

Effects of atmospheric CO₂ on longleaf pine: productivity and allocation as influenced by nitrogen and water

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Summary Longleaf pine (*Pinus palustris* Mill.) seedlings were exposed to two concentrations of atmospheric CO₂ (365 or 720 μmol mol⁻¹) in combination with two N treatments (40 or 400 kg N ha⁻¹ year⁻¹) and two irrigation treatments (target values of -0.5 or -1.5 MPa xylem pressure potential) in open-top chambers from March 1993 through November 1994. Irrigation treatments were imposed after seedling establishment (i.e., 19 weeks after planting). Seedlings were harvested at 4, 8, 12, and 20 months. Elevated CO₂ increased biomass production only in the high-N treatment, and the relative growth enhancement was greater for the root system than for the shoot system. In water-stressed trees, elevated CO₂ increased root biomass only at the final harvest. Root:shoot ratios were usually increased by both the elevated CO₂ and low-N treatments. In the elevated CO₂ treatment, water-stressed trees had a higher root:shoot ratio than well-watered trees as a result of a drought-induced increase in the proportion of plant biomass in roots. Well-watered seedlings consistently grew larger than water-stressed seedlings only in the high-N treatment. We conclude that available soil N was the controlling resource for the growth response to elevated CO₂ in this study. Although some growth enhancement was observed in water-stressed trees in the elevated CO₂ treatment, this response was contingent on available soil N.

Keywords: biomass partitioning, carbon dioxide, *Pinus palustris*, resource limitations.

Introduction

The concentration of CO₂ in the Earth's atmosphere is increasing (Keeling et al. 1989), and is expected to double during the next century (Bolin 1986). Several reviews have discussed the positive effects of CO₂-enriched air on plants, which include increased photosynthetic capacity, water-use efficiency, and growth (Rogers and Dahlman 1993, Allen and Amthor 1995, Amthor 1995, Wittwer 1995). Carbon dioxide-enriched air also often increases the proportion of biomass that is distributed to the root system, which may result in increased acquisi-

tion of essential soil resources (Prior et al. 1994, Rogers et al. 1994).

Because plant species respond differently to CO₂-enriched air, increasing CO₂ concentrations could alter competitive relationships and thereby change ecosystem structure and function (Bazzaz 1990, Mooney et al. 1991). Predicting the direction and magnitude of such changes with increasing atmospheric CO₂ concentration is difficult because we lack a detailed understanding of basic processes within natural systems (Bazzaz 1990, Mooney et al. 1991). The majority of research on the effects of CO₂-enriched air on plants has focused on crops grown under optimal conditions (Ceulemans and Mousseau 1994, Amthor 1995); however, in natural ecosystems, plants are often limited by suboptimal resource availability (e.g., soil N and water). Under conditions of resource limitation, plant growth responses to elevated CO₂ are variable. For example, some studies have shown that growth of woody species increases in response to CO₂-enriched air only when N fertility is high (Bazzaz and Miao 1993, Griffin et al. 1993), whereas other studies have shown increases in growth even under conditions of low N fertility (Conroy et al. 1992, Johnson et al. 1995). In some tree species, the relative growth enhancement in response to CO₂-enriched air is greater under drought conditions than under well-watered conditions (Conroy et al. 1986, Miao et al. 1992), whereas in other tree species growth responses to CO₂-enriched air are independent of water supply (Samuelson and Seiler 1993). These variable results, which are related, in part, to different experimental conditions (e.g., water and nutrient regimes) and species-specific differences in response to CO₂-enriched air, emphasize the importance of investigating whole-plant responses to multiple stresses of native species.

Prior to European settlement, the coastal plain forests of the southeastern United States were dominated by nearly pure stands of longleaf pine (*Pinus palustris* Mill.) with a diverse understory plant community (Peet and Allard 1993). This system now occupies only 2% of its former range (Landers et al. 1995), a loss comparable to or exceeding that of most endangered communities throughout the world 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 forests currently occupy relatively xeric sites and are often found on soils with low N availability. Null hypotheses tested in this study were: that elevated atmospheric CO₂ would have no effect on biomass productivity and allocation in longleaf pine seedlings; and that interactions of CO₂ with soil resource limitations (nitrogen and water) would have no effect on these variables.

Materials and methods

In February 1993, longleaf pine seedlings from a wild seed source were lifted from a Florida nursery, stored at 2 °C for less than 1 week, graded (root collar diameter mean = 13 mm; standard deviation = 2 mm), and planted (three per container) in 192, 45-liter plastic containers filled with a coarse sandy growing medium (pH 5.1) of low fertility (Cope et al. 1980). Deionized water was used to irrigate seedlings throughout the experiment.

Seedlings were exposed to ambient ($\approx 365 \mu\text{mol mol}^{-1}$) or elevated ($\approx 720 \mu\text{mol mol}^{-1}$) CO₂ in open-top chambers starting on March 30, 1993. The chambers, CO₂ supply, and CO₂ monitoring and dispensing systems have been described elsewhere (Mitchell et al. 1995).

