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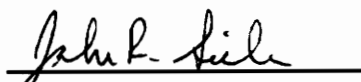
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Seasonal Effects of Elevated Carbon Dioxide, Competition, and Water Stress on Gas Exchange and Growth of Loblolly Pine and Sweetgum Grown In Open-top Chambers

by

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Forestry

(ABSTRACT)

Loblolly pine (*Pinus taeda*) and sweetgum (*Liquidambar styraciflua*) were grown in miniature stands at 7.6-cm spacings outdoors in open-top chambers (4.6 m in diameter and 3.5 m tall) for 16 months. Treatments consisted of ambient- and elevated-CO_2, drought-stressed and well-watered, and stand type (monoculture and 50:50 replacement mixture). Gas exchange was measured monthly, growth parameters bimonthly.

Loblolly pine carbon exchange rate (CER) was positive throughout the winter in all treatments and averaged 83% of summer rates. Between November 1994 and April 1995, relative crowding coefficient (RCC) of pine stem volumes increased regardless of CO_2 or water availability. RCC of pine biomass increased in

droughted stands relative to well-watered stands, while RCC of sweetgum showed the opposite response. Based on these results increased atmospheric CO_2 concentrations will not affect the competitive outcomes of loblolly pine and sweetgum mixed stands: loblolly pine will continue to be more competitive on dry sites, sweetgum on wet sites.

CER of loblolly pine and sweetgum, as well as soil respiration, were consistently significantly greater in elevated-CO_2 stands. CER in upper-canopy foliage was significantly greater than that of lower-canopy foliage for sweetgum. Loblolly pine, but not sweetgum, demonstrated a significant canopy position x CO_2 interaction, with upper-canopy CER greater only in elevated-CO_2 conditions. No consistent acclimation of CER to elevated CO_2 was statistically significant for either species, although acclimation response was stronger in sweetgum than in loblolly pine.

ACKNOWLEDGEMENTS

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

The CO_2 gradient between the atmosphere and chloroplasts is a driving force for carbon uptake in plants; for this reason, photosynthesis is often CO_2-limited under light-saturated conditions (Kramer and Kozlowski 1979, Kozlowski et al. 1991, Cropper and Gholz 1993). Therefore, doubling atmospheric CO_2 concentrations, expected by 2050, will likely have important effects on the physiology of trees (Eamus and Jarvis 1989, Kozlowski et al. 1991, Houghton et al. 1990).

Mousseau and Saugier (1992), Kimball et al. (1993), and Bowes (1993) report that elevated CO_2 concentrations commonly increased intercellular CO_2 partial pressure, increased photosynthesis, decreased photorespiration, and decreased dark respiration. These responses often result in increased net photosynthesis, although acclimation to high CO_2 levels frequently limited the enhancement (Eamus and Jarvis 1989). The causes and potential significance of this acclimation are poorly understood. It may result from changes in source/sink relations which limit photophosphorylation, reduced or damaged chloroplasts due to starch accumulation, or decreased activity or concentrations of Rubisco (Fetcher et al. 1988, Arp 1991,

1

Lewis et al. 1994). Whether acclimation will occur in field-grown trees is not known.

Concomitant changes in moisture regimes will also likely affect gas exchange in plants due to the impacts on stomatal conductance (Chaves and Pereira 1992, Tyree and Alexander 1993). Possible interactions between effects due to changes in CO_2 concentration and water availability could have important impacts on inter- and intraspecific competition (Bazzaz and Carleson 1984, Bazzaz and McConnaughay 1992, Groninger et al. 1995, Jifon et al. 1995).

Tolley and Strain (1985) found that response of carbon exchange rate (CER), the net photosynthetic assimilation of carbon, to increased water availability was higher in elevated-CO_2 conditions for individually-grown sweetgum (*Liquidambar styraciflua*) but not loblolly pine (*Pinus taeda*). The negative effect of water stress on CER was greater under low light levels for both loblolly pine and sweetgum. This suggests that lower-canopy foliage might have especially low CER in water-stress conditions. Although current silvics indicate that sweetgum is more competitive on wetter sites (Kormanik 1990) and loblolly on drier sites (Baker and Langdon 1990), Tolley and Strain (1985) concluded that competition between

2

loblolly pine and sweetgum may reverse in a future climate which might favor sweetgum on drier sites.

