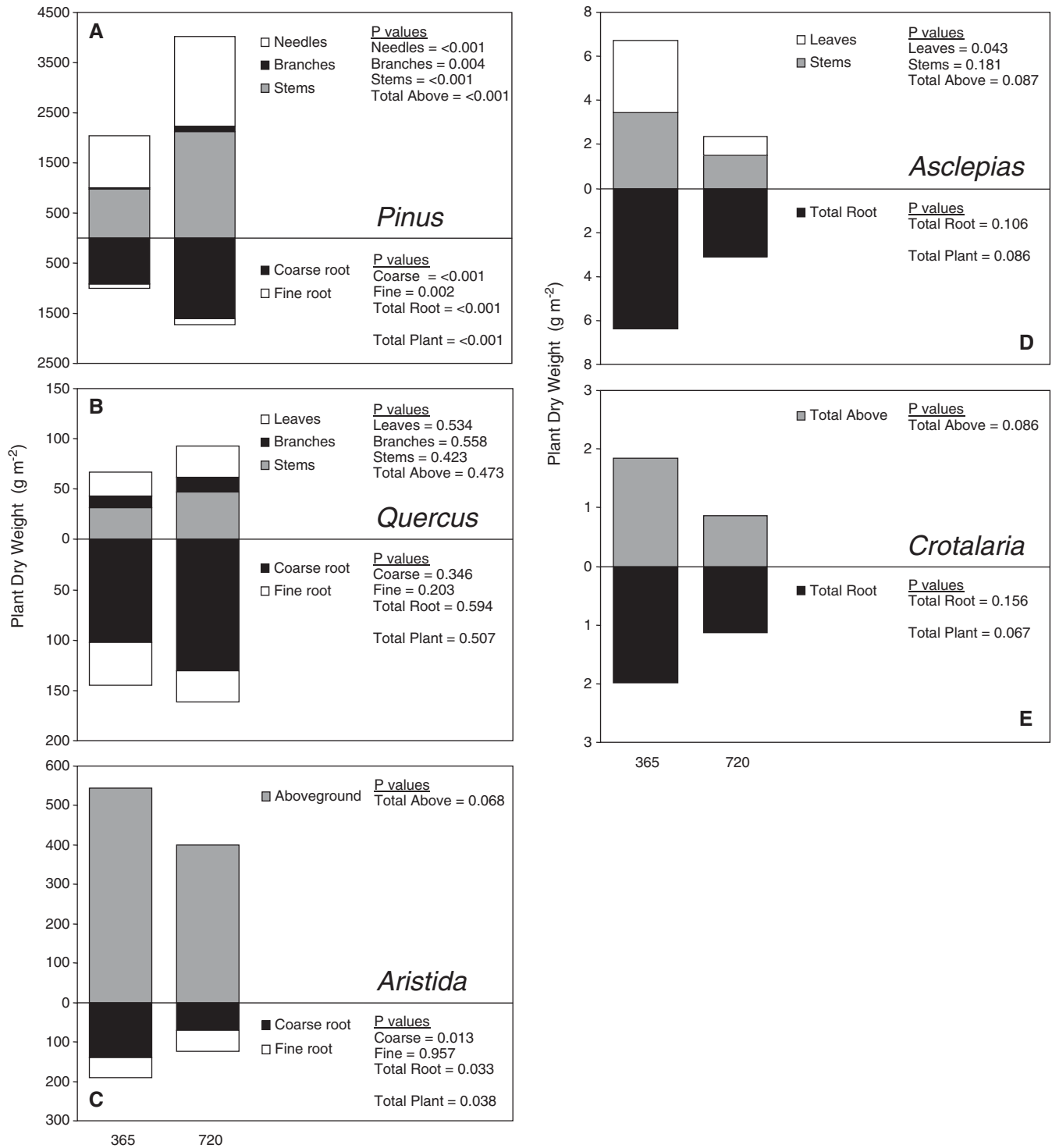
Fig. 1. Plant dry weight (g m^{-2}) for component plant parts (needles, leaves, branches, stems, total aboveground, coarse roots, fine roots, total roots, total plant as applicable for each species), with associated mean separation statistics, for longleaf pine (A), sand post oak (B), wiregrass (C), butterfly weed (D), and rattlebox (E) when grown together for 3 yr under ambient (365 μmol mol^{-1}) and elevated (720 μmol mol^{-1}) concentrations of atmospheric CO$_2$.

(Fig. 1B) parameters. There was, however, a decrease in biomass allocation to fine roots (Fig. 2B), which resulted in a trend for decreased root to shoot ratio under elevated CO$_2$ (Fig. 3).