Nitrogen treatments, which were slight modifications of those used by Bazzaz and Miao (1993), consisted of either 0.20 or 0.02 mg N g⁻¹ soil year⁻¹ (sulfur-coated urea), applied at planting and at three-month intervals thereafter. The low-N treatment provided N at amounts slightly above those of natural longleaf pine soils (Wilson et al. 1996). Nitrogen mineralization rates varied between 15 and 30 kg ha⁻¹ year⁻¹ in the upper 15 cm of soil. The high-N treatment provided N at amounts that were comparable to those at sites receiving N fertilization (i.e., former agricultural fields or fertilized forests). Other nutrients were maintained in nonlimiting amounts by applying sulfur-coated potassium (0.04 mg K g⁻¹ soil year⁻¹) and MicroMax™ Plus (P = 0.14, Ca = 0.57, Mg = 0.28, and S = 0.05 mg g⁻¹ soil year⁻¹, plus a complete complement of micronutrients) at the time containers were filled. (Trade names and products are mentioned solely for information. No endorsement by the USDA is implied.) In April 1993, iron chelate (0.007 mg Fe g⁻¹ soil) was applied.

To allow for seedling establishment, the two irrigation treatments (target values were -0.5 or -1.5 MPa xylem pressure potential for well-watered and water-stressed treatments, respectively) were not initiated until 19 weeks after planting. Teflon (5 mil FEP film) covers were installed over the chambers to exclude rainfall. Before initiating the irrigation treatments, all containers were flooded with water, allowed to drain overnight, and weighed (weights were assumed to represent field capacity values). New field capacity values were taken at the end of the first growing season (November 1993) and midway through the second growing season (July 1994) to compensate for changes in plant growth. Needle xylem pressure potential measurements were periodically taken with a pressure chamber (Scholander et al. 1965). These measure-

ments were correlated with gravimetric determinations taken with a weighing device (an electronic cable scale with pneumatic lifter). Soil in each container was brought to field capacity with deionized water when gravimetric measurements indicated that the appropriate stress point had been achieved. Containers in the well-watered treatment were irrigated every 3–4 days and containers in the water-stress treatment were irrigated every 12–20 days. Xylem pressure potentials immediately before watering averaged -0.6 and -1.3 MPa for seedlings in the well-watered and water-stressed treatments, respectively.

Treatments were arranged in a split-plot design with six replications. Carbon dioxide treatments (main plots) were randomly assigned to chambers within replicates. Nitrogen and irrigation treatments (subplots) were randomly assigned, in a 2 × 2 factorial design, to a total of 16 containers within each chamber. Container locations within each chamber were re-randomized monthly.

One container from each treatment in each chamber was destructively harvested at each of four sampling dates; July 1993, November 1993, March 1994, and November 1994, corresponding to 4, 8, 12, and 20 months after initiation of the study. Data from two containers for each chamber were combined for each N treatment at the four-month harvest, because the irrigation treatments were not imposed until after this first harvest. The aboveground variables determined at all harvests were: dry weights of leaf, stem, and total top (oven dried at 55 °C); needle number; needle area (measured photometrically); stem height; stem diameter; and stem volume (measured by the water displacement method). The belowground variables determined were: dry weights of taproot, lateral root, fine root, and total root; taproot volume; and lateral and fine root lengths. Root length was measured with a Comair Root Length Scanner (Hawker de Havilland, Port Melbourne, Australia).

Data were totaled for each seedling and averaged for each container before being subjected to an analysis of variance. Data were analyzed with the GLM procedure of the Statistical Analysis System (SAS Institute, Cary, NC 1985). In all cases, differences were considered significant at the $P \leq 0.05$ level. Values which differed at the $0.05 < P \leq 0.15$ level were considered trends.

Results

Biomass production

Total above- and belowground biomass of the longleaf pine seedlings were usually increased by the CO₂-enriched air, high-N and well-watered treatments. Interactions, primarily CO₂ by N and N by irrigation, were prevalent at most harvests (Figure 1). The interaction between CO₂ and N was significant for aboveground (4, 8, and 20 months) and belowground biomass (all dates) (Figures 1A and 1D). Effects of CO₂-enriched air on seedling growth were significant only in the high-N treatment. Relative growth enhancement in response to elevated CO₂ was greater for the root system than for the shoot

