

**The Influence of Elevated Carbon Dioxide and Water Availability
on Herbaceous Weed Development and Planted Loblolly Pine
(*Pinus taeda*) and Coppice Sweetgum (*Liquidambar styraciflua*) Growth**

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(ABSTRACT)

Loblolly pine (*Pinus taeda*) and coppiced sweetgum (*Liquidambar styraciflua*) seedlings were grown in competition with a native weed community using soil and seed bank collected near Appomattox, Virginia. Seedlings and weeds were exposed to CO₂ (ambient and elevated) and water (water stressed and well watered) treatments for approximately one growing season in closed top chambers.

Weed growth had an effect on tree growth, but the amount of variation in tree biomass explained by weed biomass was very low. It appears that the tree seedlings benefited more from available resources than the herbaceous weeds. The influence of competition with loblolly pine and elevated CO₂ did not have an influence on total weed biomass; however, it did favor C₃ weed community development regardless of water availability. This suggests that weed community composition may shift toward C₃ plants in a future elevated CO₂ atmosphere.

Loblolly pine height, diameter, needle, shoot and total biomass were significantly greater in the well watered treatment than the water stressed treatment. Pine root, needle, shoot and total biomass were significantly greater in the elevated treatment than the ambient treatment. While not significant, root biomass of water stressed pine seedlings was 63% greater in the elevated CO₂ treatment than the ambient treatment. There was a significant water and CO₂ interaction for pine root:shoot ratio. Under elevated CO₂, root:shoot ratio was significantly greater in the water stressed treatment than the well watered treatment. In contrast, root:shoot ratio in the ambient treatment was nearly identical under both water treatments. These results indicate that loblolly pine will respond favorably in an elevated CO₂ atmosphere, even under dry conditions.

The coppiced sweetgum seedlings responded favorably to well watered conditions with significant increases in leaf area, specific leaf area, leaf, shoot and total biomass compared to water stressed conditions. Leaf, root, shoot+stump and total biomass of sweetgum significantly increased and specific leaf area decreased under elevated CO₂ compared to ambient CO₂, but differences were smaller than previous findings. This indicates that coppicing may dampen the growth response to elevated CO₂, at least in the initial growth stage after coppicing.

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INTRODUCTION

The rising level of carbon dioxide (CO₂) in the atmosphere is well documented and has become a major topic of discussion in the scientific community. Of major concern is its role as a greenhouse gas and its influence on plant growth and development. Even though these levels have historically fluctuated, recent tropical deforestation and fossil fuel consumption have caused a rapid increase in atmospheric CO₂ (Dipperly et al. 1995). Pre-industrial revolution levels of CO₂ have been estimated at 270 to 280 ppm (Eamus and Jarvis 1989). In 1996 the concentration of atmospheric CO₂ had reached a level of 362 ppm and was expected to increase approximately 1.2 ppm each year (Conway et al. 1988, Keeling and Whorf 1997). The general consensus is that atmospheric CO₂ levels will double to 700 ppm by the mid to late 21st century; however, levels as high as 800 ppm have been predicted for this same time period by the Intergovernmental Panel on Climate Change (Eamus and Jarvis 1989, Houghton et al. 1990).

Along with increasing CO₂ levels, various climate modelers have also predicted changing precipitation patterns and global warming (Houghton et al. 1990). Many studies have been undertaken in which species were exposed to elevated CO₂ and varying water regimes, and findings have indicated that species will respond differently in the face of changing environmental conditions (Groninger et al. 1996). This could eventually result in an altering of species composition and stand structure due to changes in competitive abilities (Groninger et al. 1996, Ceulemans and Mousseau 1994).

Understanding how species will react in competitive ecosystems in response to elevated CO₂ will give valuable insight to land managers and aid future research direction. Surprisingly, though, there has been very little research involving competition between tree species and herbaceous weeds under elevated CO₂ levels, and the response of coppice regeneration has not yet been investigated. Findings by Groninger et al. (1995), in one of the few studies where seedlings were competitively grown under elevated CO₂ levels, underscore the importance of studying competitive interactions. In this study, loblolly pine and sweetgum were grown under elevated CO₂ levels in monoculture and mixed-stands. 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 CO₂ have consistently concluded that C₃ species have higher growth rates and out-compete C₄ species (Bazzaz and Carlson 1984, Wray and Strain 1987, Bazzaz and Garbutt 1988). In each of these studies however, species were chosen by the researchers and sown into experimental designs.

While the results of these studies contribute significantly to our understanding of competitive changes there is much that remains unanswered. For example,

herbaceous weeds exert a strong influence on tree seedling survival and growth (Britt et al. 1990, Esen 1996). However, there is no information on how these relationships may change in a future CO₂ environment or how a native herbaceous community will develop under increased CO₂. There are several other critical questions that need answering as well. Will loblolly pine seedlings react differently under elevated CO₂ to competition with a native herbaceous community? How will coppiced sweetgum sprouts develop when competing with a native herbaceous community? In order to answer these questions and gain a better understanding of the competitive responses of species grown under elevated CO₂, this study proposed:

1. To evaluate the difference in native herbaceous community development as influenced by water regime (water stressed and well watered) and ambient and elevated atmospheric carbon dioxide.

2. To determine if a difference in 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.

3. To compare the growth response of sweetgum seedling coppice sprouts when competing with a native herbaceous community developing under two water regimes (water stressed and well watered) and ambient and elevated carbon dioxide levels.

LITERATURE REVIEW

Studies involving the influence of CO₂ on plant growth date back to 1804 when de Sussure is credited with making the first observations of growth enhancement due to CO₂ enrichment (Wittwer 1986). Today, greenhouses around the world are using this knowledge to stimulate the growth of vegetation through elevated CO₂ levels (Kimball et al. 1993). While the influence of elevated CO₂ levels on plant growth is now better understood than ever before, predicting species responses in natural ecosystems is difficult because of variation in available resources and the inherent interactions between species. The influence of intra and inter-specific competition, in combination with other environmental factors, on the development of vegetation grown under elevated CO₂ levels is just now being examined. Although results from studies are sometimes conflicting, in general, researchers are beginning to better understand competitive influences.

Growth

Effects of CO₂

Many studies examining the effects of elevated CO₂ on plant growth have concluded that total growth increases due to increased carbon uptake (Eamus and Jarvis 1989, Ceulemans and Mousseau 1994). In a review of past research, Kimball et al. (1993) summarized basic conclusions concerning the effects of doubling atmospheric CO₂ concentrations:

- plant growth and yield will probably increase by an average of 30% (not considering potential climate change)
- plants will have varying degrees of responses, with C₃ species responding more than C₄ species, thus effecting competition and land distribution of these species.
- there is a strong relationship between temperature and CO₂ concentration, with increased CO₂ growth stimulation under some conditions and a decrease under others.
- stomatal conductance will probably decrease resulting in decreased transpiration per unit of leaf area and increased leaf temperature. However, leaf area will probably increase, resulting in a minimal effect on seasonal water use per unit of land area.
- plants will respond to elevated CO₂ even on nutrient-poor sites, although this response may be reduced on severely depleted soils.

These conclusions are based on a review of past research involving species which were generally grown under optimum conditions (Kimball et al. 1993). This same review found that a doubling of CO₂ concentrations resulted in average biomass

increases of 25 - 31% for agricultural C₃ crops, 34% for non-agricultural C₃ crops, 26% for woody species and 14% for C₄ crops. Other studies have shown similar results, with biomass of annual herbaceous crops increasing from 10 - 50% for C₃ crops and 0 - 10% for C₄ crops (Hunt et al. 1991). Hunt et al. (1991) studied the growth response in 11 C₃ herbaceous species, and found that those grown under elevated CO₂ levels increased their biomass 43% more than those grown under ambient conditions.