Wiregrass

Percent mortality was significantly higher under elevated than ambient CO$_2$ (Table 1). Clump diameter of wiregrass was not affected by CO$_2$ treatment. However,

Table 2. Biomass allocation among species when grown for 3 yr under ambient (365 μmol mol^{-1}) and elevated (720 μmol mol^{-1}) CO$_2$. Means with associated separation statistics and percent change (ambient to elevated) are shown.

Percent of total in species	Ambient CO$_2$	Elevated CO$_2$	Percent change	P values
		%		
		Longleaf pine		
Aboveground	76.74	88.86	15.8	<0.001
Belowground	74.04	85.46	15.4	<0.001
Total	75.81	87.81	15.8	<0.001
		Sand post oak		
Aboveground	2.50	2.06	−17.6	0.688
Belowground	10.55	8.06	−23.6	0.153
Total	5.21	3.92	−24.8	0.283
		Wiregrass		
Aboveground	20.44	9.01	−55.9	0.003
Belowground	14.81	6.28	−57.6	0.001
Total	18.57	8.16	−56.1	0.004
		Butterfly weed		
Aboveground	0.25	0.05	−80.0	0.054
Belowground	0.46	0.15	−67.4	0.016
Total	0.32	0.08	−75.0	0.021
		Rattlebox		
Aboveground	0.07	0.02	−71.4	0.041
Belowground	0.14	0.05	−64.3	0.033
Total	0.09	0.03	−66.7	0.019

total clump area was 24% lower under elevated CO$_2$ conditions (Table 1) due to increased mortality. Biomass of plant organs, with the exception of fine roots, was lower under CO$_2$–enriched conditions (Fig. 1C), resulting in 29% less total plant dry weight. However, litter was significantly increased by growth under elevated CO$_2$ (Table 1). Elevated atmospheric CO$_2$ tended to decrease biomass allocation to coarse roots, but increased allocation to fine roots (Fig. 2C); this resulted, overall, in little net change and no effect on root to shoot ratio (Fig. 3).

Butterfly Weed

Elevated CO$_2$ did not affect percent mortality, number of reproductive plants, litter dry weight, or height. However, total stem length (cumulative for all stems) was lower for plants growing under high CO$_2$ (Table 1). Biomass of all plant organs was (or tended to be) lower under CO$_2$–enriched conditions, resulting in elevated CO$_2$ plots having less than half as much biomass both above- and belowground (Fig. 1D). Elevated CO$_2$ decreased biomass allocation to leaves, but increased allocation to roots (Fig. 2D); this resulted in an increase in root to shoot ratio (Fig. 3).

Rattlebox

As with butterfly weed, elevated CO$_2$ did not affect percent mortality, number of reproductive plants, or litter dry weight (Table 1). Biomass of both above- and belowground plant parts tended to be lower under CO$_2$–enriched conditions. As with butterfly weed, this resulted in elevated CO$_2$ plots having approximately half as much biomass as ambient plots (Fig. 1E). However, unlike butterfly weed, elevated CO$_2$ did not af-

fect biomass allocation (Fig. 2E) nor root to shoot ratio (Fig. 3).

Community Level Responses

The total aboveground biomass of CO$_2$–enriched plots was 70% greater than that of ambient plots ($P < 0.001$). Increases in woody biomass (stems and branches) were responsible for 67% of the difference in aboveground response to CO$_2$. Belowground biomass was also greatly enhanced by elevated CO$_2$ (+41%, $P < 0.001$). Although fine root biomass was significantly greater in CO$_2$–enriched plots (+10%, $P = 0.007$), increases in coarse root biomass were responsible for 97% of the belowground response to elevated CO$_2$. Total leaf litter mass was 76% greater in CO$_2$–enriched plots ($P < 0.001$).

Community structure was altered by CO$_2$ enrichment. The percentage of aboveground, belowground, and total biomass comprised by longleaf pine was significantly greater (approximately 12%) in CO$_2$–enriched plots (Table 2). Biomass components for wiregrass were, concomitantly, lower (8–11%) under elevated CO$_2$ conditions. Although butterfly weed and rattlebox comprised small amounts of the overall biomass of the system, these were also significantly lower when grown under elevated than ambient CO$_2$ (Table 2). As with most other variables, the biomass contribution of sand post oak to the total system did not differ significantly between CO$_2$ treatments.