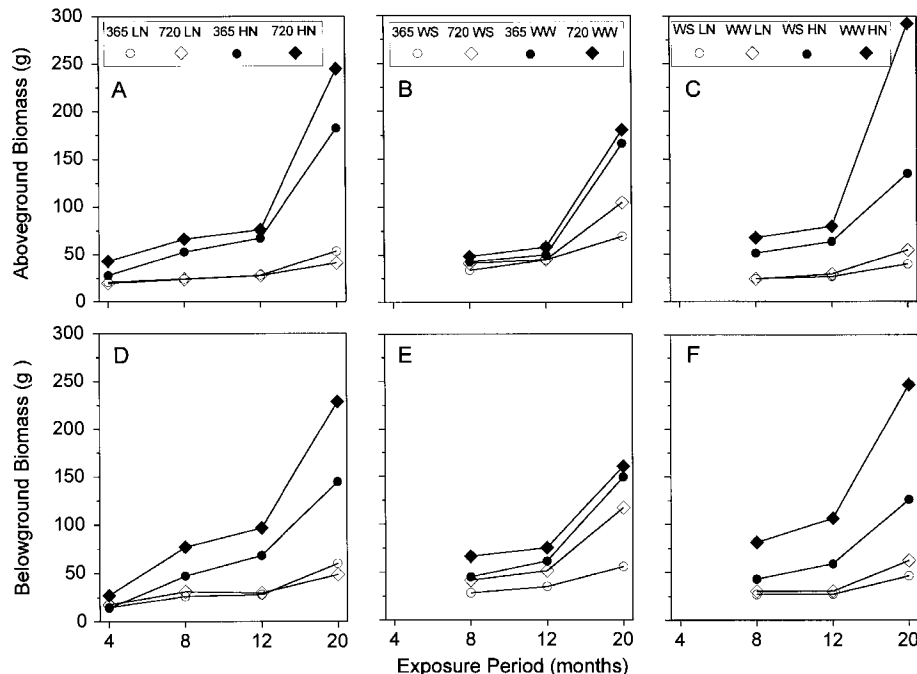


Figure 1. Above- and below-ground biomass at four harvests as affected by interactions between CO₂ and N (A and D, respectively); CO₂ and irrigation (B and E, respectively); and N and irrigation (C and F, respectively). Irrigation treatments were initiated after the first harvest. Abbreviations: 365 and 720 ($\mu\text{mol mol}^{-1}$) denote ambient and elevated CO₂ treatments, respectively; LN and HN denote low-N and high-N treatments, respectively; WS and WW denote water-stressed and well-watered treatments, respectively.

system; for example, belowground biomass increased by 58% compared to 34% for the aboveground response at the 20-month harvest. Irrigation by N interactions were significant for aboveground (8 and 20 months; trend at 12 months) (Figure 1C) and belowground biomass (all dates) (Figure 1F). Well-watered seedlings consistently had more biomass than water-stressed seedlings in the high-N treatment but not in the low-N treatment. Carbon dioxide by irrigation interactions were limited to belowground biomass at the 20-month harvest. Belowground biomass increased (110%) in response to CO₂-enriched air in water-stressed trees only.

Components of aboveground and belowground biomass responded similarly to main effects and their interactions as

described above. Biomass of all tissue was increased by the elevated CO₂ treatment only when seedlings were grown in the high-N treatment (Figure 2A). There was a significant CO₂ by irrigation interaction at 20 months when the elevated CO₂ treatment increased fine root biomass of the water-stressed trees only (Figure 2B); similar trends were observed for lateral and fine root biomass at 8 months (data not shown). Irrigation by N interactions were significant for individual root biomass variables at all harvests, whereas differences for needle and shoot biomass were noted at 8 and 20 months, and a trend was observed at 12 months. In all cases, well-watered seedlings had greater biomass than water-stressed seedlings only in the high-N treatment (Figure 2C).

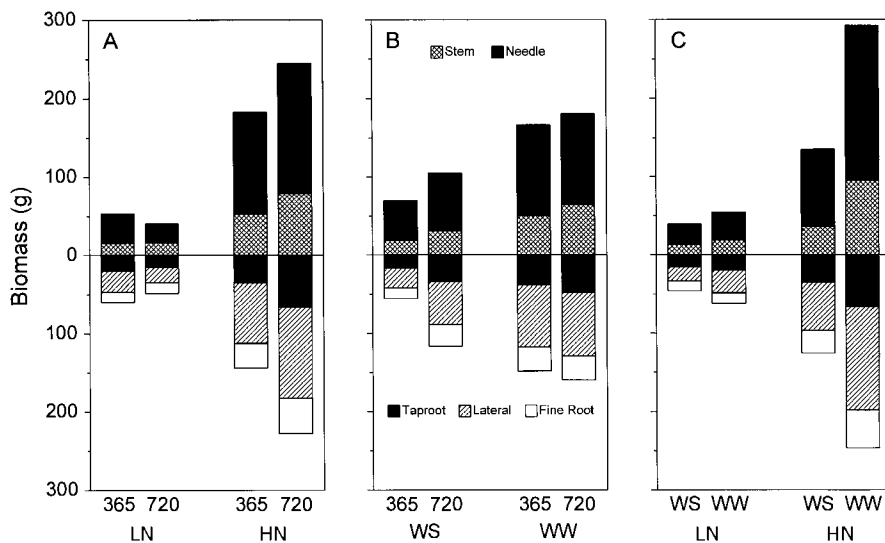


Figure 2. Biomass at the final harvest (20 months) as affected by interactions between CO₂ and N (A); CO₂ and irrigation (B); and N and irrigation (C). Data above the bisecting line represent aboveground tissues, and data below the line represent belowground tissues. Irrigation treatments were initiated after the first harvest. Abbreviations: 365 and 720 ($\mu\text{mol mol}^{-1}$) denote ambient and elevated CO₂ treatments, respectively; LN and HN denote low-N and high-N treatments, respectively; WS and WW denote water-stressed and well-watered treatments, respectively.

