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The influence of elevated carbon dioxide and water availability on herbaceous weed development and growth of transplanted loblolly pine (*Pinus taeda*)

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Abstract

Loblolly pine (*Pinus taeda* L.) seedlings were grown in competition with native weeds using soil and seed bank collected from recently chopped and burned areas near Appomattox, Virginia. One-year-old seedlings were planted and weeds allowed to germinate from the native seed bank while being exposed to CO_2 (ambient and elevated — approximately 700 ppm) and water (water stressed and well watered) treatments for approximately one growing season in a greenhouse. Elevated CO_2 did not influence total weed biomass; however, C_3 weed community development was favored over C_4 weed community development in elevated CO_2 regardless of water availability. This suggests that weed community composition may shift toward C_3 plants in a future elevated CO_2 atmosphere. Pine growth was significantly greater in the well watered and elevated CO_2 treatments compared to the water stressed and ambient treatments, respectively, even though they were competing with native herbaceous weeds for resources. There was a significant water and CO_2 interaction for pine root:shoot ratio. Under elevated CO_2, root:shoot ratio was significantly greater in the water stressed treatment than the well watered treatment. In contrast, there was no significant difference in the root:shoot ratio under the ambient CO_2 treatment for either water treatment. These results suggest that loblolly pine seedlings will respond favorably in an elevated CO_2 atmosphere, even under dry conditions and competing with herbaceous weeds. © 2000 Elsevier Science Ireland Ltd. All rights reserved.

Keywords: Biomass; CO2; Competition; Herbaceous weeds; Loblolly pine

1. Introduction

The rising level of atmospheric carbon dioxide (CO_2) is well documented and has become a major topic of discussion in the scientific community. Of major concern is CO_2's role as a greenhouse gas and its influence on plant growth and development. Historically, atmospheric CO_2 levels have

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fluctuated, but recent tropical deforestation and fossil fuel consumption have caused a rapid increase in atmospheric concentrations (Dippery et al., 1995). The level of atmospheric CO_2 has risen nearly 100 ppm since the industrial revolution, and is predicted to continue increasing approximately 1–2 ppm each year (Eamus and Jarvis, 1989; Keeling et al., 1995; Keeling and Whorf, 1999). This increase could result in atmospheric CO_2 reaching levels close to 700 ppm by the mid to late 21st century (Houghton et al., 1995; Saxe et al., 1998).

Along with increasing CO_2 levels, various climate modelers have also predicted changing precipitation patterns and global warming (Houghton et al., 1990). Studies where species have been exposed to elevated CO_2 and varying water treatments indicate that vegetative species will respond differently to changing environmental conditions (Groninger et al., 1996). Since this could eventually result in altered species composition and stand structure, understanding how species will compete for resources in response to elevated CO_2 will give valuable insight to land managers and aid in future carbon sequestration research (Ceulemans and Mousseau, 1994; Groninger et al., 1996).

Much of our current understanding about the effect of elevated CO_2 on plant growth comes from studying individual plant responses. Findings by Groninger et al. (1995) underscore the importance of studying competitive interactions under elevated CO_2 levels. In this study, monoculture and mixed stands of loblolly pine and sweetgum (*Liquidambar styraciflua* L.) seedlings where grown under elevated CO_2 levels in a greeenhouse. Data from the monoculture stands suggested that sweetgum would have a stronger growth response than loblolly pine. Data from mixed stands, however, showed no differences in the competitive abilities of these two species. Studies involving competition between herbaceous species grown under elevated CO_2 have generally concluded that C_3 species have higher growth rates and out-compete C_4 species (Bazzaz and Carlson, 1984; Wray and Strain, 1987; Bazzaz and Garbutt, 1988).