Carbon Responses

Carbon concentration (mg g^{-1}) of longleaf pine stems ($P = 0.002$) and fine roots ($P = 0.106$) tended to be higher, while that of longleaf pine litter ($P = 0.011$), sand post oak coarse roots ($P = 0.015$), and butterfly weed leaves ($P = 0.004$) were lower under elevated CO$_2$ (data not shown). Carbon concentration of all other plant tissues, as well as that for soil, was not affected by CO$_2$ treatment. Carbon content (g m^{-2}) of plant tissues and litter (data not shown) followed patterns, with regard to differences between CO$_2$ treatments and their statistical significance, exactly in accordance with tissue dry weight data (Table 1 and Fig. 1). Within this model community, total C content (g m^{-2}) of plants and litter were significantly increased (65 and 74%, respectively) by 3 yr of growth under elevated CO$_2$ (Table 3). Soil C content did not differ between CO$_2$ treatments at termination of this study. However, as soil C content was slightly higher in elevated CO$_2$ plots at initiation of the study, the overall gain in soil C was lower under elevated CO$_2$ (Table 3). Nonetheless, due to the large gain in C content in both standing plant and litter biomass, total C content and total C gain over the course of study were significantly increased by exposure to elevated atmospheric CO$_2$ (Table 3).

DISCUSSION

While much is known concerning the response of individual plants to increasing atmospheric CO$_2$ con-
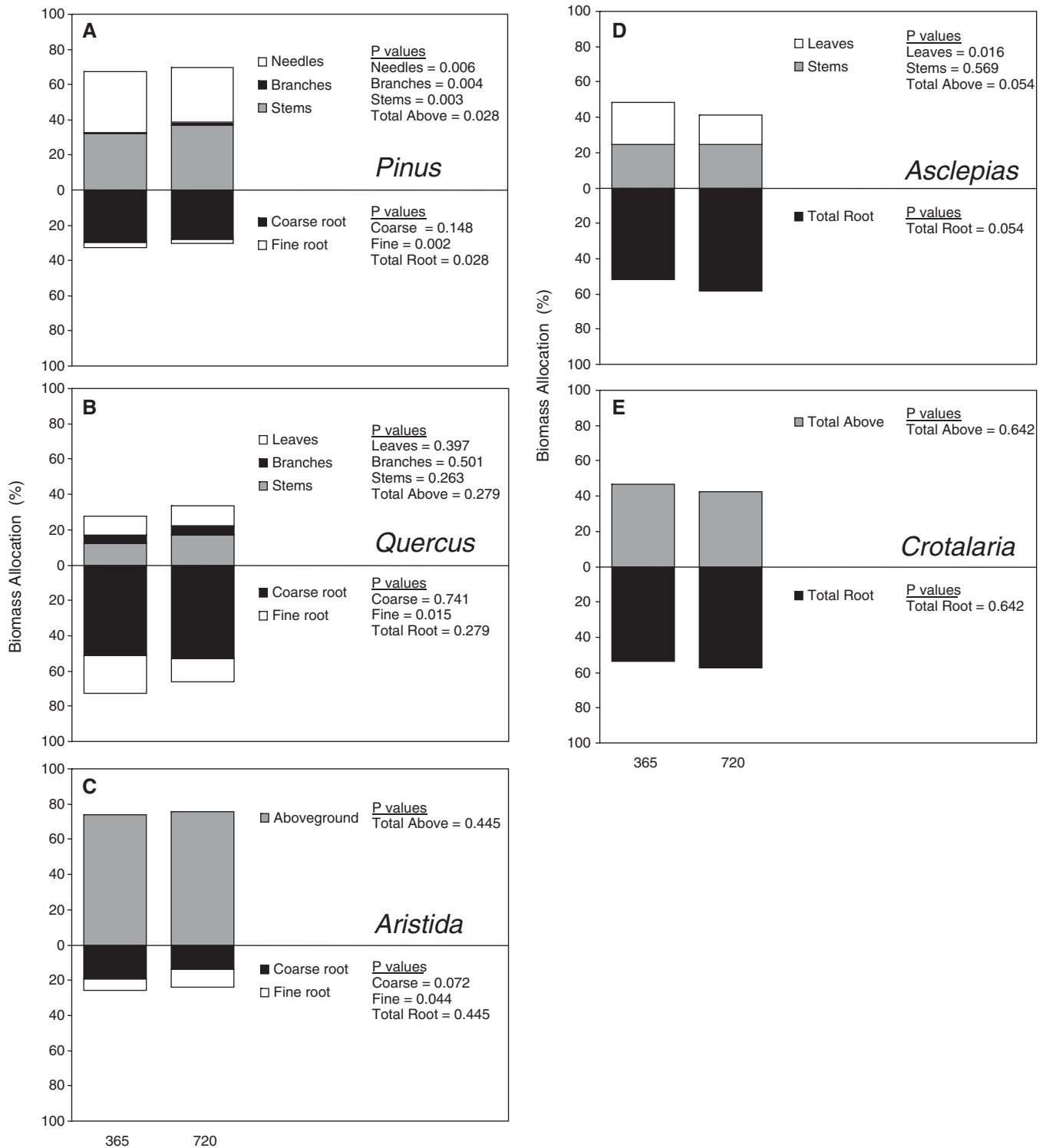
Fig. 2. Biomass allocation (%) among plant component parts (needles, leaves, branches, stems, total aboveground, coarse roots, fine roots, total roots, total plant as applicable for each species), with associated mean separation statistics, for longleaf pine (A), sand post oak (B), wiregrass (C), butterfly weed (D), and rattlebox (E) when grown together for 3 yr under ambient (365 μmol mol^{-1}) and elevated (720 μmol mol^{-1}) concentrations of atmospheric CO$_2$.