Groninger et al. (1993, 1995, 1996) found that photosynthesis of competitively grown loblolly pine and sweetgum seedlings increased under elevated CO_2. Groninger et al. (1996) reported lower photosynthetic rates per unit leaf area for whole-stand measurements than for upper canopy, excised, single-leaf measurements. The authors suggested that depressed whole-stand rates may be due to self-shading of seedlings grown at the close (2.54 cm) spacings, a particularly strong effect in the lower canopy. Design limitations prevented Groninger et al. (1995, 1996) from examining canopy-level differences in CER which might explain the whole-stand rates (Higginbotham and Strain 1973). In addition, the experimental design did not allow for winter photosynthesis by the pines. Data reviewed by Kozlowski et al. (1991) indicate that substantial differences in winter photosynthesis rates between evergreens and deciduous species could affect yields and competitive outcomes.

The study by Groninger et al. (1995) is one of the only experiments in which seedlings were grown competitively in

elevated CO_2 concentrations. While results of this project do yield important insights, there are also limitations in the experimental methods which must be addressed. The limited number of similar studies at small and intermediate scales prevents assessing how spacing affects competitive outcomes and seedling morphology. As a result, it is difficult to extrapolate results from small-scale stands to natural stands. In addition, the lack of a natural winter in the study by Groninger (1993) did not account for winter photosynthesis and growth in pines. Therefore, this study was designed to use outdoor, open-top chambers (OTCs) with the aim of answering several questions: Do different spacings of seedlings in miniature stands alter physiologic responses? Do loblolly pine seedlings gain any significant growth advantage as a result of their ability to photosynthesize during the winter when deciduous species lack foliage? What is the effect of shading on photosynthetic rates in the lower canopy? Does a decreased photosynthetic rate in the lower canopy explain depressed photosynthesis in whole-stand measurements relative to measurements on light-saturated single seedlings? The answers to these questions hold valuable information for the design and validation of experiments and models of global

climate change. Loblolly pine and sweetgum were selected for this study based on the economic importance of loblolly pine, the natural competition between the two species, and the large volume of work already published on both (Baker and Langdon 1990, Kormanik 1990).

In an effort to further understand the competitive responses of trees under elevated CO_2, this study proposed:

1. To determine how CO_2 concentrations, water stress, and competition affect gas exchange rates in loblolly pine and sweetgum at 7.6 cm spacings in outdoor, OTCs.

2. To characterize the pattern of seasonal carbon uptake in sweetgum and loblolly pine and to evaluate the significance of dormant season carbon uptake to growth and competitive outcome of loblolly pine.

3. To determine whether different photosynthetic rates in the lower and upper canopies of miniature stands of seedlings at 7.6 cm spacing explain depressed whole-stand measurements relative to measurements of single seedlings.

4. To compare relative yields of seedling stands planted outdoors in OTCs at 7.6 cm spacings to relative yields of seedlings grown indoors at 2.54 cm spacings.

LITERATURE REVIEW

Since the experiments of de Saussure in 1804, there have been many studies of the effects of elevated CO_2 on plant growth (Bowes 1991, Campagna and Margolis 1989, Kimball et al. 1993, Sage et al. 1989, and Stulen and den Hertog 1993). Most experiments have focused on plants grown individually. More recently, scientists have examined the effects of inter- and intraspecific competition on plant physiology (Bazzaz and McConnaughay 1992, and Reekie and Bazzaz 1989). It is now clear that interactions between CO_2 concentration, water availability, and competition are poorly understood. Current research suggests that different species respond differently to changing conditions, complicating the task of predicting ecosystem responses to a changing climate (Bazzaz et al. 1990, and Hollinger 1987).

Gas exchange rates

<u>Effects of CO_2</u>

As atmospheric CO_2 levels change, plants respond differently partly by altering their CER. Changes in CER may result from effects on photosynthesis, respiration, or a combination of the two. Excellent reviews have been published by Chaves and Pereira (1992), Mousseau and Saugier (1992), Kimball et al. (1993), and Bowes (1993). These sources make several general conclusions regarding CER: 1) although C_4 species are positively affected in some circumstances, C_3 are more commonly influenced by changes in CO_2 concentration; this difference results from increased intercellular CO_2 partial pressure and thus decreased photorespiration in the C_3 species 2) the initial carbon assimilation rate, or quantum yield, increases in C_3 species under higher CO_2 3) photosynthesis per unit leaf mass or leaf area may decrease even in comparison to initial ambient CER, yet biomass and yield may increase as a result of branching, increased leaf area and/or thickness, additional root growth, phenological changes, or increased numbers of mesophyll cells and/or chloroplasts. Pearcy and Bjorkman (1983) also cite increased state of activation of ribulose 1,5-bisphosphate

7

carboxylase/oxygenase (Rubisco) enzyme as an explanation for increased photosynthesis in elevated CO_2. Photorespiration was still significantly lower on *Scirpus olneyi* (C_3) after four years of exposure to elevated CO_2 (700 ppm) (Azcón-Bieto et al. 1994).