While the results of these studies contribute significantly to our understanding of competitive changes between weeds and seedlings there is much that remains unanswered. For example, herbaceous weeds exert a strong influence on tree seedling survival and growth (Britt et al., 1990; Morris et al., 1993). However, there is little information on how these relationships may change in an elevated CO_2 environment or how a native herbaceous community will develop under increased CO_2. To answer these questions and gain a better understanding of the competitive responses of seedlings and weed species grown together under elevated CO_2, this study proposed to specifically (a) evaluate the difference in native herbaceous community development as influenced by water regime (water stressed and well watered) and ambient and elevated atmospheric CO_2, and (b) determine if a difference in 1 year old (1:0) loblolly pine seedling growth occurs when competing with a native herbaceous community developing under two water regimes (water stressed and well watered) and ambient and elevated carbon dioxide levels. It was hypothesized that native weed growth would respond more favorably to elevated CO_2 and thereby limit the growth response of loblolly pine seedlings to elevated CO_2. Further, it was also hypothesized that C_3 weeds would tend to replace C_4 weeds under elevated CO_2 levels.

2. Materials and methods

2.1. Soil

This experiment was conducted in a greenhouse on the Virginia Polytechnic Institute and State University campus, with the goal of simulating regeneration on a post drum chop and burn Piedmont site. Soil (Tatum series, Clayey, mixed, thermic Typic Hapludults) was randomly collected in early March 1997 across three recently chopped and burned sites in the Piedmont region near Appomattox, Virginia. Approximately 0.2 m^3 of subsoil and 0.03 m^3 of topsoil were collected from ten randomly selected locations on each site (approximately 2 ha). The topsoil layer consisted of the upper A and E horizons (approximately 3.0 cm in depth). All topsoil collected was thoroughly

mixed in order to evenly distribute the seed bank and create a homogeneous mixture. Subsoil (below 3.0 cm) collected was also thoroughly mixed. Both soil types were refrigerated at 2°C until the start of the experiment to prevent premature native weed seed germination.

2.2. Seedling culture

1:0 loblolly pine seedlings (*Pinus taeda* L.), obtained from the Virginia Department of Forestry, were used in this study, and kept in cold storage (2°C) until the start of the experiment to sustain dormancy. To mimic a typical Piedmont growing season, this experiment began 5 April, 1997. It ended on 28 August, 1997, when weeds were beginning to go through natural senescence. At the start of the experiment approximately 0.008 m^3 (18 cm) of subsoil and 0.001 m^3 (2.5 cm) of topsoil were stratified in 40 plastic containers (24 cm in diameter, 23 cm deep, approximately 0.010 m^3). Soil was saturated with water and one loblolly pine seedling was planted in the middle of each container. Containers were then moved into chambers for CO_2 and water treatments.

Container size was selected in order to eliminate root binding during the study. Using large containers created a microcosm inside each chamber whereby seedlings and weeds grew and competed as they would after a typical hand planting operation on a chopped and burned Virginia Piedmont site. No fertilizer was added to the containers. Nutrition was limited to the native fertility already present in the soil, as is the case in most planting operations involving loblolly pine seedlings.

2.3. CO_2 treatments

Two growth chambers, 0.91 × 1.07 × 1.52m in dimension, were constructed of 6 ml polyvinyl plastic with a 75% light transmittance. Ambient air from outside the greenhouse was pulled into each chamber through a PVC tube 2.5 m above the ground. A regenerative blower was used to distribute the air at the same rate into each chamber. To provide elevated CO_2 to a chamber, pure (99.99%) liquid CO_2 was injected into blower air before entering the chamber. The design for airflow, CO_2 flow and measuring systems are fully described by Samuelson and Seiler (1993). Air for each chamber was sampled on a time-shared system for 10-min periods three times each hour. CO_2 concentrations were measured with an infrared gas analyzer (ADC Mk III, Hoddeson, England) and strip chart recorder.