centration (Amthor, 1995), few experiments have addressed community level responses to elevated CO$_2$; this paucity of data is particularly severe for forest ecosystems (Arnone, 1996). Forests are both ecologically and economically important in that they contribute as much

as two-thirds to the world's photosynthesis (Kramer, 1981), they dominate many terrestrial ecosystems, and they provide raw materials for a multi-billion dollar industry each year. Thus, understanding how global change (including the effects of elevated CO$_2$) will
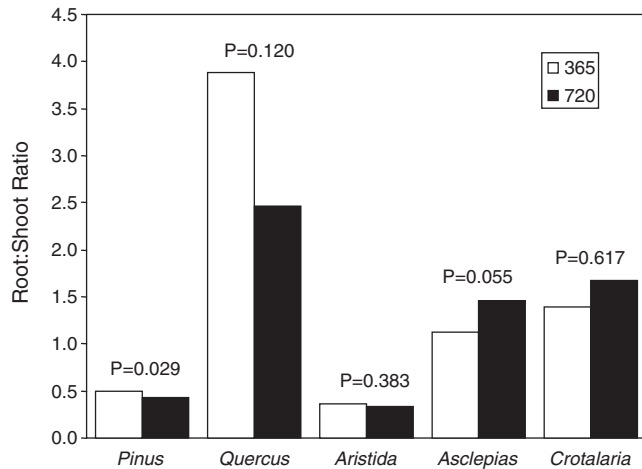
Fig. 3. Root to shoot ratios, with associated mean separation statistics, for longleaf pine, sand post oak, wiregrass, butterfly weed, and rattlebox when grown together for 3 yr under ambient (365 μmol mol^{-1}) and elevated (720 μmol mol^{-1}) concentrations of atmospheric CO_2.

Table 3. Carbon content of various longleaf pine community components when grown for 3 yr under ambient (365 μmol mol^{-1}) and elevated (720 μmol mol^{-1}) CO_2. Means with associated separation statistics and percent change (ambient to elevated) are shown.

Component	Ambient CO_2	Elevated CO_2	Percent change	P values
	g m^{-2}			
Total plants	1886.2	3106.7	64.7	<0.001
Total litter	217.1	378.3	74.3	<0.001
Initial soil	1764.3	1942.0	10.1	0.097
Final soil	3042.3	2974.7	−2.2	0.281
Gain in soil	1278.0	1032.7	−19.2	0.040
Total	5145.5	6459.6	25.5	<0.001
Total gain	3381.3	4517.6	33.6	<0.001

influence the structure and function of forest communities is critical to accurately predict how the biosphere may be impacted.

Integrating knowledge from the CO_2 effects literature (particularly physiology, symbiotic relationships, and nutrient acquisition of individual plants) with our prior research on the effects of CO_2 on longleaf pine (Prior et al., 1997; Runion et al., 1997, 1999), this research was developed to test four hypotheses concerning how plants from differing functional guilds would respond to elevated CO_2 when grown in a community. Briefly, we predicted $C_3 > C_4$ plants, broadleaf > conifers, N-fixers > non-N-fixers, and that the influence of elevated CO_2 on these competitive relationships would alter structure of this forest community and its capacity for storing atmospheric carbon.