Another positive impact on CER due to elevated CO_2 is decreased stomatal conductance. Hollinger (1987) found that CER increased while stomatal conductance decreased significantly in Monterey pine (*P. radiata*), Douglas-fir (*Pseudotsuga menziensii*), and New Zealand red beech (*Nothofagus fusca*) between 310 ppm and 620 ppm CO_2. Such decreased stomatal conductance accompanied by increased CER results in large increases in plant water use efficiency (WUE) (Tyree and Alexander 1993).

Respiration may decrease in elevated CO_2, partially accounting for an increase in net photosynthesis (Ryan 1991, Mousseau and Saugier 1992). Norby et al. (1992) measured decreased leaf-level respiration rates and increased photosynthesis in yellow-poplar (*Liriodendron tulipifera*) saplings grown under high CO_2. Decreased leaf respiration was also found in white oak (*Quercus alba*) grown under elevated CO_2 (Wullschleger and Norby 1992). In sweet chestnut (*Castanea sativa*), shoot dark-respiration was significantly

8

lower in CO_2-enriched plants during the growing season, but the difference was negligible by fall (Mousseau 1993). Wullschleger and Norby (1992) point out that decreased leaf respiration may result from improved efficiency either in foliage production or from more efficient tissue and enzyme maintenance. Reuveni and Gale (1985) ascribe 80% of the decrease in total plant respiration to lower maintenance respiration of alfalfa (*Medicago sativum*) seedlings after short-term exposure to elevated CO_2. In white oak grown at 664 ppm CO_2 for three years, growth respiration and maintenance respiration decreased by 31 and 45 percent respectively (Wullschleger and Norby 1992).

The current average concentration of CO_2 in soil (>1000 ppm) is approximately three times the concentration of atmospheric CO_2, so direct effects on soil processes will likely change little even with doubled atmospheric levels (van Veen et al. 1991). Therefore, plant-soil responses, such as root respiration, will be responsible for much of the change in soil respiration rates. Poorter et al. (1988) measured short-term (3 weeks) increases in root respiration rates of *Plantago major* under CO_2-enriched conditions; stem respiration was not affected. Den Hertog et al. (1993), also studying *P. major*, found

no significant changes in root respiration as a result of CO_2 enrichment during the three-week experiment. Gifford et al. (1985) found long-term depressed root respiration rates in wheat (*Triticum* spp.) and increased root respiration in sunflowers (*Helianthus* spp.) grown at increased CO_2 levels. In shortleaf pine (*P. echinata*) seedlings, CO_2 concentration had no effect on the percentage of carbon lost in root respiration (Norby et al. 1987).

Shoot and root respiration in loblolly pine seedlings may be inversely related as suggested by Drew and Ledig (1981) who found that root respiration increased in the fall and winter. A similar relationship was demonstrated in *P. major* by Den Hertog et al. (1993).

Acclimation

Although increases in CER are commonly reported, long-term exposure to elevated CO_2 often leads to an acclimation, a downward shift in photosynthesis, transpiration, and growth rates (Eamus and Jarvis 1989). Research reviewed by Arp (1991) shows that photosynthesis rates may plateau or even drop relative to initial rates at elevated CO_2. In contrast, Gunderson et al. (1993) concluded that enhanced photosynthesis was sustained over three years in

yellow-poplar and white oak at 500 ppm and 650 ppm CO_2.
Groninger (1995) measured acclimation in loblolly pine but not in
sweetgum grown at 800 ppm CO_2 for 42 weeks.

The physiology of acclimation remains largely unexplained
although several hypotheses have been suggested. One theory is that
source/sink relations limit photosynthesis. Arp (1991) outlined this
process:

o increased photosynthesis and insufficient sink strength lead
to photosynthate accumulation in the leaves.

o excessive sucrose in the leaves causes a negative feedback
on enzymes responsible for sucrose production.

o changes in enzyme concentrations results in decreased
amounts of inorganic orthophosphate (P_i), causing
increased starch production.

o if P_i concentrations are forced low enough, the rate of
photophosphorylation is affected.

o photosynthesis is now limited by photophosphorylation rates
and not CO_2 or O_2 concentrations.