The ambient treatment had a daily mean (± SD) of 357 ppm (± 33) CO_2 and a nightly mean of 404 ppm (± 27) CO_2. The elevated treatment had a daily mean of 660 ppm (± 41) CO_2 and a nightly mean of 736 ppm (± 46) CO_2. Daily and nightly temperature and relative humidity (RH) were monitored with recording hygrothermographs, which were calibrated weekly with mercury thermometers. The mean temperature and RH of the ambient treatment were 26.4°C (± 4.8) and 56.0% (± 10.7), respectively, during the day, and 23.4°C (± 4.2) and 61.2% (± 11.5) at night. Mean temperature and RH of the elevated treatment in this experiment were 26.4°C (± 4.5) and 57.8% (± 8.1), respectively, during the day, and 23.8°C (± 4.6) and 62.9% (± 9.7) at night.

2.4. Water treatments

Two water treatments (well watered and water stressed) were administered in order to simulate different moisture levels in a future Piedmont clear-cut. Treatment levels were defined as atmospheric inputs rather than plant stress levels. While no attempt was made to keep the different water treatments at constant plant stress levels, watering levels were consistent within treatments.

Water stressed (1.27 cm H_2O/week) and well watered (2.54 cm H_2O/week) treatments were administered to designated containers in both chambers. Water was applied twice each week. During each watering, water stressed treatments received 300 ml per container, and well watered treatments received 600 ml per container. This amount of water combined with the large size of containers resulted in negligible leaching through the bottoms of the containers.

2.5. Biomass determinations and measurements

To determine the influence of treatments on herbaceous community development and tree growth, all species were destructively harvested at the end of the experiment. Weeds were separated by genus (i.e. *Panicum* spp.) and CO_2 fixation biochemistry (C_3 or C_4). Dry biomass of weed roots and tops (stem and leaves) were determined and compared, as was pine height, diameter and dry biomass of roots, needles and shoots. Beginning pine height above the root-collar and diameter were also measured for use as a possible covariant in the analysis. Root:shoot ratio was calculated by dividing dry root biomass by dry shoot biomass for each seedling.

Plant water potential was measured immediately prior to the final watering (approximately 4 h after photo-period began). Five seedlings were randomly selected from each treatment and foliage was measured using a pressure bomb (PMS Instruments Inc., Corvallis, OR).

2.6. Experimental design and analysis

This experiment was conducted as a factorial experiment and analyzed as a completely randomized design, with CO_2 concentration (ambient and elevated) and water level (water stressed and well watered) being the treatments analyzed. There were 10 replications for each treatment combination, for a total of 40 containers (20 in each chamber). Containers were rotated within chambers once a week in order to average out any variability and eliminate any confounding caused by the chambers (i.e. shade effects). Containers and CO_2 treatments were also rotated between chambers once a week in order to average out any chamber differences (i.e. one chamber being cooler than the other). This rotating ensured that all containers spent approximately equal amounts of time in all locations within both chambers (Samuelson and Seiler, 1992, 1993). Statistical analysis was performed with SAS (SAS Institute Inc., Cary, NC) statistical software. Analysis of variance was used to compare biomass of weeds and trees between treatments, and also to determine if there were any changes in weed species composition (i.e. C3 vs. C4 weeds). Regression analysis was used to determine weed effects on plant growth by correlating total biomass of tree seedlings with total biomass of weeds. Statistical differences were considered significant at $P \leq 0.05$. Values of $P \leq 0.10$ are noted and discussed when appropriate.

3. Results

3.1. Plant water potential

Plant water potential prior to final watering was significantly lower in the water stressed treatment (-2.17 MPa) than in the well watered treatment (-1.66 MPa). Measurements for the CO_2 treatments were significantly lower in the elevated treatment (-2.06 MPa) than in the ambient treatment (-1.77 MPa). There was no significant CO_2 and water interaction.