It is apparent that there is much species specific variation in growth responses under elevated CO₂ levels. Further complicating our understanding and predictive abilities is the inherent variation between experimental designs, such as length of experiment and growth conditions. In a comparative study by Dippery et al. (1995), total biomass of *Abutilon theophrasti* (C₃) significantly increased while *Amaranthus retroflexus* (C₄) remained relatively unchanged when grown under elevated CO₂ levels. In contrast, Bazzaz et al. (1989) found that elevated CO₂ caused a larger initial biomass increase in *Am. retroflexus* than in *Ab. theophrasti*. Furthermore, neither species had a significant difference in final biomass after 40 days when compared to individuals grown at ambient CO₂ levels. The initial biomass increase in *Am. retroflexus* led the authors to conclude that C₄ species can increase growth just as much as C₃ species in elevated CO₂ atmospheres (Bazzaz et al. 1989). These contradictory results appear to be related to differences in experimental design. The study by Dippery et al. (1995) lasted just 35 days and species were grown at constant irradiance levels of 1000 $\mu\text{mol photons m}^{-2}\text{s}^{-1}$. The study by Bazzaz et al. (1989), on the other hand, lasted 60 days and used natural lighting where irradiance levels were sometimes as high as 2000 $\mu\text{mol photons m}^{-2}\text{s}^{-1}$. Dippery et al. (1989) explained the growth in *Am. retroflexus* as being related to the higher irradiance levels used in the Bazzaz et al. experiment, since C₄ species have shown increased growth under high irradiance (Sionit and Patterson 1984). It would seem though, that natural lighting, as opposed to a constant lower irradiance, would give a more accurate prediction of species response. In general though, plants grown under elevated CO₂ levels are heavier than those grown under ambient levels, and this is partially attributed to an increase in dry weight per unit stem length (Enoch and Zieslin 1988, Ford and Thorne 1967).

Carbon dioxide has also been shown to influence dry matter partitioning in plants (Enoch and Zieslin 1988), but again, results are sometimes contradictory. The experiment by Dippery et al. (1995) found a significant increase in the root:shoot ratio due to increased root biomass for *Ab. theophrasti*, but Bazzaz et al. (1989) found no significant differences. Likewise, Rogers et al. (1983) found a significant increase in root:shoot ratio of maize (C₄), while Sionit et al. (1982) did not. In reviewing the effects of elevated CO₂ on plant growth, Enoch and Zieslin (1988) found that root:shoot ratios generally increase. The authors blamed contradictory results on differences in experimental designs, citing unfavorable environmental conditions and too short a period of CO₂ enrichment as primary

causes (Enoch and Zieslin 1988). These authors also concluded that root:shoot ratios are generally higher in both C₃ and C₄ species grown in elevated CO₂ due to weakened apical dominance and an increase in side shoot development. Increased root:shoot ratios have also been attributed to an increased partitioning of photosynthate to root tissues (Dippery et al. 1995). The review by Enoch and Zieslin (1988) also concluded that plants grown under elevated CO₂ generally show large increases in leaf dry weight. Other studies have concurred with this statement, and have attributed the increase in dry leaf biomass to an accumulation of starch (Sage et al. 1989, Eamus and Jarvis 1989).

Ceulemans and Mousseau (1994) reviewed woody plant responses to elevated CO₂ under a variety of experimental conditions and species ages, and reported the following:

- there is much variation between and within species.
- total plant growth of seedlings and young trees is enhanced due to increased carbon uptake.
- increases in total biomass averaged 38% in evergreen conifers and 64% in broadleaf deciduous species.
- distinctive root:shoot balances develop as a result of extra assimilates being partitioned into different plant parts (Eamus and Jarvis 1989).
- dry weight of unit leaf area increases due to an accumulation of starch and/or additional cell layers (Eamus and Jarvis 1989).

Ceulemans and Mousseau (1994) also reported that CO₂ generally contributes to an extra root storage rather than shoot storage, especially in experiments where pots do not constrict root growth. This response appears to be species dependent; however, as other studies have reported that CO₂ has no effect on root:shoot ratio (Hurd 1968, Sionit et al. 1985), and in some cases even induces a decrease (Wulff and Strain 1982, Tolley and Strain 1984b). In several experiments where trees were grown in nutrient poor soils, substantial increases in root:shoot ratios (Norby et al. 1986b, O'Neill et al. 1987) and fine root growth (Norby et al. 1986a, El Kohen et al. 1992, Mousseau and Saugier 1992) were observed. This response would benefit species by allowing them to explore larger areas in search of soil nutrients.

There appear to be many variables that can influence the effect of elevated CO₂ on plant growth. As previously mentioned, pot size and length of exposure are two influential variables. One five month study involving containerized loblolly pine seedlings exposed to elevated CO₂ reported that biomass was 59% higher than those grown at ambient levels (Thomas et al. 1994). In a similar study lasting 17 months the increase in biomass due to elevated CO₂ was only 33% (Strain and Thomas 1992). Differences are even more extreme in an experiment where loblolly

pine seedlings were grown in an abandoned field at elevated CO₂ levels for 19 months. Under these conditions, Tissue et al. (1995) reported that the increase in biomass due to elevated CO₂ decreased from 233% after one year to 111% after 19 months. As these results indicate, large initial increases in biomass are often reduced after extended exposure to elevated CO₂ levels (Tissue et al. 1995, Ceulemans and Mousseau 1994).

Experiments examining effects of elevated CO₂ on growth of individually grown loblolly pine seedlings have generally reported consistent results. Three such experiments ranging from 59 days to 19 months of exposure to doubled CO₂ reported that loblolly pine total biomass, stem weight, leaf weight and root weight were all significantly higher under elevated levels than they were under ambient levels (Sionit et al. 1985, Tschaplinski et al. 1993, Tissue et al. 1995). Each of these studies also reported slight decreases in root:shoot ratios, but the differences were not significant.

Studies of individually grown sweetgum seedlings have shown similar responses to elevated CO₂. Tolley and Strain (1984a & b) reported that height, basal stem diameter, total biomass, stem weight, leaf weight and root weight were all significantly higher under elevated levels than they were under ambient levels. Both of these studies also found slight decreases in root:shoot ratios, but again, the differences were not significant.

Effects of water

The main effect of water stress on plants appears to be through its influence on stomatal aperture and growth, with stomata generally being the main limiting factor to carbon uptake in most species (Chaves and Pereira 1992). Furthermore, these effects seem to be greatest when there are other contributing factors (i.e. high light and high temperature) which cause an increase in photoinhibition, and as a result decrease quantum yield (Chaves and Pereira 1992). It also appears that water stress effects the photosynthetic capacity of older leaves more than expanding leaves (Chaves and Pereira 1992), so the timing of water stress can be an influential factor as well.

Davies et al. (1989) reported that plants often respond to water stress by partitioning biomass to root systems. In spite of this partitioning, many studies have shown a decrease in root systems when under water stress. Tschaplinski et al. (1993) found that water stress caused a 45% and 32% decrease in loblolly pine root and shoot dry weight, respectively. These authors also reported that stem and dry needle weight significantly decreased and root:shoot ratios decreased, although not significantly, under water stressed conditions. Other studies have also concluded that root and shoot dry weights decreased as a result of water stress, with the shoots generally affected more than the roots (Seiler and Johnson 1985, Bongarten and Teskey 1987). Groninger et al. (1993) observed slight decreases in

average stem volume of water stressed loblolly pines, but this change was not significant. While low soil moisture is generally a hindrance to sweetgum establishment (Ceulemans and Mousseau 1994), Tolley and Strain (1985) found no significant changes in growth as a result of withholding water until total plant water potential reached -2.5 MPa. Groninger et al. (1993) reported significant decreases after one growing season in average stem volume of water stressed sweetgums. After two growing seasons in a study of similar design, root, shoot and total biomass increased 36, 73 and 33% respectively, under the higher levels of water availability (Groninger et al. 1995).