Growth responses from the destructive harvest reported here (3 yr) are in general agreement with a previous report from this study which used allometric equations to estimate biomass following 2 yr of exposure to elevated and ambient CO_2 (Davis et al., 2002). Aboveground community biomass was estimated to be 109% greater in response to CO_2 enrichment (compared with 70% reported here based on actual harvested material). One major difference between the previous report and data presented here was the response of wiregrass to the CO_2 treatments. After 2 yr, wiregrass aboveground biomass was 24% greater in elevated than ambient CO_2 plots (Davis et al., 2002). However, after the third year, wiregrass aboveground biomass was actually 26% less in CO_2–enriched chambers. This difference in wiregrass biomass response to CO_2 was primarily due to the increased mortality which occurred between the two reporting periods (i.e., 5% for both treatments after 2 yr compared with 9.7% and 19.1% for ambient and elevated CO_2 treatments after 3 yr) which is most likely due to shading effects of longleaf pine.

Data from this study support our first hypothesis in that biomass of C_3 plants, as a whole, responded positively to elevated CO_2, while survival and growth of the C_4 species (wiregrass) was reduced. Unexpectedly, and counter to our second hypothesis, increased atmospheric CO_2 strongly favored the C_3 conifer (longleaf pine) over the broadleaf C_3 species (sand post oak, rattlebox, and butterfly weed). Longleaf pine begins in a grass stage, where it remains for 3 to 6 (even up to 12) years (Harlow and Harrar, 1969). Once out of the grass stage, longleaf pine generally grows very rapidly due to its extensive tap root system developed during the grass stage. Plants grown under elevated CO_2 tended to bolt out of the grass stage earlier than those in ambient plots and were 30 cm taller 2 yr after planting (Davis et al., 2002). By the end of the third year the increase from high CO_2 was almost 50 cm. This early and rapid height growth under high CO_2 is the most likely reason for the poorer performance of the other species (including the C_3 broadleaves) in this study (i.e., other plants did not put on rapid height growth, could not compete for light, and succumbed to shading by longleaf pine).

A previous study (Runion et al., 1997) demonstrated that, due both to increased root length and increased colonization, ectomycorrhizae approximately doubled on longleaf pine exposed to elevated CO_2. Further, it has been suggested that vesicular–arbuscular mycorrhizae (which occur on grasses, legumes, and forbes) tend to be less responsive to elevated CO_2 than do ectomycorrhizae (O'Neill, 1994). Although not measured in this study, increased ectomycorrhizal colonization might also help explain the strong response of longleaf pine to elevated CO_2 (compared with other C_3 species). However, this explanation would not hold for sand post oak, which also has ectomycorrhizal associations, as it showed no significant response to high CO_2. It should be noted that longleaf pine, as an evergreen conifer, is capable of photosynthesis and root growth (thus, exploration for soil resources) during the overwintering period giving it a possible competitive advantage over neighboring deciduous species, regardless of any potential impacts on mycorrhizal associations.

Our third hypothesis is also not supported by data from this study. Rattlebox, the C_3 N-fixing legume in this study, did not respond positively to elevated CO_2 and did not perform any better than butterfly weed (a similar, albeit non-N-fixing, C_3 herbaceous perennial) or wiregrass (a C_4 grass). The fact that tissue N concentration was unaffected by CO_2 treatment for all species (data not

shown), suggests that plant growth in this study was not limited by soil N availability. Therefore, the ability to fix N did not provide rattlebox with any substantial benefit over the other understory species and it, too, was negatively affected by shading from longleaf pine. Grasses, such as wiregrass, have been shown to compete strongly for soil resources, including N (Mitchell et al., 1993; Perry et al., 1993, 1994). Thus, it is possible that wiregrass may have moderated response of the C$_3$ understory species (rattlebox, butterfly weed, and sand post oak) to elevated CO$_2$. Given the large growth response of longleaf pine, it appears likely that it did not suffer from competition with wiregrass for soil resources.

In both the initial report (Davis et al., 2002) and here, community structure was altered by CO$_2$ enrichment (Hypothesis 4). However, it is important to note that shifts in individual species responses occurred between these two reports, with the most notable changes observed for the keystone species, longleaf pine and wiregrass. Previously, the percentage of aboveground biomass comprised by longleaf pine was only 4% greater in CO$_2$–enriched plots (Davis et al., 2002), while at the destructive harvest 1 yr later this difference was increased threefold (approximately 12%). After 2 yr, wiregrass comprised only 2% less of the total system biomass in CO$_2$–enriched chambers (Davis et al., 2002). After the third year, the contribution of wiregrass to total system biomass was greatly decreased (11%) under high CO$_2$ conditions. This difference in wiregrass response to CO$_2$ is primarily due to the increased mortality which occurred between the two reporting periods (i.e., 5% for both treatments after 2 yr compared with 9.7 and 19.1% for ambient and elevated CO$_2$ treatments after 3 yr) which is most likely due to shading effects of longleaf pine.