3.2. Loblolly pine biomass

Both loblolly pine seedling height and diameter were significantly greater ($p = 0.001$ and 0.009, respectively) in the well watered treatment than in the water stressed treatment, with increases of 21% and 12%, respectively (Table 1). There were no significant differences between CO_2 treatments for either height or diameter at $P \leq 0.05$; however, height was 9% greater in the elevated treatment compared to the ambient treatment ($P = 0.086$). No significant CO_2 and water interactions were detected. Root biomass was 33% greater ($P = 0.014$) in the elevated treatment than the ambient treatment, but there were no significant differences between water treatments and no CO_2 and water interaction (Table 1).

Needle, shoot and total biomass were all significantly greater in the well watered treatment than the water stressed treatment, with increases of 34, 31 and 23%, respectively. Shoot and total biomass were significantly greater in the elevated CO_2 treatment than the ambient CO_2 treatment, with increases of 23 and 22%, respectively. Needle biomass was 16% greater in the elevated CO_2 treatment than the ambient CO_2 treatment

Table 1
Loblolly pine seedling diameter, height, needle, root, shoot and total biomass responses to CO_2 and water treatments[a]

Treatment	Diameter (mm)	Height (cm)	Needle (g)	Root (g)	Shoot (g)	Total (g)
CO_2						
Ambient	7.93	35.46[c]	9.23[c]	4.17[b]	5.29[b]	18.69[b]
Elevated	8.49	38.52	10.67	5.53	6.52	22.73
Water						
Water stressed	7.74[b]	33.44[b]	8.52[b]	4.94	5.12[b]	18.57[b]
Well watered	8.68	40.54	11.38	4.76	6.70	22.85

[a] Values are the mean for 20 samples.
[b] Means significantly different at $P \leq 0.05$.
[c] Means significantly different at $P \leq 0.10$.

($P = 0.076$). None of these variables had a significant CO_2 and water interaction.

There was a significant CO_2 and water interaction for root:shoot ratio ($P = 0.002$). Under elevated CO_2, loblolly pine root:shoot ratio was 80% greater ($P = 0.001$) in the water stressed treatment than the well watered treatment. In contrast, the root:shoot ratio in the ambient treatment was nearly identical under both water treatments ($P = 0.939$).

3.3. Weed biomass

Total weed biomass was significantly greater (433%) in the well watered treatment than in the water stressed treatment (Table 2). Surprisingly, there were no significant differences between the CO_2 treatments, and there were no significant CO_2 and water interactions. Water treatment had a significant influence on the total biomass of C_3 and C_4 weeds, with respective increases of 832 and 230% in the well watered treatment compared to the water stressed treatment (Table 2). There were no significant differences between CO_2 treatments and no CO_2 and water interactions for either variable.

The percentage of biomass that the C_3 and C_4 weeds contributed toward total weed biomass was influenced by treatment level. However, differences in total weed biomass were not significant at a P-value of 0.05 (Table 3). The C_4 weeds contributed 66% of the total biomass in the water stressed treatment, but only 41% of the total weed biomass in the well watered treatment. Under the ambient treatment, C_4 weeds contributed 53% of the total weed biomass, but their contribution decreased to 35% under the elevated treatment, an overall reduction of 33% ($P = 0.098$). There were no CO_2 and water interactions.

The three most predominant weeds, in terms of contribution to total weed biomass were *Erechtites* spp., *Panicum* spp. and *Phytolacca* spp. (Table 3). *Panicum* spp. (a C_4 weed), *Erechtites* spp. and *Phytolacca* spp. (C_3 weeds) respectively combined to make up 80 and 78% of the total weed biomass in the ambient and elevated CO_2 treatments. *Panicum* spp. contributed 46% to total weed biomass in the ambient CO_2 treatment, but only 28% of the total weed biomass in the elevated treatment. Under the water stressed treatment, *Panicum* spp. contributed 56% to the total weed biomass, but only 35% of the total weed biomass in the well watered treatment.