Interactions of CO₂ and water

It appears that increases in biomass due to elevated CO₂ levels can offset the negative effects of water stress. As previously stated, stomata play an important role in the effects of water stress on plant growth. The effect of CO₂ on stomates is equally significant, and may help to counteract plant losses due to water stress. It has been reported that elevated CO₂ results in a partial closing of stomates, and this in turn reduces water loss through transpiration (Kimball et al. 1993). Morison (1987) did not find any significant differences in stomatal conductance between C₃ and C₄ plants when reviewing the effects of CO₂ enhancement, suggesting that both groups of species could derive similar amounts of drought tolerance from elevated CO₂ (Kimball et al. 1993). In addition, dry matter production in water stressed plants grown under elevated CO₂ has been shown to increase to the same extent as non-water stressed plants grown under ambient levels (Morison 1993). This could have a significant influence on species distribution in the future.

Studies of loblolly pine responses to elevated CO₂ and water availability have not shown any significant interactions between these two factors (Tolley and Strain 1985, Tschaplinski et al. 1993, Groninger et al. 1993, 1995 and 1996). Tolley and Strain (1985) did report that under elevated CO₂ levels, water stress had less of an effect on dry matter production than in controls. Groninger et al. (1995 and 1996) reported growth increases of 5 to 9% in water stressed loblolly pines grown under elevated CO₂. Growth of water stressed sweetgum seedlings in elevated CO₂ have shown significant increases, 48 to 50%, over water stressed seedlings grown at ambient levels (Groninger et al. 1995 and 1996). Tolley and Strain (1985) also reported that elevated CO₂ delayed the effects of water stress on plant water potential by as much as six days, leading the authors to conclude that establishment of sweetgum stands could be more prevalent on dryer sites in the future.

Competition

All species growing in natural ecosystems will have to compete with other species for nutrients and sunlight throughout most of their life cycles. The rapid

growth of herbaceous species, both above and below ground, is a vital part of their competitive strategy that enables them to propagate and dominate many landscapes. The influence of herbaceous and woody species on loblolly pine growth has been examined in several studies, and results have shown strong competitive interactions that negatively effect loblolly pine growth as early as the first growing season after planting (Nelson et al. 1981, Morris et al. 1989, Perry et al. 1993). The Perry et al. (1993) study examined the first year growth response of 1:0 loblolly pine seedlings when competing with different densities of sweetgum and broomsedge sprouts. The results indicated that loblolly pine stem volume (height x diameter²) was significantly reduced by the beginning of May when competing with sweetgum, and by the beginning of June when competing with broomsedge. After this time, the amount of variation in loblolly pine growth due to competition increased, as did the magnitude of the response (Perry et al. 1993). Morris et al. (1989) reported similar findings. The Perry et al. (1993) study also found that while low densities of competition greatly decreased loblolly pine stem volume, the effect was lessened as density increased. Loblolly pine stem volume was decreased 60% when competing with 4 broomsedge/m², but only decreased an additional 22% when competing with 16 broomsedge/m². When competing with one sweetgum/m², loblolly pine stem volume was decreased 75%, but only decreased an additional 4% and 16% when competing with 2 and 4 sweetgums/m², respectively.

Significant competitive interactions between loblolly pine and both herbaceous and woody species is not just limited to the first year after planting. In a three year study of loblolly pine seedlings grown in Virginia, Bacon and Zedaker (1987) found that herbaceous vegetation had the greatest impact on tree growth during the first two growing seasons. While the survival rate of the young trees was not significantly reduced by herbaceous competition after three years, tree height and ground line diameter were significantly greater in plots not competing with herbaceous species. This and other studies (Miller et al. 1991, Weiner and Thomas 1992, Holbrook and Putz 1989) have also reported that competition reduces diameter more than height growth. While the mechanism for this is not completely understood, it is believed to be due to a phytochrome response (Perry et al. 1993).

The influence of herbaceous vegetation on tree growth is generally not a factor once a tree becomes well established. While this time period will vary between species, Clason (1978) found that herbaceous control in the seventh year did not significantly enhance loblolly pine growth. In another study, Miller et al. (1991) examined the influence of both herbaceous and woody competition on loblolly pine growth during the first five years after planting. Fourteen locations within the southeastern US received treatments controlling either woody species, herbaceous species or both herbaceous and woody species. Average increases in pine volume after five years were 67%, 171% and 424% for the woody, herbaceous and total control treatments, respectively. While competition with herbaceous species decreased loblolly pine volume more than woody species during the first five years,

the competitive effect of woody species was becoming more of a factor by the end of the study.

Effects of CO₂

In order to predict the growth and development of future ecosystems, it is necessary to understand how elevated CO₂ levels will effect inter and intra-specific competition. Unfortunately, the majority of information available on plant responses to elevated CO₂ is based on individually grown species (Bazzaz and McConnaughay 1992). Results from these experiments have led to the popular assumption that C₃ plants will gain a competitive advantage over C₄ plants, thus altering the complexion of future ecosystems (Kimball et al. 1993, Patterson and Flint 1990). Several studies involving competitive arrays have given credence to this assumption. In a study by Wray and Strain (1987), *Aster pilosus* (C₃) and *Andropogon virginicus* (C₄) were grown individually and in competitive arrays under elevated CO₂ levels. The authors found that biomass of *Aster pilosus* was significantly greater when grown in competition with *Andropogon virginicus* than when grown in monoculture. Furthermore, biomass of *Andropogon virginicus* was smaller when grown in competition with *Aster pilosus* than when grown in monoculture. Studies by Carter and Peterson (1983) and Patterson et al. (1984) have reported similar findings. Bazzaz and Garbutt (1988) studied the responses of two C₃ and two C₄ species grown in all possible combinations under elevated CO₂ levels, and concluded that biomass of C₄ species was suppressed in the presence of C₃ species more than when grown with only C₄ species.

The rather simplistic view that C₃ species will dominate C₄ species does not, however, hold up over the vast range of competitive systems. Zangerl and Bazzaz (1984) found that in six-species mixtures grown under elevated CO₂ levels, biomass was greater in two of the C₃ species, but remained unchanged in the other C₃ and C₄ species. These results suggest that plant responses to elevated CO₂ may be strongly density dependent (Stewart and Potvin 1996). While the reasons for this are not completely understood, sub-ambient CO₂ levels have been reported in dense stands (Yabuki et al. 1967, Reicosky 1989) suggesting that individual leaf surfaces may not benefit from elevated CO₂ as much as others in dense stands (Bazzaz and McConnaughay 1992).

Loblolly pine seedlings have shown varying responses to competition when grown under elevated CO₂ levels. When grown with red maple (*Acer rubrum*) seedlings, total and stem biomass of loblolly pine seedlings significantly increased when compared to growth in monocultures (Groninger et al. 1996). This study also found that height to diameter ratios in mixed stands were significantly lower than in the monocultures. When grown in competition with sweetgum seedlings, however, loblolly pine seedling root, shoot and total biomass decreased 33, 27 and

28% percent, respectively, compared to monocultures (Groninger et al. 1995). In this same study, sweetgum seedling root:shoot ratio and shoot biomass significantly increased in mixed stands versus monoculture. In a similar study, total yields were not significantly different between monocultures of sweetgum and loblolly pine versus mixed 50:50 stands, regardless of CO₂ concentration (Groninger et al. 1993).