In addition, limited soil volume may decrease the carbon sink
strength, thereby depressing photosynthetic rates (Eamus and Jarvis

11

1989). Therefore, studies investigating the effects of elevated CO_2 on tree growth should carefully consider available rooting volume.

Arp (1991) mentioned three other possible agents of acclimation: i) starch accumulation in the leaf may damage chloroplasts and reduce chlorophyll ii) increased mesophyll thickness impinges upon CO_2 diffusion to chloroplasts iii) decreased activity and/or concentrations of Rubisco. Acclimation due to alterations of Rubisco activity and concentrations may be the result of changes in nitrogen allocation away from Rubisco or from phosphorous deficiency (Conroy et al. 1987, Chaves and Pereira 1992, Lewis et al. 1994)

Carbon source/sink relations differ significantly between seedlings and mature trees, making generalizations from seedling experiments tenuous; experimental design difficulties further complicate attempts to understand acclimation in mature trees (Mousseau and Saugier 1992). Eamus and Jarvis (1989) add that acclimation to gradual changes in global CO_2 levels may affects plants quite differently than sudden, experimental increases in CO_2.

Effects of water

The negative impact of water deficit on photosynthesis has been well documented (Kramer 1983, Chaves and Pereira 1992). The main effects of water stress on photosynthesis are most likely due to stomatal closure as stomata limit carbon uptake. The actual photosynthetic mechanism is usually quite resistant to irreparable damage due to low relative water content (Chaves and Pereira 1992). As stomatal conductance decreases, transpiration generally decreases (Eamus and Jarvis 1989). A review by Tyree and Alexander (1993) concludes that this decrease in transpiration is partially responsible for increases in WUE. Tolley and Strain (1985) found that gas exchange was significantly lower in water-stressed loblolly pine (14-day drying cycle) and sweetgum (10-day drying cycle) at ambient CO_2 levels.

Soil respiration is positively affected by increasing soil moisture but only to a point (Schlentner and van Cleve 1985). In aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), and black spruce plots (*Picea mariana*) plots, respiration reached a peak plateau between 150% and 250% soil moisture content.

13

Interactions of CO_2 and water

Combined effects due to increased CO_2 level and water-stress are complicated by decreased stomatal conductance resulting from both the increased CO_2 and decreased water levels. Although intercellular partial pressure of CO_2 (C_i) increases in general with elevated atmospheric CO_2, water-stressed plants will have a lower C_i than well-watered plants (Chaves and Pereira 1992). Tolley and Strain (1985) found that total plant water potential for stressed loblolly pine seedlings decreased gradually over time regardless of CO_2 level. However, the same experiment revealed that water potential in stressed sweetgum remained higher at increased levels of CO_2. For the seedlings in general, stomatal conductance and photosynthesis were also maintained longer at the higher CO_2 concentrations but still decreased as a result of prolonged water stress. Seedlings in this experiment were not grown in competition. Groninger et al. (1993) grew loblolly pine and sweetgum competitively in monoculture and 50:50 mixture. Results indicated that there was no water x CO_2 interaction effect on photosynthetic rates for either species.

Effects of light and shading

Groninger (1995) demonstrated a decreased CER of whole-stand measurements relative to measurements from single leaves. In a study of four co-occurring tree species, loblolly pine was most sensitive to shading; pines were more sensitive than hardwoods in general (Groninger 1995). Maximum photosynthesis, dark respiration, and light compensation point decreased by 26, 34, and 36 percent respectively for pine grown under 80 percent shade cloth for one growing season. Similar results on *P. major* indicate a significant, negative correlation between total leaf area and whole-plant photosynthesis (Poorter et al. 1988). Instead, projected leaf area (the area of the ground covered by canopy) is a better predictor of whole-plant photosynthesis.