Biomass partitioning

More biomass was partitioned to aboveground tissue in ambient atmospheric CO₂ than in CO₂-enriched air, as a result of increased allocation to needles (Table 1). Conversely, belowground partitioning was greater than aboveground partitioning in the elevated CO₂ treatment and was associated with increased allocation to lateral and fine roots (Table 2). These distribution patterns resulted in increased root to shoot ratios (R:S) in the elevated CO₂ treatment at all harvests (data not shown). Although less biomass was partitioned to stems in the high-N treatment than in the low-N treatment, the high-N treatment increased total aboveground distribution (except at 12 months) as a result of large increases in allocation to the needle fraction. Root:shoot ratios were decreased by the high-N treatment at 4, 8, and 20 months (data not shown). An increase in belowground partitioning in the low-N treatment was the result of increased allocation to taproots and fine roots and occurred despite reduced partitioning to lateral roots. Water stress increased the proportion of biomass aboveground (except at 20 months) by increasing allocation to needles (Table 1) and reducing allocation to lateral roots (Table 2).

Interactions among treatments on biomass partitioning were infrequent and generally occurred only at the 12-month harvest (data not shown). Elevated CO₂ increased the proportion of biomass belowground only in the high-N treatment, as a result of greater allocation to lateral roots. Ambient CO₂ increased partitioning aboveground only in the high-N treatment as a result of a trend for greater distribution to needles. Likewise, ambient CO₂ increased aboveground distribution only under

conditions of water stress as a result of a drought-induced increase in biomass partitioning to needles (12 and 20 months). Increased R:S in elevated CO₂ occurred only in water-stressed seedlings at 20 months, although a similar trend was noted at 12 months (data not shown). Elevated CO₂ increased total belowground distribution only for water-stressed seedlings. Water-stressed seedlings distributed more biomass aboveground (in needles) and less belowground (in lateral roots) when grown in the high-N treatment but not when grown in the low-N treatment (8 and 12 month harvests). At the 12-month harvest, but not at the other harvests, R:S was higher for well-watered seedlings than for water-stressed seedlings in the high-N treatment but not in the low-N treatment.

Shoot and root morphology

Elevated CO₂ increased total needle number and foliar surface area only at the initial harvest (Figure 3), whereas the high-N treatment increased needle number and foliar surface area at all harvests. The well-watered treatment increased needle number (20 months) and foliar surface area (8 and 20 months, with similar trends at 12 months). Carbon dioxide by N interactions indicated needle numbers (4 and 20 months) and foliar surface area (4, 8 and 20 months) increased in response to elevated CO₂ only in the high-N treatment (Figures 3A and 3D). Elevated CO₂ increased both variables only in water-stressed seedlings at 20 months (Figures 3B and 3E) and a similar trend was noted at the 12 month harvest for foliar surface area. Well-watered seedlings had higher needle number (20 months) and foliar surface area (8 and 20 months; trend

Table 1. Main treatment effects for longleaf pine partitioning variables for seedlings harvested at four periods following initiation of CO₂ exposure. Water stress treatments were initiated after the first harvest.

Sample date	CO ₂ Concentration ($\mu\text{mol mol}^{-1}$)		N Fertility regime ($\text{kg ha}^{-1} \text{year}^{-1}$)		Water stress regime (MPa)	
	365	720	40	400	-1.5	-0.5
<i>% Needle</i> ¹						
July 93 (4) ²	52.7	47.8** ³	45.1	55.5***	–	–
November 93 (8)	42.0	36.0*	35.2	42.8***	41.6	36.4***
March 94 (12)	40.8	35.4**	37.2	39.0	40.4	35.8**
November 94 (20)	36.9	30.8*	29.5	38.2***	34.6	33.2
<i>% Stem</i>						
July 93 (4)	10.1	9.3	10.9	8.5***	–	–
November 93 (8)	8.8	8.8	10.4	7.2***	8.8	8.7
March 94 (12)	10.2	10.8	12.0	9.1***	10.6	10.4
November 94 (20)	15.1	17.3	16.9	15.6	15.1	17.4
<i>% Aboveground</i>						
July 93 (4)	62.8	57.1**	55.9	63.9***	–	–
November 93 (8)	50.7	44.8*	45.6	50.0**	50.5	45.1**
March 94 (12)	51.0	46.2*	49.2	48.1	51.1	46.2**
November 94 (20)	52.1	48.2*	46.4	53.9***	49.7	50.5

¹ % Needle = % of total biomass represented by needles; % Stem = % of total biomass represented by stems; and % Aboveground = % of total biomass represented by aboveground biomass.