Effects of water

The effect of water on competition is highly dependent on the species involved. Under drought conditions, C₄ species generally have an advantage over C₃ species since stomatal closure due to water stress can lead to photoinhibition in C₃ species. In addition, species with high water use efficiencies (WUE) will be more competitive in dry environments than those with a lower WUE (Carlson and Bazzaz 1980). In a competitive study involving three C₃ and one C₄ species, Bazzaz and Carlson (1984) found that the heights of all four species were taller in a moist treatment than in a dry treatment. Additionally, the C₄ species, *Amaranthus retroflexus*, responded best in the dry soil treatment. This same response was reported for C₄ species in a simulated grassland community (Campbell et al. 1995).

Studies involving mixed stands of loblolly pine and sweetgum seedlings have indicated that sweetgum is more competitive than loblolly pine on wet sites, but neither species gains a competitive edge on dry sites. Groninger et al. (1993 and 1995) grew loblolly pine and sweetgum seedlings in 50:50 competitive arrays, and reported that loblolly pine had a higher, although non-significant, growth rate when compared to monocultures. The proportion of each species in the drought treatment, however, was nearly equal. Under well watered conditions, height of the sweetgum seedlings in the mixed stand was nearly twice as high as those grown in monoculture. Furthermore, the sweetgums were dominant in the mixed stands under well watered conditions.

Interactions of CO₂ and water

The interaction of CO₂ and water has been shown to induce opposite responses in C₃ and C₄ species when grown in competitive arrays. In the study by Bazzaz and Carlson (1984) the contribution of *Amaranthus retroflexus* (C₄) to community biomass decreased as CO₂ levels increased in the dry treatment. *Polygonum pensylvanicum* (C₃), on the other hand, was able to increase its contribution to community biomass in the dry treatment to a level that was similar to what it achieved in the well watered treatment at ambient levels. Campbell et al. (1995) found that C₃ species in their grassland community study reacted more favorably than C₄ species under well watered conditions at elevated CO₂. Following a simulated drought, however, the C₄ species significantly became the dominant contributor to the community.

No significant CO₂ x water interactions have been found for loblolly pine/sweetgum or loblolly pine/red maple competitive stands (Groninger et al. 1993, 1995 and 1996). Groninger et al. (1993) did find that stem biomass of sweetgums significantly increased under well watered and elevated CO₂ conditions when competing with loblolly pines. A trend was also observed where loblolly pine appeared to gain a competitive advantage over sweetgums under elevated CO₂ and low water conditions (Groninger et al. 1993, Burdick 1996). Another study of similar design, however, showed that elevated CO₂ and dry conditions did not affect the growth of either species in competitive arrays (Groninger et al. 1995).

Seed germination and emergence

Studies involving the influence of elevated CO₂ on vegetative growth have been primarily concerned with growth responses following emergence from the soil. Few studies have actually examined the influence of elevated CO₂ on seed germination and seedling emergence. Part of the reason for this may be that seeds often experience subsurface CO₂ concentrations between 2500 and 7000 ppm (Ziska and Bunce 1993). However, many seeds lay near the soil surface where CO₂ concentrations are close to those in the ambient air above (Ziska and Bunce 1993).

St. Omer and Horvath (1983) examined the germination response of three winter annuals under ambient (300ppm) and elevated (700, 1400, and 2100 ppm) CO₂ levels. Nondormant six month old seeds were placed in a mixture of vermiculite and pumice and exposed to natural lighting and temperature that was consistent with their native habitat. The results of this study were that elevated CO₂ levels did not have a significant effect on seed germination for any of the species.

In another study, Ziska and Bunce (1993) evaluated seed germination and emergence for individually grown crop and weed seeds under elevated CO₂ (700 ppm). The results indicated that only one (alfalfa) of the six crop species had a significantly greater germination percentage compared to the controls. None of the crop species had significantly different emergence percentages compared to the controls. Three of the four weed species had a significantly greater germination percentage, and two of the four had a significantly greater emergence percentage. This experiment was conducted entirely in plastic trays, so comparisons with natural conditions can not be made. Ziska and Bunce (1993) also studied seed germination and emergence from soil in outdoor open-top CO₂ chambers. After rototilling the soil to remove all standing weed biomass, plots were exposed to elevated CO₂. After three weeks, the number of emerged weeds was compared to control plots. Results indicated that elevated CO₂ caused a significant increase in the number to emerged weeds. Of the most predominant weeds counted, the number of grasses (not separated by species) and *Amaranthus* spp. present was significantly greater than the control plots. The three other most abundant species (*Chenopodium album*, *Portulaca oleracea* and *Lepidium virginicum*) increased in

elevated CO₂, but not significantly. These results led the authors to conclude that elevated CO₂ levels could cause changes in the germination and emergence of crops and weeds. A questionable assumption in this study was that the weed seeds were equally distributed across the different plots. One interesting finding in this study was that changes in germination and emergence occurred primarily with the smaller seeds. The authors concluded that smaller seeds could have a larger surface to volume ratio, resulting in a greater diffusion capacity for CO₂ (Ziska and Bunce 1993).

METHODS AND MATERIALS

Soil

Two separate experiments, each with the goal of simulating the regeneration of a post drum chop and burn Piedmont site, were conducted in a greenhouse on the Virginia Tech campus. Soil (Tatum series, Clayey, mixed, thermic Typic Hapludults) was randomly collected across three recently chopped and burned sites in the Piedmont region near Appomattox, Virginia. Approximately 200 dm³ of subsoil and 32 dm³ of topsoil was 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 each experiment to prevent native weed seed germination.

Seedling culture - Experiment I, Loblolly Pine

1:0 loblolly pine seedlings, obtained from the Virginia Department of Forestry, were used for this study. Seedlings were kept in cold storage (2° C) until the start of the experiment to sustain dormancy. In order to mimic a typical Piedmont growing season, this experiment began April 5, 1997 and ended on August 28, 1997, when some of the weeds were going through natural senescence. At the start of the experiment approximately 7.5 dm³ of subsoil and 1.2 dm³ (approximately 2.5 cm) of topsoil were stratified in plastic containers (24 cm in diameter, 23 cm deep, approximately 10.4 dm³). Soil was saturated with water and one loblolly pine seedling was planted in the middle of each container. Seedlings were then moved into chambers for CO₂ and water treatments.

Seedling culture - Experiment II, Sweetgum

Sweetgum seeds obtained from a commercial vendor (FM Schumaker, Sandwich, MA) were sown in a flat in January 1997, germinated and allowed to grow for one month. The seedlings were then transplanted into D40 containers (6.4 cm in

diameter, 25 cm deep, approximately 0.8 dm³) (Stuewe & Sons, Inc., Corvallis, OR) with a 50:50 peat moss/sand mixture. After transplanting, three grams of 15:10:10 slow release fertilizer (Grace Sierra General Purpose, Milpitas, CA) was added to each container. Seedlings were repotted July 7, 1997 into plastic containers (24 cm in diameter, 23 cm deep, approximately 10.4 dm³) containing 7.5 dm³ of subsoil, and received 100 ml of 200 ppm N, 87 ppm P and 166 ppm K as 20:20:20 water soluble fertilizer (Peters General Purpose, Fogelsville, PA). Seedlings were then grown through the fall so that a large root system could develop, and normal patterns of leaf senescence and carbon storage to the root system could take place. On November 26, 1997, following leaf senescence, 0.9 dm³ (approximately 2 cm) of top soil was added and seedlings coppiced by cutting the stems approximately 2.5 cm above the soil line. Seedlings were then moved into chambers for CO₂ and water treatments. Supplemental sodium vapor lighting was used in order to simulate 16 hour photoperiods. This experiment ended on February 12, 1998, when some of the weeds were going through natural senescence and seed set.