Table 2
Effects of CO_2 and water treatments on total, C_3 and C_4 weed biomass (g)[a]

Treatment	Total	C_3	C_4
CO_2			
Ambient	2.42 (0.148)	1.15 (0.335)	1.27 (0.098)
Elevated	1.89	1.23	0.66
Water			
Water stressed	0.68 (0.001)	0.23 (0.001)	0.45 (0.007)
Well watered	3.63	2.14	1.49

[a] Values are the mean for 20 samples. Numbers in parentheses indicate within treatment P-values.

Table 3
Treatment responses of individual weeds, expressed as percent contribution toward total weed biomass[a]

	CO_2 treatment		Water treatment	
Weed species	Ambient	Elevated	Water stressed	Well watered
C_4				
Acalypha spp.	3.3	0.3	0.7	2.2
Carex spp.	0.7	2.2	2.1	1.4
Cyperus spp.	2.4	1.0	0.7	2.4
Danthonia spp.	0.0	2.5	6.8	0.0
Panicum spp.	46.2	28.3	55.5	35.0
Poa spp.	0.1	0.4	0.4	< 0.1
Total[b]	52.6	35.2	66.3	41.0
C_3				
Antenaria spp.	0.7	1.6	0.3	1.2
Ceanothus spp.	0.0	1.6	0.0	0.8
Equisetum spp.	0.0	0.4	1.1	0.0
Erechitites spp.	17.0	30.3	6.0	26.0
Lechea spp.	0.1	0.5	0.2	0.3
Liriodendron spp.	0.2	1.4	0.0	0.8
Lysimachia spp.	2.1	1.5	2.9	1.6
Phytolacca spp.	16.8	19.7	20.7	17.6
Pinus spp.	0.0	0.8	0.0	0.4
Potentella spp.	0.0	2.2	0.0	1.1
Rubus spp.	8.3	1.9	1.8	6.2
Solanum spp.	1.2	0.0	0.0	0.8
Solidago spp.	0.2	2.0	0.0	1.2
Stellaria spp.	0.5	0.5	0.4	0.5
Trifolium spp.	0.1	0.1	0.3	< 0.1
Vaccinium spp.	0.3	0.0	0.0	0.2
Viola spp.	0.0	0.6	0.0	0.3
Total[b]	47.4	64.8	33.7	59.0

[a] Values are the mean for 20 samples.
[b] Totals do not always equal the sum of the individual weed species due to rounding.

Water treatment had a significant influence on C_3, C_4 and total weed shoot biomass, with respective increases of 1195, 210 and 440% in the well watered treatment compared to the water stressed treatment (Table 4). There was no significant difference between CO_2 treatments at a P-value of 0.05; however, total weed root:shoot ratio was 35% smaller in the elevated treatment ($P = 0.097$). There were no CO_2 and water interactions for any of these variables.

Total weed, C_3 and C_4 root biomass was significantly greater in the well watered treatment than the water stressed treatment, with increases of 424, 601 and 267%, respectively (Table 4). Total weed and C_3 root biomass was not influenced by CO_2; however, C_4 root biomass was significantly less (54%) in the elevated CO_2 treatment compared to the ambient treatment. Water and CO_2 treatments did not have a significant effect on total, C_3 and C_4 root:shoot ratios (Table 4). There were no CO_2 and water interactions for any of these variables.

Total weed biomass affected total loblolly pine biomass but only explained a small amount of the variability in loblolly pine seedling growth ($r^2 = 0.10$). The level of CO_2 and water treatments did not influence this relationship, as r^2-values were similar within each treatment.

4. Discussion

Even in the presence of competing herbaceous weeds, loblolly pine seedlings exhibited growth responses similar to those found in previous studies involving CO_2 and water treatments. Height and diameter were both higher (9 and 7%, respectively) in the elevated CO_2 treatment than the ambient CO_2 treatment, but only height differences were significant at $p \leqslant 0.10$. Groninger et al. (1996) also reported a significant increase (14%) in loblolly pine seedling height when growing in competition with red maple (*Acer rubrum*) seedlings for two growing seasons. This is consistent with previous findings by Bacon and Zedaker (1987), Miller et al. (1991) and Weiner and Thomas (1992) where competition affected tree height growth more than diameter growth.