The rapid growth of longleaf pine, particularly in height, under high CO$_2$ likely affected not only wiregrass mortality, but the response of the other understory species. Since longleaf pine was one of the more densely planted species, its rapid height growth under elevated CO$_2$ tended to produce a greater shading effect (Davis et al., 2002), which likely dampened the response of understory species. Regardless of the cause(s), elevated CO$_2$ did alter species composition in this study. Davis et al. (2002) suggested that the CO$_2$–induced changes in community structure noted after 2 yr would probably not alter community function as both of the keystone species (longleaf pine and wiregrass) performed well under high CO$_2$. Results from this third year clearly demonstrate that the performance of wiregrass under elevated CO$_2$ was not sustainable and suggest that the effects on community function could be dramatic. For example, longleaf pine–wiregrass ecosystems are fire-dependent and fire is critical in nutrient cycling in these systems. The primary pyric species in this system are longleaf pine and wiregrass. Thus, the pyric characteristics of these ecosystems may lessen as CO$_2$ concentration continues to rise, given the poor response of wiregrass to elevated CO$_2$, unless it is replaced by another pyric understory grass species. On the other hand, given the increased litter production noted here, fire intensity in these systems may increase or fire management may need to be altered (increased frequency) as CO$_2$ continues to rise.

The apparent increased competitive ability of longleaf pine under elevated CO$_2$ may impact the survival of many of the threatened and endangered species found in these ecosystems (Walker, 1997). Also, given that the small understory species (rattlebox and butterfly weed) did not perform well under CO$_2$ enrichment, species diversity could be reduced in these communities which may reduce total ecosystem response to elevated CO$_2$ (Reich et al., 2001). This contention by Reich et al. (2001) is not supported by the current study. Although understory species did not perform well (and could possibly be eliminated) under rising CO$_2$, the community as a whole (due to the response of longleaf pine) showed a strong positive response to CO$_2$ enrichment. In fact, total C content of plants and litter were significantly increased by 3 yr of growth under elevated CO$_2$ resulting in a gain of 11.4 Mg C ha^{-1}. Given that this increased C was largely allocated to woody biomass, the ability of longleaf pine ecosystems to sequester carbon will likely increase as CO$_2$ rises, assuming the response to elevated CO$_2$ continues.

CONCLUSIONS

Individual species within this model community did not always respond in the manner we hypothesized. Perhaps this is not surprising given it has often been noted that response of individual species cannot be reliably predicted—even when based on factors known to influence response to CO$_2$—when species are grown in communities. Although rising CO$_2$ may alter community structure in ways which could impact ecosystem function, productivity and the ability of longleaf pine forests to sequester carbon will likely be enhanced by rising levels of atmospheric CO$_2$. It seems apparent that competition among plants confounds our understanding of ecosystem function. This fact highlights the need for additional studies which examine the effects of elevated CO$_2$ on these processes.

REFERENCES

Abrahamson, W.G., and D.C. Hartnett. 1990. Pine flatwoods and dry prairies. p. 103–149. *In* R.L. Myers and J.J. Ewel (ed.) Ecosystems of Florida. Univ. of Central Florida Press, Orlando.

Amthor, J.S. 1995. Terrestrial higher-plant response to increasing atmospheric [CO$_2$] in relation to the global carbon cycle. Glob. Change Biol. 1:243–274.

Arnone, J.A. 1996. Predicting responses of tropical plant communities to elevated CO$_2$: Lessons from experiments with model ecosystems. p. 101–122. *In* C. Körner and F.A. Bazzaz (ed.) Carbon dioxide, populations, and communities. Academic Press, San Diego, CA.

Bazzaz, F.A. 1990. The response of natural ecosystems to the rising global CO_2 levels. Annu. Rev. Ecol. Syst. 21:1671–1696.

Bazzaz, F.A., and R.W. Carlson. 1984. The response of plants to elevated CO_2 I. Competition among an assemblage of annuals at two levels of soil moisture. Oecologia 62:196–198.

Bazzaz, F.A., and K.D.M. McConnaughay. 1992. Plant-plant interactions in elevated CO_2 environments. Aust. J. Bot. 40:547–563.

Bowes, G. 1993. Facing the inevitable: Plants and increasing atmospheric CO_2. Annu. Rev. Plant Physiol. Plant Mol. Biol. 44:309–332.

Ceulemans, R., and M. Mousseau. 1994. Effects of elevated atmospheric CO_2 on woody plants. New Phytol. 127:425–446.