CO₂ treatments

Two growth chambers, 0.91m x 1.07m x 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 CO₂ to a chamber, pure (99.99%) liquid CO₂ was injected into blower air before entering the chamber. In order to eliminate variability caused by different chambers, containers and CO₂ treatments were rotated between chambers weekly. The design for air flow, CO₂ flow, and measuring systems are fully described by Samuelson and Seiler (1993). Air for each chamber was sampled on a time shared system for ten minute periods three times each hour. CO₂ concentrations were measured with an infrared gas analyzer (ADC Mk III, Hoddeson, England) and strip chart recorder.

The ambient treatment for Experiment I had a daily mean of 357 (\pm 33 standard deviations) ppm CO₂ and a nightly mean of 404 (\pm 27) ppm CO₂. The elevated treatment for this experiment had a daily mean of 660 (\pm 41) ppm CO₂ and a nightly mean of 736 (\pm 46) ppm CO₂. The ambient treatment for Experiment II had a daily mean of 408 (\pm 16) ppm CO₂ and a nightly mean of 411 (\pm 17) ppm CO₂. The elevated treatment for this experiment had a daily mean of 668 (\pm 41) ppm CO₂ and a nightly mean of 688 (\pm 50) ppm CO₂.

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 in Experiment I were 26.4° C (\pm 4.8 standard deviations) and 56.0% (\pm 10.7), respectively, during the day, and 23.4° C (\pm 4.2) and 61.2% (\pm 11.5) at night. Mean

temperature and RH of the elevated treatment in this experiment were 26.4° C (\pm 4.5) and 57.8% (\pm 8.1), respectively, during the day, and 23.8° C (\pm 4.6) and 62.9% (\pm 9.7) at night. The mean temperature and RH of the ambient treatment in Experiment II were 23.8° C (\pm 2.7) and 37.7% (\pm 12.9), respectively, during the day, and 22.9° C (\pm 3.1) and 38.0% (\pm 14.9) % at night. Mean temperature and RH of the elevated treatment in this experiment were 23.7° C (\pm 2.7) and 37.1% (\pm 10.0), respectively, during the day, and 22.1° C (\pm 2.7) and 36.8% (\pm 12.8) at night.

Water treatments

Water stressed (600 ml H₂O/week) and well watered (1200 ml H₂O/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 - approximating 1.27 cm and 2.54 cm of water per week, respectively.

Biomass determinations and measurements

In order to determine the influence of treatments on herbaceous community development and tree growth, all species were destructively harvested at the end of each experiment. Weeds were separated by genus (i.e. *Panicum spp.*) and CO₂ fixation biochemistry (C₃ or C₄). Dry biomass of weed roots and tops was determined and compared, as was dry biomass of roots, leaves and shoots of loblolly pine and sweetgum. Beginning and ending loblolly pine height above root-collar and dry biomass of sweetgum shoots prior to coppicing were also determined for use as possible covariates in the analysis. Root:shoot ratio for both experiments was determined by dividing dry root biomass by dry shoot biomass for each seedling. Experiment II also included a root:shoot ratio determined by dividing dry root biomass by dry shoot + dry stump biomass.

Sweetgum leaf area was measured with a LI-COR Area Meter (LI-COR Inc., Lincoln, Nebraska). Three measurements were taken and averaged in order to estimate total leaf area for each seedling. Specific leaf area (SLA) was calculated by dividing each leaf area estimate by the corresponding dry leaf weight.

Water potential was measured immediately prior to the final harvest in each experiment. Five seedling were randomly selected from each treatment and foliage was measured using a pressure bomb (PMS Instruments Inc., Corvallis, OR).

Experimental design and analysis

Each experiment was conducted as a factorial experiment in a completely randomized design, with CO₂ 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 within chambers (i.e. shade effects). Containers and CO₂ treatments were also rotated between chambers once a week in order to average out any differences across treatment combinations (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. All statistical information 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 distribution (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 always considered significant at $p \leq 0.05$. All p -values are presented and values of $p \leq 0.1$ are noted and discussed when appropriate.

RESULTS - EXPERIMENT I

Water potential

Water potential measurements at final harvest were significantly lower in the water stressed treatment (-2.17 MPa) than in the well watered treatment (-1.66 MPa). Measurements for the CO₂ treatments were significantly lower in the elevated treatment (-2.06 MPa) than in the ambient treatment (-1.77 MPa). There was no significant CO₂ and water interaction.

Loblolly pine biomass

Diameter and height growth

Loblolly pine height and diameter were both significantly greater 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 CO₂ treatments for either height or diameter at a p -value of 0.05; however, height was significantly different at $p = 0.086$, with an increase of 9% in the elevated treatment compared to the ambient treatment. No CO₂ and water interactions were detected.

Root, shoot, needle, and total biomass and root:shoot ratio

Root biomass was significantly larger (33%) in the elevated treatment than the ambient treatment (Table 1). There were no significant differences between water treatments, and no CO₂ and water interaction.

Table 1. Loblolly pine seedling diameter, height, needle, root, shoot and total biomass responses to CO₂ and water treatments. Numbers in parentheses indicate treatment *p*-values.

<u>Treatment</u>	<u>Diameter</u> (mm)	<u>Height</u> (cm)	<u>Needle</u> (g)	<u>Root</u> (g)	<u>Shoot</u> (g)	<u>Total</u> (g)
<u>CO₂</u>						
Ambient	7.93 (.114)	35.46 (.086)	9.23 (.076)	4.17 (.014)	5.29 (.017)	18.69 (.019)
Elevated	8.49	38.52	10.67	5.53	6.52	22.73
<u>Water</u>						
Water Stressed	7.74 (.009)	33.44 (.001)	8.52 (.001)	4.94 (.736)	5.12 (.003)	18.57 (.014)
Well Watered	8.68	40.54	11.38	4.76	6.70	22.85

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 CO₂ treatment than the ambient CO₂ treatment, with increases of 23% and 22%, respectively. Needle biomass was significantly greater in the elevated treatment at $p = 0.076$. None of the variables had a significant CO₂ and water interaction.

There was a significant CO₂ and water interaction for root:shoot ratio (Table 2). Under elevated CO₂, loblolly pine root:shoot ratio was significantly greater (80%) 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.

Weed biomass

Total and species biomass

Total weed biomass was significantly greater (433%) in the well watered treatment than in the water stressed treatment (Table 3). There were no significant differences between the CO₂ treatments, and no CO₂ and water interaction.

Water treatment had a significant influence on the total biomass of C₃ and C₄ weeds, with respective increases of 832% and 230% in the well watered treatment compared to the water stressed treatment (Table 3). There were no significant differences between CO₂ treatments and no CO₂ and water interactions for either variable.

The percentage of biomass that the C₃ and C₄ weeds contributed toward total weed biomass was influenced by treatment level; however, differences were not significant at a p -value of 0.05 (Table 4). C₄ weeds contributed 66% of the total biomass in the water stressed treatment, but only 41% in the well watered treatment. Under the ambient treatment, C₄ weeds contributed 53% of the total biomass, but their contribution decreased to 35% under the elevated treatment, an overall 33% reduction ($p = 0.098$). There were no CO₂ and water interactions.

The three most dominant weeds, in terms of contribution to total biomass were *Erechtites spp.*, *Panicum spp.* and *Phytolacca spp.* (Table 4). *Panicum spp.* (a C₄ weed), *Erechtites spp.* and *Phytolacca spp.* (C₃ weeds) combined to make up 80% and 78% of the total weed biomass in the ambient and elevated treatments, respectively. *Panicum spp.* contributed 46% to total weed biomass in the ambient treatment, but only 28% in the elevated treatment. Under the water stressed treatment, *Panicum spp.* contributed 56% to the total weed biomass, but only 35% in the well watered treatment.

Table 2. Loblolly pine root:shoot ratio response to CO₂ and water treatment. Numbers in parentheses indicate within CO₂ treatment by water treatment *p*-values.