Seasonal effects on CER

The possibility of positive CER in conifers during dormancy (Kozlowski et al. 1991) while deciduous species respire (negative CER) means that seasonal differences in CER could have important impacts on competitive outcomes between loblolly pine and sweetgum. Net CER of loblolly pine seedlings remained positive throughout the year in New Haven, CT, and in Durham, NC (McGregor

15

and Kramer 1963, Drew and Ledig 1981). Decreased photosynthetic rates associated with fall season were delayed in big-toothed aspen (*Populus grandidentata*) and in loblolly but not sweetgum by doubling the CO_2 concentration (Rogers et al. 1983, Curtis and Teeri 1992). Data gathered by Decker indicated that shoot respiration in loblolly pine increased from summer to winter but never exceeded photosynthesis (cf. McGregor and Kramer 1963). Chloroplasts in the twigs and bark of hardwoods, including sweetgum, allowed positive net photosynthesis during the winter when temperatures rose above 0°C for an hour (Perry 1971). Perry (1971) observed biomass increases of 42% and 68% for sweetgum and loblolly pine, respectively, between December 20 and April 1 near Raleigh, NC.

Growth

Effects of CO_2

Many studies of the effects of long-term CO_2 enrichment have shown an increase in plant growth relative to control plants (Eamus and Jarvis 1989). Mousseau and Saugier (1992) provided a summary of the major morphologic changes in plants due to CO_2 enrichment:

o   increase in leaf number, leaf area, and leaf weight per

plant. Leaf area increase may be due to more

numerous or larger cells.

o   higher specific leaf weight due to thicker leaves often

with a second layer of palisade cells.

o   increase (sometimes a decrease) in root/shoot ratio.

However, results vary considerably; biomass

partitioning is detailed below.

Although increase in leaf area due to greater carbon assimilation results in positive feedback, this cycle is self-limiting due to increased shading. Garcia et al. (1994) determined that the increase in foliar area, resulting mostly from an increase in number of needles, was responsible for a 50 percent increase in whole-tree photosynthesis. This enhancement was maximized in the CO2 treatment of 678 ppm; as the authors mentioned, the effect will be less important in competitive stands where shading from neighbors further limits whole-tree photosynthesis.

In loblolly pine and sweetgum seedlings, total biomass, root biomass, and shoot biomass increased significantly as a result of CO_2 enrichment (Groninger et al. 1993, Groninger et al. 1995). In the

same pine and sweetgum stands, very-fine root length density (RLD) increased insignificantly (Jifon et al. 1995). In mixed stands, RLD increased the most under resource-rich conditions where sweetgum RLD accounted for more than 75 percent of the total RLD. The authors concluded that below-ground competition between loblolly pine and sweetgum on rich sites will intensify in future conditions of elevated CO_2.

Elevated CO_2 led to greater translocation of photosynthate to fine roots, greater fine root:coarse root ratio, and increased mycorrhizal density in shortleaf pine (Norby et al. 1987). Increased growth of fine roots also occurred in yellow-poplar grown for three years under elevated CO2; despite sustained increases in photosynthesis and growth efficiency, there was no effect on above-ground mass, total root mass, root:shoot ratio, nor on tree morphology (Norby et al. 1992). The authors explain this lack of growth enhancement by the loss of carbon through turnover of increased fine root matter.

Tolley and Strain (1984a) found that sweetgum height, basal stem diameter, and leaf area increased 31, 20, and 44 percent respectively under elevated CO_2; however, there was little or no

effect on growth of loblolly pine due to CO_2 enrichment. In the same study, sweetgum dry weights increased by 73 percent while loblolly pine dry matter did not change significantly. For both species, the effects of CO_2 on growth decreased with prolonged exposure. Siniot et al. (1985) found that both sweetgum and loblolly pine seedlings increased their size and total weight significantly under elevated CO_2; sweetgum responded more quickly and maintained height dominance throughout the experiment. In addition, the number of branches per seedling increased significantly for sweetgum (122 percent) but not for loblolly pine. This differential response in morphology may result in important increases in self-shading for sweetgum, limiting productivity.

Rogers et al. (1983) measured growth of one year old loblolly pine and sweetgum raised in separate pots at ambient (612 ppm) [higher than current global ambient levels] and elevated (936 ppm) CO_2 for 10 weeks. Dry weights for pine stems and roots increased significantly under elevated CO_2; dry weights of sweetgum decreased slightly at 936 ppm. Stem diameter and wood density increased significantly while height and wood volume increased insignificantly for sweetgum exposed to high CO_2 levels. For loblolly pine, stem

diameter, wood volume, and height increased insignificantly while wood density decreased slightly at 936 ppm CO_2. Rogers et al. (1992) also found large increases in root growth (length, diameter, dry weight) of soybean, although the number of roots did not increase as the result of CO_2 fertilization. These authors also noted differential increase of lateral root length relative to taproot length. Increases in root length and volume imply greater sorption capacity. Increases in lateral root growth could have important impacts on competition between neighbors, particularly if these effects are species-specific. The fact that stem basal area and the cumulative root cross-sectional area are strongly correlated allows scientists to make conclusions about root growth based solely on stem diameter measurements (Carlson and Harrington 1987).