Davis, M.A., S.G. Pritchard, R.J. Mitchell, S.A. Prior, H.H. Rogers, and G.B. Runion. 2002. Elevated atmospheric CO_2 affects structure of a model regenerating longleaf pine community. J. Ecol. 90:130–140.

Dijkstra, P., G. Hymus, D. Colavito, D.A. Vieglais, C.M. Cundari, D.P. Johnson, B.A. Hungate, C.R. Hinkle, and B.G. Drake. 2002. Elevate atmospheric CO_2 stimulates aboveground biomass in a fire-regenerated scrub-oak system. Glob. Change Biol. 8:90–103.

Drake, B.G. 1992. A field study of the effects of elevated CO_2 on ecosystem processes in a Chesapeake Bay wetland. Aust. J. Bot. 40:579–595.

Fajer, E.D. 1989. How enriched carbon dioxide environments may alter biotic systems even in the absence of climatic changes. Conserv. Biol. 3:318–320.

Hainds, M.J. 1995. Legume population dynamics in a frequently burned longleaf pine-wiregrass ecosystem. M.S. thesis. Auburn Univ., Auburn, AL.

Harlow, W.M., and E.S. Harrar. 1969. Textbook of dendrology. 5th ed. McGraw-Hill Book Co., New York.

Hartwig, U.A., S. Zanetti, T. Hebeisen, A. Lüscher, M. Frehner, B. Fischer, C. van Kessel, G.R. Hendrey, H. Blum, and J. Nösberger. 1996. Symbiotic nitrogen fixation: One key to understand the response of temperate grassland ecosystems to elevated CO_2? p. 253–264. In C. Körner and F.A. Bazzaz (ed.) Carbon dioxide, populations, and communities. Academic Press, San Diego, CA.

Jacqmain, E.I. 1996. Controls on oak composition and population size structure in frequently burned longleaf pine-wiregrass savannahs. M.S. thesis. Auburn Univ., Auburn, AL.

Joel, G., F.S. Chapin, III, N.R. Chiarello, S.S. Thayer, and C.B. Field. 2001. Species-specific responses of plant communities to altered carbon and nutrient availability. Glob. Change Biol. 7:435–450.

Keeling, C.D., and T.P. Whorf. 1994. Atmospheric CO_2 records from the sites in the SIO air sampling network. p. 16–26. In T.A. Boden, D.P. Kaiser, R.J. Sepanski, and F.W. Stoss (ed.) Trends '93: A compendium of data on global change. ORNL/CDIAC-65. The Carbon Dioxide Information Analysis Center, Oak Ridge Natl. Lab., Oak Ridge, TN.

Körner, C., and J.A. Arnone III. 1992. Responses to elevated carbon dioxide in artificial tropical ecosystems. Science 257:1672–1675.

Kramer, P.J. 1981. Carbon dioxide concentration, photosynthesis, and dry matter production. Bioscience 31:29–33.

Landers, J.L., D.H. van Lear, and W.D. Boyer. 1995. Longleaf pine forests of the southeast: Requiem or renaissance? J. For. 93:39–44.

Littell, R.C., G.A. Milliken, W.W. Stroup, and R.D. Wolfinger. 1996. SAS System for mixed models. SAS Inst., Cary, NC.

Mitchell, R.J., G.B. Runion, S.A. Prior, H.H. Rogers, J.S. Amthor, and F.P. Henning. 1995. Effects of nitrogen on Pinus palustris foliar respiratory responses to elevated atmospheric CO_2 concentration. J. Exp. Bot. 46:1561–1567.

Mitchell, R.J., B.R. Zutter, T.H. Green, M.A. Perry, D.H. Gjerstad, and G.R. Glover. 1993. Spatial and temporal variation in competitive effect on soil moisture and pine responses. Ecol. Appl. 3:167–174.

Morgan, J.A., D.E. Pataki, C. Korner, H. Clark, S.J. Del Grosso, J.M. Grunzweig, A.K. Knapp, A.R. Mosier, P.C.D. Newton, P.A. Niklaus, J.B. Nippert, R.S. Nowak, W.J. Parton, W.J. Polley, and M.R. Shaw. 2004. Water relations in grasslands and desert ecosystems exposed to elevated atmospheric CO_2. Oecologia 140:11–25.

Norby, R.J., S.D. Wullschleger, C.A. Gunderson, D.W. Johnson, and R. Ceulemans. 1999. Tree response to rising CO_2 in field experiments: Implications for the future forest. Plant Cell Environ. 22:683–714.

Noss, R.F. 1989. Longleaf pine and wiregrass: Keystone components of an endangered ecosystem. Nat. Areas J. 9:211–213.