² Values in parentheses following sample date represent months of exposure to CO₂ and N treatments.

³ Asterisks refer to the probability of a greater *F* value calculated for the split-plot design: * = 0.01 < *P* ≤ 0.05; ** = 0.001 < *P* ≤ 0.01; *** = *P* ≤ 0.001.

Table 2. Main treatment effects for longleaf pine partitioning variables for seedlings harvested at four periods following initiation of CO₂ exposure. Water stress treatments were initiated after the first harvest.

Sample date	CO ₂ Concentration ($\mu\text{mol mol}^{-1}$)		N Fertility regime ($\text{kg ha}^{-1} \text{ year}^{-1}$)		Water stress regime (MPa)	
	365	720	40	400	-1.5	-0.5
<i>% Taproot</i> ¹						
July 93 (4) ²	15.6	16.5	18.5	13.6*** ³		
November 93 (8)	16.3	16.7	19.7	13.2***	16.6	16.4
March 94 (12)	14.8	16.1	17.1	13.8***	15.9	15.0
November 94 (20)	15.3	16.0	18.5	12.8***	16.1	15.2
<i>% Lateral root</i>						
July 93 (4)	13.3	15.0*	15.0	13.3**		
November 93 (8)	21.3	24.5**	20.7	25.1***	20.1	25.7***
March 94 (12)	23.6	25.5	21.7	27.3***	22.2	26.9***
November 94 (20)	21.7	23.3	21.5	23.4	21.4	23.5
<i>% Fine root</i>						
July 93 (4)	8.3	11.5**	10.6	9.2		
November 93 (8)	11.7	14.0*	14.0	11.7**	12.9	12.8
March 94 (12)	10.6	12.2	12.0	10.8	10.9	11.9
November 94 (20)	11.0	12.6*	13.7	9.9***	12.8	10.8*
<i>% Belowground</i>						
July 93 (4)	37.2	42.9**	44.1	36.1***		
November 93 (8)	49.3	55.2*	54.4	50.0**	49.5	54.9**
March 94 (12)	49.0	53.8*	51.9	51.9	48.9	53.8**
November 94 (20)	48.0	51.8*	53.6	46.1***	50.3	49.5

¹ % Taproot = % of total biomass represented by taproot; % Lateral root = % of total biomass represented by lateral roots; % Fine root = % of total biomass represented by fine roots; % Belowground = % of total biomass represented by belowground biomass.

² Values in parentheses following sample date represent months of exposure to CO₂ and N treatments.

³ Asterisks refer to the probability of a greater *F* value calculated for the split-plot design: * = 0.01 < *P* ≤ 0.05; ** = 0.001 < *P* ≤ 0.01; *** = *P* ≤ 0.001.

at 12 months) only in the high-N treatment (Figures 3C and 3F).

Stem height was not affected by CO₂ treatment, but stem diameters were larger in the elevated CO₂ treatments at all except the first harvest. Stem heights and diameters were larger in plants in the high-N treatment than in plants in the low-N treatment at most harvests. Water-stressed seedlings were shorter and had smaller stem diameters than well-watered seedlings at 8, 12, and 20 months (trend for stem height at 12 months). The elevated CO₂ treatment increased diameters (all harvests) and heights (4 and 8 months) of seedlings only in the high-N treatment (Figures 3G and 3J), and both growth measures (8 and 20 months, trends at 12 months) were larger for well-watered seedlings than for water-stressed seedlings in the high-N treatment but not in the low-N treatment (Figures 3I and 3L). There were no CO₂ by irrigation interactions (Figures 3H and 3K).

Stem and taproot volume (Figure 4) exhibited similar responses to treatments and their interactions as stem height and diameter. Increases in tissue density, based on measures of stem and taproot dry weights and volumes (data not shown), occurred in seedlings in CO₂-enriched air (4 and 20 months, trend for taproot density at 12 months) and in seedlings in the low-N treatment (4, 8, and 12 months, trend for taproot density

at 20 months). No differences between water treatments and no significant interactions on tissue density were observed.

Root length

Total lateral and fine roots were longer in the elevated CO₂ treatment than in the ambient CO₂ treatment, except for lateral root length at 8 months and both root lengths at 20 months (Figure 4). At 8, 12 and 20 months, total lateral and fine roots were longer in the high-N treatment than in the low-N treatment (similar trend at 4 months for fine roots). At all harvest dates, both root length variables were lower in water-stressed seedlings than in well-watered seedlings.

Elevated CO₂ increased lateral root length (20 months, trend at 4 months) and fine root length (4 months, trend at 8 and 20 months) of seedlings in the high-N treatment but not in the low-N treatment (Figures 4G and 4J). Elevated CO₂ increased total fine root length only in water-stressed seedlings at 20 months (Figures 4H and 4K). Well-watered seedlings consistently had longer lateral roots (8 and 12 months, trend at 20 months) and fine roots (8 and 20 months, trend at 12 months) in the high-N treatment than in the low-N treatment (Figures 4I and 4L).