<u>CO₂</u>	<u>Water Stressed</u>	<u>Well Watered</u>
Ambient	0.78 (.939)	0.77
Elevated	1.17 (.001)	0.65

Table 3. Total weed biomass and weed type responses to CO₂ and water treatments. Numbers in parentheses indicate treatment *p*-values.

<u>Treatment</u>	<u>Total</u> (g)	<u>C₃</u> (g)	<u>C₄</u> (g)
<u>CO₂</u>			
Ambient	2.42 (.148)	1.15 (.335)	1.27 (.098)
Elevated	1.89	1.23	0.66
<u>Water</u>			
Water Stressed	0.68 (.001)	0.23 (.001)	0.45 (.007)
Well Watered	3.63	2.14	1.49

Table 4. Treatment responses of individual weeds, expressed as percent contribution toward total weed biomass.

Weed Species	CO ₂ Treatment		Water Treatment	
	<u>Ambient</u>	Elevate d	<u>Water Stressed</u>	<u>Well Watered</u>
<u>C₄</u>				
<i>Acalypha spp.</i>	3.3	0.3	0.7	2.2
<i>Carex spp.</i>	0.7	2.2	2.1	1.4
<i>Cyperus spp.</i>	2.4	1.0	0.7	2.4
<i>Danthonia spp.</i>	0.0	2.5	6.8	0.0
<i>Panicum spp.</i>	46.2	28.3	55.5	35.0
<i>Poa spp.</i>	<u>0.1</u>	<u>0.4</u>	<u>0.4</u>	<u>< 0.1</u>
Total ¹	52.6	35.2	66.3	41.0
<u>C₃</u>				
<i>Antenaria spp.</i>	0.7	1.6	0.3	1.2
<i>Ceanothus spp.</i>	0.0	1.6	0.0	0.8
<i>Equisetum spp.</i>	0.0	0.4	1.1	0.0
<i>Erechitites spp.</i>	17.0	30.3	6.0	26.0
<i>Lechea spp.</i>	0.1	0.5	0.2	0.3
<i>Liriodendron spp.</i>	0.2	1.4	0	0.8
<i>Lysimachia spp.</i>	2.1	1.5	2.9	1.6
<i>Phytolacca spp.</i>	16.8	19.7	20.7	17.6
<i>Pinus spp.</i>	0.0	0.8	0.0	0.4
<i>Potentilla spp.</i>	0.0	2.2	0.0	1.1
<i>Rubus spp.</i>	8.3	1.9	1.8	6.2
<i>Solanum spp.</i>	1.2	0.0	0.0	0.8
<i>Solidago spp.</i>	0.2	2.0	0.0	1.2
<i>Stellaria spp.</i>	0.5	0.5	0.4	0.5
<i>Trifolium spp.</i>	0.1	0.1	0.3	< 0.1
<i>Vaccinium spp.</i>	0.3	0.0	0.0	0.2
<i>Viola spp.</i>	<u>0.0</u>	<u>0.6</u>	<u>0.0</u>	<u>0.3</u>
Total ¹	47.4	64.8	33.7	59.0

¹ Totals do not always equal the sum of the individual weed species due to rounding.

Total weed biomass affected total loblolly pine biomass but only explained 10% of the variability. The level of CO₂ and water treatments did not influence this relationship.

Root:shoot ratio, root and shoot biomass

Water treatment had a significant influence on C₃, C₄ and total weed shoot biomass, with increases of 1195%, 210% and 440%, respectively, in the well watered treatment compared to the water stressed treatment (Table 5). There was no significant difference between CO₂ treatments at a *p*-value of 0.05; however, total weed root:shoot ratio was significantly smaller in the elevated treatment at *p* = 0.097. There were no CO₂ and water interaction for any of these variables.

Total weed, C₃ and C₄ root biomass was significantly greater in the well watered treatment than the water stressed treatment, with increases of 424%, 601% and 267%, respectively (Table 5). Only CO₂ main effects on C₄ weed root biomass was significant, with a decrease of 53% in the elevated treatment compared to the ambient treatment. There were no CO₂ and water interactions.

Water and CO₂ treatments did not have a significant effect on total, C₃ and C₄ root:shoot ratios (Table 5). There were no CO₂ and water interactions for any of these variables.

DISCUSSION - EXPERIMENT I

The loblolly pine seedlings exhibited growth responses similar to those found in previous studies involving CO₂ and water treatments. Height and diameter were both higher (9% and 7%, respectively) in the elevated CO₂ treatment than the ambient treatment, but only height differences were significant. Sionit et al. (1985) reported non-significant increases in loblolly pine height and diameter after growing in monoculture for 8 months. Groninger et al. (1996), however, reported a significant increase (14%) in loblolly pine 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), Weiner and Thomas (1992) and Holbrook and Putz (1989) where competition affected 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 CO₂ treatments, because water is a more limiting factor than CO₂.

Table 5. Total weed, C₃ and C₄ weed shoot, root and root shoot ratio responses to CO₂ and water treatments. Numbers in parentheses indicate treatment *p*-values.

	Treatment			
	CO ₂ Level		Water Level	
	<u>Ambient</u> (g)	<u>Elevated</u> (g)	<u>Water stressed</u> (g)	<u>Well Watered</u> (g)
<u>Total Weed</u>				
Shoot	1.30 (.663)	1.50	0.38 (.001)	2.07
Root	1.42 (.158)	0.74	0.30 (.001)	1.56
Root:shoot	0.98 (.097)	0.64	0.72 (.411)	0.89
<u>C₃</u>				
Shoot	0.53 (.386)	0.72	0.09 (.001)	1.16
Root	0.62 (.613)	0.51	0.14 (.001)	0.98
Root:Shoot	1.25 (.214)	0.79	0.90 (.519)	1.14
<u>C₄</u>				
Shoot	0.78 (.157)	0.43	0.29 (.015)	0.91
Root	0.50 (.044)	0.24	0.16 (.002)	0.58
Root:Shoot	4.17 (.878)	4.83	4.22 (.896)	4.78

The water and CO₂ treatments resulted in significant increases in loblolly pine needle, shoot and total biomass in both the elevated CO₂ treatment and the well watered treatment. These findings were also reported by Groninger et al. (1996), Sionit et al. (1985), Tschaplinski et al. (1993) and Tissue et al. (1995). 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 CO₂ 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 effected more than root biomass (Seiler and Johnson 1985, Bongarten and Teskey 1987). While no significant CO₂ and water interaction was detected for root biomass, a potential interaction ($p = 0.063$) was detected. Further investigating revealed that root biomass in the water stressed loblolly pine seedlings was 63% larger in the elevated CO₂ treatment than the ambient CO₂ treatment. This could result in an increased ability for loblolly pine to exploit resources when growing in dry conditions under elevated CO₂.

Root:shoot ratio showed a significant CO₂ and water interaction. This interaction is in contrast to findings by Tolley and Stain (1985), Tschaplinski et al. (1993) and Groninger et al. (1993, 1995 and 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 CO₂ resulted in a significantly larger root:shoot ratio for these seedlings.

Water availability had a much greater impact on total weed biomass than did CO₂ level. Both C₃ and C₄ species had significantly larger total biomass in the well watered treatment than the water stressed treatment. Water stress, however, favored the C₄ weeds while well watered conditions favored the C₃ weeds. These findings were also reported by Campbell et al. (1995).

The CO₂ 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 C₄ biomass under elevated CO₂. Total biomass of the C₃ weeds was 84% larger than C₄ weeds in the elevated treatment; however, when water was limiting under elevated CO₂, biomass was nearly equal in both weed types. While there was no significant CO₂ and water interaction, the combined effect of water stress and elevated CO₂ resulted in a 143% increase in total C₃ biomass and a 38% decrease in total C₄ biomass compared to the water stressed weeds under ambient CO₂ levels. Under well watered conditions, elevated CO₂ did not influence biomass of C₃ weeds, but resulted in a 52% decrease in C₄ weed biomass. Bazzaz and Carlson (1984) and Campbell et al. (1995) reported similar findings indicating that elevated CO₂ may benefit C₃ species more than C₄ species.