Under experimental conditions, the timing of onset of experimentally elevated CO_2 relative to the plant phenology may have a significant impact on plant growth (Campagna and Margolis 1989). Therefore, trees must be allowed to grow for more than one full year or results may be incomplete or misleading. For example, acclimation to near-freezing temperatures allowed loblolly pines to increase dry weights even during the winter (Perry 1971). This

suggests that pines may gain a competitive advantage over sweetgum by assimilating carbon throughout the year. Such an effect might become even more critical in an elevated-CO_2 atmosphere.

Effects of water

As previously discussed, water stress has many effects on plant physiology, most notably on stomatal conductance. In addition to a decrease in net photosynthesis, there are other effects of water stress on anatomy and physiology which alter plant growth. At ambient CO_2 levels, water-stressed loblolly pine showed a significant decrease in dry weights of shoots, stems, needles, and roots (Tschaplinski et al. 1993). Significantly decreased root growth (but not shoot growth) was also measured in loblolly pine (Seiler and Johnson 1985) and red spruce (*Picea rubens*) (Samuelson and Seiler 1993). Tolley and Strain (1984b) concluded that individually grown sweetgum seedlings had no significantly change in growth parameters as a result of water stress; growth of loblolly pine seedlings did decrease significantly during the recovery period following water stress. Loblolly pine growth did not respond

significantly to water availability while sweetgum growth was significantly reduced by drought treatment (Groninger et al. 1993).

Interactions of CO_2 and water

Under many circumstances, it appears that the gains due to CO_2 enrichment outweigh adverse effects of water stress; under elevated CO_2 and water-stressed conditions, plant growth will likely increase relative to well-watered plants grown at ambient CO_2 concentrations (Tolley and Strain 1984b, Bowes 1993, Kimball et al. 1993, Samuelson and Seiler 1993). Experiments have found no statistical interaction between water stress and CO_2 level in loblolly pine (Tschaplinski et al. 1993) nor in red spruce (Samuelson and Seiler 1993). In sweetgum monoculture, CO_2-induced increases in stand volume were significant only under droughted conditions; in competitive arrays with loblolly pine, sweetgum volume increases were significant only in well-watered treatments (Groninger et al. 1993).

Effects of light and shading

In a study of seven co-occurring tree species, beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), and hemlock (*Tsuga canadensis*), the three shade tolerant species studied, showed the

greatest growth response to elevated CO_2, suggesting that interspecific differences in growth response may be partly due to variation in shade tolerance (Bazzaz et al. 1990). There was no evidence that the age of seedlings affected the response to CO_2 levels.

The total biomass of loblolly pines grown under 80 percent shade cloth was only nine percent of the biomass of open-grown loblolly pines (Groninger 1995). In comparison, red maple (*A. rubrum*) and yellow-poplar maintained 48 and 47 percent growth under similar shading. Furthermore, stem height decreased for shaded loblolly pine and increased significantly for shaded yellow-poplar; white pine (*P. strobus*) and red maple did not change in height. Light reduction increased specific leaf area in all species. Growth differences in general increased during the second growing season. These results suggest that species-specific effects due to shading by neighbors could alter competitive outcomes differently at various spacings and over different durations. Consequently, studies of small-scale stands need to consider implications of both spatial as well as temporal effects.

Models of light interception indicate a linear relationship between photosynthetic active radiation (PAR) interception and

above-ground biomass in Monterey pine on fertile sites, regardless of thinning and light pruning (Grace et al. 1987).

Allocation

Allocation of photosynthates is usually measured as the dry-mass ratio of roots to shoots. Conclusions about the allocation of photosynthates under elevated CO_2 are conflicting (Stulen and Den Hertog 1993, Tyree and Alexander 1993). Effects due to CO_2 concentrations and water stress appear to be dependent on species, season, phenology, CO_2 concentration and exposure duration, and competition for light, water, and nutrients (Chaves and Pereira 1992, Eamus and Jarvis 1989, Farrar and Williams 1991, Jenkins 1974, Kolb and Steiner 1990, Kuhns and Gjerstad 1991a and 1991b, Mousseau and Saugier 1992, Schier 1970, Sionit et al. 1985). Comparisons among different experimental results are, therefore, difficult. However, some general trends do appear.