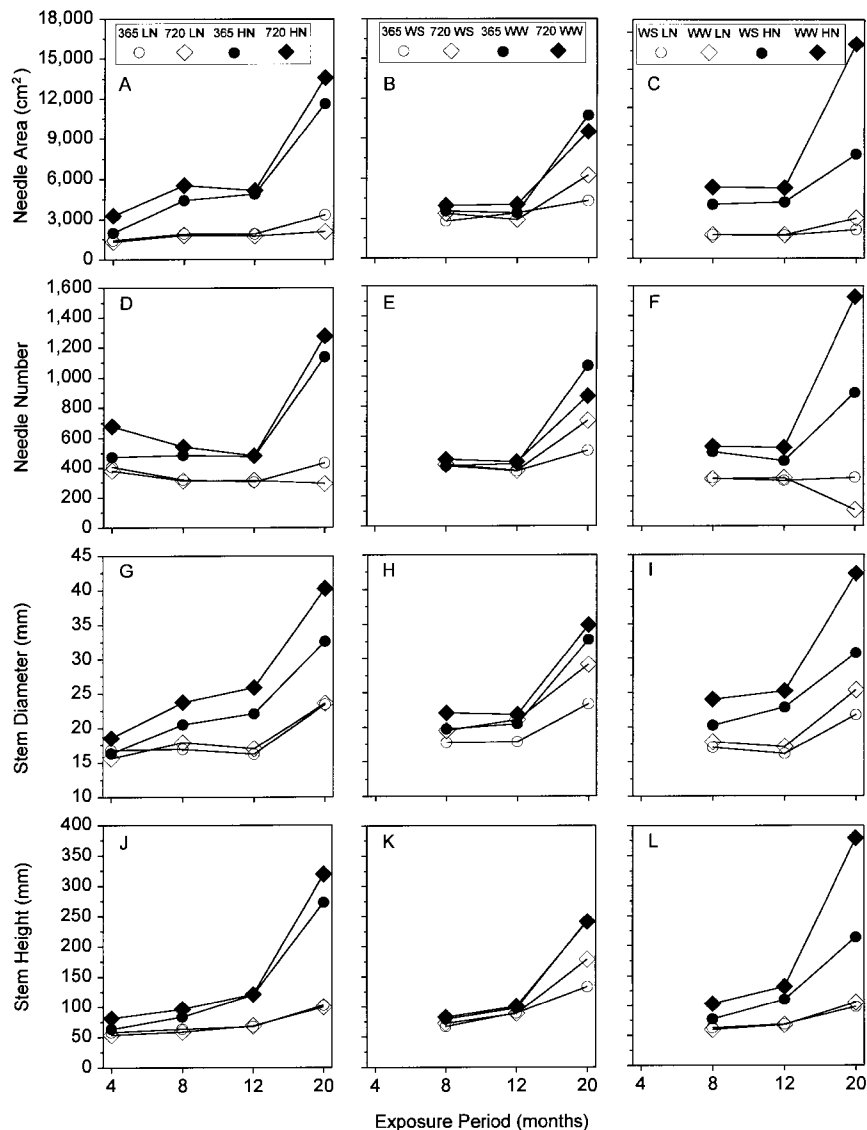


Figure 3. Aboveground parameters (needle area, needle number, stem diameter, and stem height) at four harvests as affected by interactions between CO₂ and N (A, D, G, and J, respectively); CO₂ and irrigation (B, E, H, and K, respectively); and N and irrigation (C, F, I, and L, respectively). Irrigation treatments were initiated after the first harvest. Abbreviations: 365 and 720 ($\mu\text{mol mol}^{-1}$) denote ambient and elevated CO₂ treatments, respectively; LN and HN denote low-N and high-N treatments, respectively; WS and WW denote water-stressed and well-watered treatments, respectively.

Discussion

The elevated CO₂ treatment increased seedling growth only when N availability was high. These findings resulted in rejection of both null hypotheses tested. Similar findings have been reported for loblolly pine (*P. taeda* L.; Griffin et al. 1993) and other early successional trees (*Betula populifolia* Marsh., *Fraxinus americana* L., *Acer rubrum* L.; Bazzaz and Miao 1993). However, positive growth responses to CO₂-enriched air even under conditions of low soil N availability have been reported for ponderosa pine (*P. ponderosa* Dougl. ex Laws.; Johnson et al. 1995) and for flooded gum (*Eucalyptus grandis* W. Hill ex Maiden.; Conroy et al. 1992). These conflicting results indicate that the interactive effects of CO₂ and N availability may not only reflect different experimental protocols but may also be species dependent. The relative enhancement of biomass production in response to CO₂-enriched air was greater for the root system than for aboveground tissues provided that soil N was not limiting. The elevated CO₂ treatment

also resulted in increased fine root length at all but the final harvest, which may have been the result of increased turnover of fine roots in response to CO₂-enriched air (Pregitzer et al. 1995). Changes in root density and turnover may have important implications for rates of root decomposition and nutrient cycling in an altered CO₂ environment.