O'Neill, E.G. 1994. Responses of soil biota to elevated atmospheric carbon dioxide. Plant Soil 165:55–66.

Peet, R.K., and D.J. Allard. 1993. Longleaf pine vegetation of the southern Atlantic and eastern gulf coast regions: A preliminary classification. p. 45–81. In S.M. Hermann (ed.) Proc. Tall Timbers Fire Ecology Conf. no. 18. Tall Timbers Res. Stn., Tallahassee, FL.

Perry, M.A., R.J. Mitchell, B.R. Zutter, G.R. Glover, and D.H. Gjerstad. 1993. Competitive responses of loblolly pine to gradients in loblolly pine, sweetgum and broomsedge densities. Can. J. For. Res. 23:2049–2058.

Perry, M.A., R.J. Mitchell, B.R. Zutter, G.R. Glover, and D.H. Gjerstad. 1994. Seasonal variation in competitive effect on water stress and pine responses. Can. J. For. Res. 24:1440–1449.

Poorter, H. 1993. Interspecific variation in the growth response of plants to elevated CO_2 concentration. Vegetatio 104/105:77–97.

Prior, S.A., G.B. Runion, R.J. Mitchell, H.H. Rogers, and J.S. Amthor. 1997. Effects of atmospheric CO_2 on longleaf pine: Productivity and allocation as influenced by nitrogen and water. Tree Physiol. 17:397–405.

Prior, S.A., G.B. Runion, H.A. Torbert, and D.C. Erbach. 2004. A hydraulic coring system for soil-root studies. Agron. J. 96:1202–1205.

Pritchard, S.G., M.A. Davis, R.J. Mitchell, S.A. Prior, D. Boykin, H.H. Rogers, and G.B. Runion. 2001. Effects of CO_2 enrichment on root dynamics in a model regenerating longleaf pine ecosystem. Environ. Exp. Bot. 46:55–69.

Pritchard, S.G., C. Mosjidis, C.M. Peterson, G.B. Runion, and H.H. Rogers. 1998. Anatomical and morphological alterations in longleaf pine needles resulting from growth in elevated CO_2: Interactions with soil resource availability. Int. J. Plant Sci. 159:1002–1009.

Reekie, E.G., and F.A. Bazzaz. 1989. Competition and patterns of resource use among seedlings of five tropical trees grown at ambient and elevated CO_2. Oecologia 79:212–222.

Reich, P.B., J. Knops, D. Tilman, J. Craine, D. Ellsworth, M.G. Tjoelker, T.D. Lee, D. Wedin, S. Naeem, D. Bahauddin, G. Hendrey, S. Jose, K. Wrage, J. Goth, and W. Bengston. 2001. Plant diversity enhances ecosystem responses to elevated CO_2 and nitrogen deposition. Nature 410:809–812.

Rogers, H.H., W.W. Heck, and A.S. Heagle. 1983. A field technique for the study of plant responses to elevated carbon dioxide concentrations. Air Pollut. Control Assoc. J. 33:42–44.

Runion, G.B., R.J. Mitchell, T.H. Green, S.A. Prior, H.H. Rogers, and D.H. Gjerstad. 1999. Longleaf pine photosynthetic response to soil resource availability and elevated atmospheric carbon dioxide. J. Environ. Qual. 28:880–887.

Runion, G.B., R.J. Mitchell, H.H. Rogers, S.A. Prior, and T.K. Counts. 1997. Effects of nitrogen and water limitation and elevated atmospheric CO_2 on ectomycorrhiza of longleaf pine. New Phytol. 137:681–689.

Saxe, H., D.S. Ellsworth, and J. Heath. 1998. Tree and forest functioning in an enriched CO_2 atmosphere. New Phytol. 139:395–436.

Walker, J. 1997. Ground layer vegetation in longleaf pine landscapes: An overview for restoration and management. p. 2–13. In J.S. Kush (ed.) Proc. Longleaf Pine Ecosystem Restoration Symp. Longleaf Alliance Rep. no. 3. Alabama Agric. Exp. Stn., Auburn, AL.

Ward, J.K., and B.R. Strain. 1999. Elevated CO_2 studies: Past, present and future. Tree Physiol. 19:211–220.

Wray, S.M., and B.R. Strain. 1987. Competition in old field perennials under CO_2 enrichment. Ecology 68:1116–1120.

Ziska, L.H. 2003. Evaluation of yield loss in field sorghum from a C_3 and C_4 weed with increasing CO_2. Weed Sci. 51:914–918.