There was a strong response to water availability, as height and diameter were both significantly greater in the well watered treatment than the water stressed treatment. The Groninger et al. (1996) study reported similar findings, but the magnitude of the responses was larger. This difference can be explained by the longer duration of their study. The differences in magnitude were not as pronounced in the CO_2 treatments, suggesting that water was a more limiting factor than CO_2 in this study.

The water and CO_2 treatments resulted in significant increases in loblolly pine needle, shoot and total biomass in both the elevated CO_2 treatment and the well watered treatment. These findings were also reported by Sionit et al. (1985), Tschaplinski et al. (1993), Tissue et al. (1996) and Groninger et al. (1996). The decreases in shoot and total biomass (31 and 23%, respectively) under water stressed conditions were similar in magnitude to those reported by Groninger et al. (1995). Root biomass was significantly greater in the elevated CO_2 treatment than the ambient treatment; however, water availability did not result in a significant difference. Water potential readings did indicate a degree of stress in the water stressed treatment, but this did not have an effect on root biomass. Tschaplinski et al. (1993) reported a 45% decrease in root biomass due to water stress, but other studies have found that shoot biomass is affected more than root biomass (Seiler and Johnson, 1985; Bongarten and Teskey, 1987). While no significant CO_2 and water interaction was detected for root biomass, a potential interaction ($P = 0.063$) was detected. Root biomass in the water stressed loblolly pine seedlings was 63% larger in the elevated CO_2 treatment than the ambient CO_2 treatment. This could result in an increased ability for loblolly pine to exploit resources when growing in dry conditions under elevated CO_2.

Table 4
Total weed, C_3 and C_4 weed shoot (g), root (g) and root:shoot ratio responses to CO_2 and water treatments[a]

	CO_2 treatment		Water treatment	
	Ambient	Elevated	Water stressed	Well Watered
Total weed				
Shoot	1.30 (0.663)	1.50	0.38 (0.001)	2.07
Root	1.42 (0.158)	0.74	0.30 (0.001)	1.56
Root:shoot	0.98 (0.097)	0.64	0.72 (0.411)	0.89
C_3				
Shoot	0.53 (0.386)	0.72	0.09 (0.001)	1.16
Root	0.62 (0.613)	0.51	0.14 (0.001)	0.98
Root:shoot	1.25 (0.214)	0.79	0.90 (0.519)	1.14
C_4				
Shoot	0.78 (0.157)	0.43	0.29 (0.015)	0.91
Root	0.50 (0.044)	0.24	0.16 (0.002)	0.58
Root:shoot	4.17 (0.878)	4.83	4.22 (0.896)	4.78

[a] Values are the mean for 20 samples. Numbers in parentheses indicate within treatment P-values.

Root:shoot ratio showed a significant CO_2 and water interaction for loblolly pine seedlings. This interaction is in contrast to findings by Tolley and Strain (1985), Tschaplinski et al. (1993) and Groninger et al. (1993), Groninger et al. (1995) and Groninger et al. (1996)), but can be explained by the response of root biomass. The large increase in root biomass exhibited by water stressed seedlings grown under elevated CO_2 resulted in a significantly larger root:shoot ratio for these seedlings.

Water availability had a much greater impact on total weed biomass than did CO_2 level. Both C_3 and C_4 species had significantly larger total biomass in the well watered treatment than the water stressed treatment. Water stress, however, favored the C_4 weeds while well watered conditions favored the C_3 weeds. These findings were also reported by Campbell et al. (1995).