There were no significant treatment differences between the root:shoot ratios of either the C₃ or the C₄ weed species. Bazzaz et al. (1989) and Sionit et al. (1982) also did not find significant differences between weed root:shoot ratios when different weed types were competitively grown under elevated CO₂. There has been much variation in the response of weed root:shoot ratios in previous studies due to differences in experimental design. 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 C₃ and C₄ 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.

As has been found in previous studies by Morris et al. (1989), Perry et al. (1993) and Bacon and Zedaker (1987) weed biomass did have an effect on loblolly pine growth, but the level of CO₂ and water did not make a difference. The amount of variation explained by weed biomass was very low ($r^2 = .10$), and it appears that the loblolly pine seedlings benefited more from available resources than the weed species. There was no evidence that either the weed species or the loblolly pines became pot bound in this study, eliminating any potential variability caused by pot size.

CONCLUSIONS - EXPERIMENT I

The growth response of loblolly pine when competing with a native herbaceous community under elevated CO₂ and different levels of water availability was similar to previous studies involving loblolly pine and the same treatments. Total loblolly pine seedling biomass was significantly greater under the elevated CO₂ and well watered treatment levels. The well watered treatment resulted in significant increases in height and diameter. Height and diameter were both greater in elevated CO₂ than ambient CO₂, but only differences in height were significant. Unlike previous studies, there was a significant interaction between CO₂ 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 CO₂, due to a larger root biomass under elevated CO₂ 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 CO₂ levels.

Herbaceous weed community development was similar to other studies involving elevated CO₂ and different levels of water availability. Elevated CO₂ appears to favor C₃ weed community development, regardless of water availability. This suggests that weed community composition may shift towards C₃ plants in a future elevated CO₂ atmosphere.

Total biomass of the well watered weeds was significantly larger than the water stressed weeds. Elevated CO₂ did not result in more total weed growth. In fact, 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 true under elevated CO₂.

RESULTS - EXPERIMENT II

Water potential

Water potential measurements at final harvest were significantly lower in the water stressed treatment (-1.98 MPa) than in the well watered treatment (-1.27 MPa). Water potentials for the CO₂ treatments were not significantly different ($p = 0.977$). There was no significant CO₂ and water interaction.

Sweetgum biomass

Leaf area, specific leaf area (SLA), leaf and shoot biomass

Sweetgum leaf area, SLA, leaf and shoot biomass were all significantly greater in the well watered treatment than in the water stressed treatment, with increases of 89%, 8%, 77% and 80%, respectively (Table 6). Only CO₂ main effects on SLA were significant at a p -value of 0.05, with a decrease of 7% in the elevated treatment compared to the ambient treatment (Table 6). Sweetgum leaf biomass was significantly greater in the elevated treatment at $p = .074$. None of these variables had a significant CO₂ and water interaction.

Root:shoot ratios, root, total, stump and stump+shoot biomass

Root:shoot ratios (root biomass/shoot biomass and root biomass/(shoot biomass + stump

biomass)) were both significantly affected by the water treatments, with decreases of 38% and 15%, respectively, in the well watered treatment compared to the water stressed treatment (Table 7). Total and stump+shoot biomass were also significantly affected by the water treatment, with increases of 27% and 35%, respectively, in the well watered treatment compared to the water stressed treatment. Root and stump biomass were not significantly effected by the water treatments. There were no significant differences between CO₂ treatments for these variables at a p -value of 0.05. Sweetgum total, root, stump and shoot+stump biomass were all significantly greater in the elevated treatment at respective p -values of 0.065, 0.108, 0.107 and 0.073. There were no CO₂ and water interactions.

Table 6. Sweetgum seedling leaf area, specific leaf area (SLA), leaf and shoot biomass responses to CO₂ and water treatments. Numbers in parentheses indicate treatment *p*-values.

<u>Treatment</u>	<u>Leaf Area</u> (sq. cm)	<u>SLA</u> (sq. cm/g)	<u>Leaf</u> (g)	<u>Shoot</u> (g)
<u>CO₂</u>				
Ambient	1097.1 (.229)	274.3 (.021)	4.00 (.074)	1.81 (.184)
Elevated	1249.8	255.6	4.89	2.17
<u>Water</u>				
Water Stressed	811.1 (.001)	255.4 (.019)	3.21 (.001)	1.42 (.001)
Well Watered	1535.7	274.6	5.67	2.56

Table 7. Sweetgum seedling root:shoot ratios, root, total, stump, and stump+shoot biomass responses to CO₂ and water treatments. Numbers in parentheses indicate treatment *p*-values.

<u>Treatment</u>	<u>Root:shoot</u> ¹	<u>Root:shoot</u> ²	<u>Root</u> (g)	<u>Total</u> (g)	<u>Stump</u> (g)	<u>Shoot+Stump</u> (g)
<u>CO₂</u>						
Ambient	8.01 (.307)	3.66 (.543)	11.97 (.108)	19.34 (.065)	1.62 (.107)	3.40 (.073)
Elevated	7.18	3.51	13.95	22.93	1.86	4.06
<u>Water</u>						
Water Stressed	9.36 (.001)	3.87 (.022)	12.24 (.227)	18.63 (.010)	1.77 (.739)	3.18 (.004)
Well Watered	5.84	3.29	13.69	23.64	1.72	4.28

¹ Root:shoot ratio = root biomass/shoot biomass

² Root shoot ratio = root biomass/(shoot biomass + stump biomass)

Weed biomass

Total weed biomass was significantly greater (154%) in the well watered treatment than in the water stressed treatment at a p -value of 0.063 (Table 8). There were no significant differences between the CO₂ treatments, and no CO₂ and water interaction.

Water treatment had an influence on total C₃ and C₄ weed biomass, with respective increases of 173% and 88% in the well watered treatment compared to the water stressed treatment (Table 8). Neither response was significant at a p -value of 0.05; however, total C₃ weed biomass was significantly greater at $p = 0.065$. There were no significant differences between CO₂ treatments, and no CO₂ and water interactions for either variable. The contribution of C₃ weeds to total biomass was consistently greater than the contribution of C₄ weeds, accounting for approximately 80% of the total biomass in each treatment level (Table 9). The response of individual weed species to water and CO₂ was variable, and no apparent pattern was detected.

Only total shoot biomass of C₃ weeds was significantly affected by water availability, with a 76% increase in the well watered treatment compared to the water stressed treatment (Table 10). C₃, C₄ and total weed root and shoot biomass and root:shoot ratios were not affected by the CO₂ treatments and there were no CO₂ and water interactions.

Total weed biomass did not significantly effect total sweetgum biomass ($p = 0.81$) and only explained 0.2% of the variability. The level of CO₂ and water treatments did not influence this relationship.

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approximately 80% of the total biomass in each treatment level (Table 9). The response of individual weed species to water and CO₂ was variable, and no apparent pattern was detected.

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Table 8. Total weed biomass and weed type responses to CO₂ and water treatments. Numbers in parentheses indicate treatment p -values.

<u>Treatment</u>	<u>Total</u> (g)	<u>C₃</u> (g)	<u>C₄</u> (g)
<u>CO₂</u>			
Ambient	0.216 (.884)	0.184 (.762)	0.032 (.689)
Elevated	0.203	0.159	0.044
<u>Water</u>			
Water Stressed	0.119 (.063)	0.092 (.065)	0.027 (.418)
Well Watered	0.301	0.251	0.050

Table 9. Treatment responses of individual weeds, expressed as percent contribution toward total weed biomass.