Increased stem biomass was mainly associated with increased stem diameter and volume rather than changes in seedling height. Additionally, the elevated CO₂ treatment increased stem tissue density (cf. Conroy et al. 1990). Such shifts, if they also occur in mature trees, may have implications for wood quality in terms of forest production.

Needle biomass and surface area increased in response to CO₂ enrichment as a result of an increase in needle number rather than needle size. Although these increases were small, they could affect whole-plant photosynthetic capacity. Increases in dry weight per unit leaf area have been observed in CO₂-enriched air and have been attributed to an additional cell

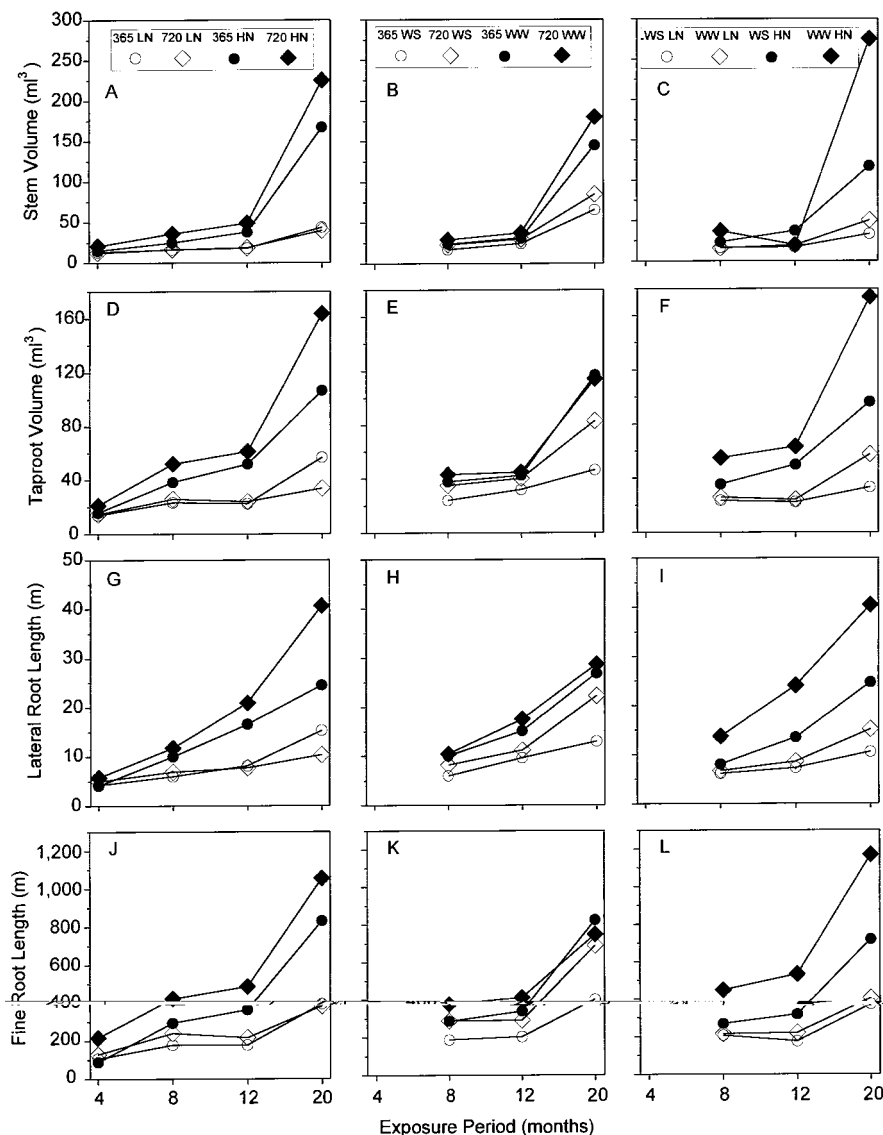


Figure 4. Aboveground (stem volume) and belowground (taproot volume, lateral root length, and fine root length) parameters at four harvests as affected by interactions between CO₂ and N (A, D, G, and J, respectively); CO₂ and irrigation (B, E, H, and K, respectively); and N and irrigation (C, F, I, and L, respectively). Irrigation treatments were initiated after the first harvest. Abbreviations: 365 and 720 ($\mu\text{mol mol}^{-1}$) denote ambient and elevated CO₂ treatments, respectively; LN and HN denote low-N and high-N treatments, respectively; WS and WW denote water-stressed and well-watered treatments, respectively.

layer (Rogers et al. 1983, Thomas and Harvey 1983) or starch accumulation, or both (Acock and Pasternak 1986). Although CO₂ enrichment resulted in higher concentrations of needle starch at the initial harvest (Mitchell et al. 1995), we found no CO₂-induced increase in dry weight per unit leaf area at any harvest. This apparent discrepancy may be associated with longleaf pine's strong taproot growth habit, which, coupled with the use of large containers, resulted in sufficient belowground C sink capacity to reduce the magnitude of foliar starch accumulation.