The CO_2 treatments did not result in any significant differences in total weed biomass. Total weed biomass was, surprisingly, 22% smaller in the elevated treatment than the ambient treatment due largely to a 78% decrease in C_4 biomass under elevated CO_2. Total biomass of the C_3 weeds was 84% greater than C_4 weeds in the elevated treatment; however, when water was limiting under elevated CO_2, biomass was nearly equal in both weed types. Although there was no significant CO_2 and water interaction, the combined effect of water stress and elevated CO_2 resulted in a 143% increase in total C_3 biomass and a 38% decrease in total C_4 biomass compared to the water stressed weeds under ambient CO_2 levels. Under well watered conditions, elevated CO_2 did not influence biomass of C_3 weeds, but resulted in a 52% decrease in C_4 weed biomass. Bazzaz and Carlson (1984) and Campbell et al. (1995) reported similar findings indicating that elevated CO_2 may benefit C_3 species more than C_4 species.

There were no significant CO_2 treatment differences between the root:shoot ratios of either the C_3 or the C_4 weed species. Sionit et al. (1982) and Bazzaz et al. (1989) reported similar findings, but there has been much variation in the response of weed root:shoot ratios in other studies. Most studies involved hand planting the weed species (as either seed or freshly germinated seedlings) at predetermined spacings, making comparisons with the present study difficult. Both C_3 and C_4 weed root and shoot biomass in this study were effected by water availability, with significant increases in the well watered treatment compared to the water stressed treatment.

Previous studies have found that weed biomass effects young loblolly pine growth (Bacon and Zedaker, 1987; Morris et al., 1989; Perry et al., 1993). In this study, CO_2 and water level did not influence the relationship between weed biomass and tree growth. The amount of variation explained by weed biomass was very low ($r^2 = 0.10$), suggesting that the loblolly pine seedlings benefited more from available resources than the weed species. During visual inspection at final harvest there was no evidence that any tree or weed species became pot bound, eliminating pot size as a source of variability.

5. Conclusions

Loblolly pine seedling growth was similar to previous studies involving loblolly pine and similar treatments. The major difference in this study; however, was that the seedlings were competing for resources with a native herbaceous community. While the magnitude of response was smaller than in other studies where seedlings were grown in monoculture, elevated CO_2 still resulted in a significantly greater growth response for loblolly pine seedlings compared to ambient CO_2.

Total loblolly pine seedling biomass was significantly greater under the elevated CO_2 and well watered treatment levels. The well watered treatment resulted in significant increases in height and diameter. Height and diameter were both greater in the elevated CO_2 treatment, but only differences in height were significant at $P \leq 0.10$. Unlike previous studies, there was a significant interaction between CO_2 and water for loblolly pine root:shoot ratio. There was a significant increase in the root:shoot ratio of water stressed seedlings grown under elevated CO_2, due to a larger root biomass under elevated CO_2 and water stressed conditions. This increase in root biomass may contribute to an improved ability of loblolly

pine to compete against weeds on dry sites under elevated CO_2 levels.

Herbaceous weed community development was similar to other studies involving elevated CO_2 and different levels of water availability. Elevated CO_2 appears to favor C_3 weed community development, regardless of water availability. This suggests that weed community composition may shift towards C_3 plants in a future elevated CO_2 atmosphere.

Total biomass of the well watered weeds was significantly larger than the water stressed weeds. Elevated CO_2 did not result in more total weed growth. Instead, it resulted in a smaller, although not significant ($P = 0.15$), total weed biomass. Even though the weed community did have a negative effect on loblolly pine biomass, it was so small that it appears the pine seedlings benefited the most from available resources. This was particularly evident under elevated CO_2.

The significant increases in loblolly pine growth lead us to reject our hypothesis that competition with a native herbaceous community in an elevated CO_2 atmosphere would limit the growth response of loblolly pine seedlings. Elevated CO_2 did stimulate pine seedling growth compared to ambient levels, while overall weed biomass was lower (although not significantly). Our second hypothesis that C_3 weeds would tend to replace C_4 weeds under elevated CO_2 was accepted based on the species composition changes for these two weed types. Even though C_3 weed biomass was not significantly larger under elevated CO_2, C_4 weed biomass decreased by nearly half.

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