Weed Species	CO ₂ Treatment		Water Treatment	
	<u>Ambient</u>	<u>Elevated</u>	<u>Water Stressed</u>	<u>Well Watered</u>
	----- % -----			
<u>C₄</u>				
<i>Carex spp.</i>	3.7	1.1	8.1	0.2
<i>Chenopodium spp</i>	0	11.7	0	7.9
<i>Cyperus spp.</i>	0.3	1.7	0	1.3
<u><i>Panicum spp.</i></u>	<u>11.1</u>	<u>7.2</u>	<u>14.3</u>	<u>7.2</u>
Total ¹	15.0	21.7	22.4	16.6
<u>C₃</u>				
<i>Barbarea spp.</i>	0	1.1	0	0.7
<i>Carduus spp.</i>	12.3	0	0	8.8
<i>Erechtites spp.</i>	0	0.7	0	0.5
<i>Erigeron spp.</i>	0.2	4.4	3.5	1.7
<i>Lespedeza spp.</i>	12.0	25.2	37.1	11.0
<i>Lotus spp.</i>	17.8	7.8	10.3	14.0
<i>Lysimachia spp.</i>	0	0.1	0	<0.1
<i>Oxalis spp.</i>	5.1	23.2	3.9	17.8
<i>Phytolacca spp.</i>	0	1.1	0	0.7
<i>Pinus spp.</i>	0.4	4.7	8.9	0
<i>Potentilla spp.</i>	3.6	0.8	0	3.1
<i>Pyxidanthaera spp.</i>	0	4.7	8.0	0
<i>Quercus spp.</i>	30.4	0	0	21.9
<i>Similax spp.</i>	3.3	0	6.0	0
<u><i>Solanum spp</i></u>	<u>0</u>	<u>4.7</u>	<u>0</u>	<u>3.1</u>
Total ¹	85.0	78.3	77.6	83.4

¹ Totals do not always equal the sum of the individual weed species due to rounding.

Table 10. Total, C₃ and C₄ weed shoot, root and root:shoot ratio responses to CO₂ and water treatments. Numbers in parentheses indicate treatment *p*-values.

	Treatment			
	CO ₂ Level		Water Level	
	<u>Ambient</u>	<u>Elevated</u>	<u>Water stressed</u>	<u>Well watered</u>
<u>Total</u>				
Shoot	0.148 (.936)	0.154	0.088 (.056)	0.214
Root	0.068 (.644)	0.049	0.030 (.178)	0.087
Root:shoot	0.338 (.792)	0.372	0.284 (.285)	0.425
<u>C₃</u>				
Shoot	0.121 (.946)	0.118	0.065 (.041)	0.173
Root	0.063 (.589)	0.041	0.027 (.219)	0.077
Root:Shoot	0.410 (.621)	0.338	0.330 (.547)	0.418
<u>C₄</u>				
Shoot	0.027 (.716)	0.036	0.023 (.470)	0.040
Root	0.005 (.594)	0.008	0.004 (.261)	0.010
Root:Shoot	0.094 (.538)	0.131	0.080 (.288)	0.145

DISCUSSION - EXPERIMENT II

Sweetgum root:shoot ratio and shoot biomass were not significantly affected by elevated CO₂. There was a small non-significant decrease in root:shoot ratio which was similar in magnitude to the findings of Sionit et al. (1985) in a study involving sweetgum seedlings and similar CO₂ treatments. Total, leaf, root, stump and shoot+stump biomass were all significantly larger in the elevated CO₂ treatment than the ambient treatment. These findings were also reported by Sionit et al. (1985), Tolley and Strain (1984 a & b) and Burdick (1996); however, the magnitude of differences in these studies was much greater than those found in the present study. This was especially true for total biomass. Coppicing may result in a dampening of the response to elevated CO₂ in sweetgum, at least in the initial growth stages after coppicing. This dampening is likely related to the amount of carbon reserves in sweetgum root systems prior to coppicing. The amount present will have a large influence on the response to coppicing, and could result in a smaller initial response to elevated CO₂.

Sweetgum SLA was significantly lower under elevated CO₂ than ambient CO₂, partly due to a 22% and 14% increase in leaf biomass and leaf area, respectively, under elevated CO₂. These findings are similar to those reported by Sionit et al. (1985) and Tolley and Strain (1984a), however the magnitudes are much less in the present study. Tolley and Strain (1984) attributed the decrease in SLA to increased leaf thickness and/or increased starch accumulations in the leaves.

Water availability significantly affected sweetgum growth, with increases in SLA, leaf area, total, shoot and leaf biomass and a decrease in root:shoot ratio under the well watered treatment. Burdick (1996) and Groninger et al. (1993), reported similar findings, but also reported a significant increase in root biomass under well watered conditions which was not found in this study. Previous studies by Groninger et al. (1995 and 1996), Tolley and Strain (1985) and Burdick (1996) involving sweetgum seedlings have also reported that water stressed seedlings increased biomass in elevated CO₂ to a greater extent than in ambient CO₂. This led the authors to conclude that establishment of sweetgum stands could be more prevalent on drier sites in the future. The present study does not support this conclusion for coppiced sweetgum sprouts. While water stressed sweetgums did have a greater biomass in elevated CO₂ than in ambient CO₂, it was only 9% greater and not significant.

Weed community development was significantly greater for C₃ weeds than C₄ weeds at all treatment levels, contributing approximately 80% of the total biomass. Analysis of weed community development is hampered by the limited number of weeds in this study. Under the ambient CO₂ treatment, *Quercus spp.* contributed 30.4% of the total biomass; however, *Quercus spp.* was found in only one container. Likewise, one *Chenopodium spp.* contributed over 50% of the total C₄ weed biomass

in the elevated CO₂ treatment. When analyzed with the *Quercus spp.* and *Chenopodium spp.* removed, the contribution of total C₄ weed biomass was 48% lower in

the elevated treatment compared to the ambient treatment. Total C₄ weed biomass was also 45% lower in the well watered treatment than the ambient treatment. The contribution of C₃ weeds to total weed biomass increased 13% in both the elevated treatment and the well watered treatment compared to the ambient and water stressed treatments, respectively. These species composition shifts under the different treatments are similar to those found in Experiment I. Total weed biomass, however, was nearly 90% less in Experiment II than in Experiment I, and the weed types present were considerably different. Since the soil in each of these studies was selected from the same mix, these differences must be related to senescence of weed seeds during extended cold storage and/or the longer photoperiod used in Experiment II.

CONCLUSIONS - EXPERIMENT II

Coppiced sweetgum sprouts responded to CO₂ by increasing biomass under the elevated treatment. Sweetgum seedling total, stump, shoot+stump, root and leaf biomass were all significantly greater in the elevated treatment than the ambient treatment. This agrees with previous findings involving sweetgum seedlings; however, the magnitude of the responses in this study was much less. This is possibly due to the fact that they were coppiced plants. Elevated CO₂ also caused a partitioning of biomass toward shoots, which resulted in smaller root:shoot ratios. CO₂ main effects were also significant for SLA, which was smaller under elevated CO₂ due to a greater partitioning of biomass to leaf weight than leaf area.

Water availability had a significant effect on growth, with the exception of root and stump biomass. SLA, leaf area, leaf, shoot and total biomass were significantly greater and root:shoot ratios were significantly smaller under well watered conditions than water stressed conditions. While these responses, as well as those under elevated CO₂, were smaller in magnitude than previous findings, it may be due to the coppicing of shoots prior to treatment exposure. A longer study is necessary in order to determine if this dampening effect will have long term implications.

Herbaceous community development did not have an effect on sweetgum growth, but this can be attributed to the limited number of weeds that germinated and became established. This is likely due to senescence of weed seeds during extended cold storage. As a result, an accurate analysis of herbaceous weed community development in this study is not possible.

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