In addition to N limitations, longleaf pines are frequently subjected to periodic episodes of water stress. Water stress reduced biomass production, irrespective of the CO₂ treatment. The initial growth enhancement due to CO₂ enrichment was similar in both irrigation treatments. The positive effects of CO₂-enriched air on aboveground growth diminished by the end of the study in both irrigation treatments. At the final harvest, however, a significant CO₂ by irrigation interaction

indicated increased foliar surface area and total root biomass for CO₂-enriched seedlings grown under water-stress conditions. Greater total seedling biomass in response to elevated CO₂ under water-limited conditions has been observed by some workers (Conroy et al. 1986, Miao et al. 1992), whereas others have found that growth enhancement in response to CO₂-enriched air is independent of water supply (Samuelson and Seiler 1993). By the end of our study, total fine root length had increased in plants grown in CO₂-enriched air under conditions of water stress. In addition, increases in the ratio of leaf area to fine root length in response to CO₂-enriched air may mean that seedlings are more drought tolerant. Collectively, these data indicate that increases in atmospheric CO₂ concentration may ameliorate the negative effects of water stress on seedling growth (Tolley and Strain 1984, 1985, Hollinger 1987), possibly through increased water-use efficiency (Rogers et al. 1983).

We note that the belowground growth enhancement observed for water-stressed seedlings grown in CO₂-enriched air was contingent on soil N availability. Irrigation by N interactions indicated that no increased growth occurred in the low-N treatment regardless of water supply. Soil resources (i.e., N and water) are often assumed to affect plants in a similar manner (Tilman 1982, Wilson 1988); however, our data indicate that this may not be a valid assumption because N tended to moderate the CO₂ response, whereas CO₂ tended to moderate the water response. We conclude that soil N availability was the overall controlling resource because CO₂ moderation of water response was contingent on soil N availability. If true, it follows that if reduced N source strength diminishes C sink strength (i.e., as a result of reduced belowground growth), then the positive growth effects due to increased atmospheric CO₂ concentration or water availability will be unrealized.

Partitioning of resources is reflected by adjustments in shoot and root growth and in R:S. Low N supply enhanced biomass partitioning to roots and increased R:S (cf. Green et al. 1994, Mooney et al. 1995). In general, increased C supply in response to elevated atmospheric CO₂ preferentially induced the distribution of photosynthates belowground (cf. Lekkerkerk et al. 1990, Ceulemans and Mousseau 1994, Rogers et al. 1994). This pattern was detected in the current study in that a higher proportion of biomass was distributed to the root system which was reflected by increased R:S. Such shifts confer an advantage to seedlings in CO₂-enriched air in terms of exploring the soil, thereby potentially attaining more resources such as water and nutrients to meet growth demands. In contrast, seedlings grown in ambient CO₂ had a greater proportion of biomass distributed to aboveground tissue, primarily in needles. Similarly, high-N availability resulted in a greater proportion of biomass being distributed to needles. These data support the contention that plants allocate photosynthate to tissues needed to acquire the most limiting resource (Chapin et al. 1987). This idea is also supported by the finding that water-stressed trees grown in CO₂-enriched air had a greater proportion of biomass in roots, which was reflected by increased R:S. In comparison, water-stressed seedlings grown in ambient CO₂ had a higher proportion of aboveground biomass partitioned to needles suggesting that CO₂ was the most limiting resource. These data again indicate that CO₂-enriched air ameliorated the effects of water stress; however, it was only under conditions of sufficient N availability that the benefits of elevated CO₂ were realized.

The lack of a growth response to elevated CO₂ in seedlings in the low-N treatment is of interest because suboptimal concentrations of N are often found in longleaf pine savannas. In addition, because longleaf pine forests currently occupy the more xeric sites in the southeast, the observed response to conditions of water stress suggests that this species is able to sustain greater productivity in an elevated CO₂ atmosphere, provided that N is made available. However, in nature, soil resources occur along spatial and temporal gradients; e.g., fertile pockets of nutrients may result from decomposing above- and belowground tissue of neighboring trees and understory species. Rapid root proliferation patterns in fertile-soil

microsites have been reported for native species (Jackson and Caldwell 1989). Large increases in longleaf pine root growth during the winter may further enhance acquisition of needed resources in the field. This dormant season root proliferation may be particularly important because Caldwell et al. (1987) have shown that direct competition between neighboring plants, in terms of shifts in nutrient acquisition from interspaces shared with defoliated plants, occurs rapidly. Potential changes in plant competition for soil resources as a result of increasing atmospheric CO₂ may increase the importance of fire in this ecosystem for controlling broadleaf plant competitors and for facilitating the release of needed N found in residue litter. It is also possible that N₂-fixing plants native to this ecosystem will play an increasingly important role (i.e., as a potential source of N) in determining how longleaf pine savannas respond to the predicted increase in atmospheric CO₂ concentration. Results from this study suggest that rising atmospheric CO₂ concentrations have important implications for management of longleaf pine.

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