Effects of CO_2

In the experiments reviewed by Eamus and Jarvis (1989), increased CO_2 resulted in a decrease or no change in root: shoot ratio when nutrients were not limiting. Under nutrient-limiting

24

conditions, root: shoot ratios increased dramatically. Allocation to fine roots in particular may increase under elevated CO_2 conditions (Petterson and McDonald 1992, Norby et al. 1987, and Norby et al. 1992). An increase in root: shoot ratio may result from the balancing of a plant's needs to fix carbon and acquire nutrients. Under elevated CO_2, nutrients are more likely to be limiting than carbon; allocation of resources therefore goes toward root development (Norby et al. 1992).

Groninger et al. (1995), experimenting with competitive arrays of seedlings, reported no significant changes in total root: total shoot ratio of loblolly pine nor in sweetgum as a result of CO_2 level; in the same experiment, very-fine root: foliage mass ratio was not affected by CO_2 enrichment either (Jifon 1994). Groninger et al. (1995) suggested that competition for light might force resource allocation toward foliage even under CO_2-enriched conditions. For this reason, experiments using a competitive-stand design may yield valuable information about allocation and seedling allometry. Furthermore, measurements of canopy light extinction would allow for a quantification of light competition in pure and mixed stands.

Effects of water

Tolley and Strain (1984a) found that root: shoot ratios for sweetgum increased significantly at high CO_2 as a result of water stress. Allocation was not significantly changed for sweetgum at low CO_2 levels, nor were there any significant differences for loblolly pine. Root: shoot ratio decreased (Seiler and Johnson 1985) or was not affected by water stress (Tschaplinski et al. 1991) in loblolly pine seedlings. Water-stressed black alder (*Alnus glutinosa*) exhibited increased root: shoot ratio (Seiler and Johnson 1984). It is possible that water deficits, even in a high-CO_2 environment, could significantly alter not only biomass partitioning but also limit foliage display (Chaves and Pereira 1992). Kuhns and Gjerstad (1991b) found that loblolly pine sugar production increased at the expense of starch and structural compounds at increased levels of water stress; allocation of ^{14}C to roots and other sinks decreased in water stressed seedlings as the result of weakened sink strength.

Interactions of CO_2 and water

Carbon partioning may be more a function of interactions between CO_2 levels and other environmental variables, such as water and nutrient availability, than the result of effects of a single

parameter (Tolley and Strain 1984a, 1985, and Stulen and Den Hertog 1993). Tschaplinski et al. (1991) concluded that loblolly pine was unaffected by either CO_2 or water stress and that there were no interactions between these two treatments.

Effects of light and shading

Although red maple did allocate growth to leaves at the expense of roots, this did not occur in loblolly pine, white pine, nor in yellow-poplar (Groninger 1995). In both pine species, but neither hardwood, shading induced greater leaf weight: stem weight ratio. Only loblolly exhibited increased allocation to leaves relative to combined stem and root biomass. For trees grown in elevated CO_2 conditions, shading may limit the expected increase in root:shoot ratio, making water availability critical especially as increased leaf area raises transpiration rates.

Competition

Recent experiments have found significant differences between outcomes of individually-grown plants and plants grown in competition (Bazzaz and McConnaughay 1992, Groninger 1995). The effects of competition vary among species as a result of differences

in morphology, physiology, and neighbor identities (Bazzaz and Garbutt 1988, Reekie and Bazzaz 1989). However, congeneric neighbors may have similar responses to changes in CO_2 concentration, minimizing changes in competitive outcomes (Rochefort and Bazzaz 1922). Competitive outcomes may also differ due to main effects and interactions of CO_2, moisture availability, and stand composition (Groninger et al. 1993, Shainsky and Radosevich 1986, Williams et al. 1986).

Groninger et al. (1993, 1995) and Jifon et al. (1995) grew loblolly pine and sweetgum seedlings in 5 x 5 competitive arrays (monoculture and 50:50 mixture) at 2.54-cm spacings. Although the design they used allows for measurements of tree physiology under controlled conditions, the authors acknowledge that differences in scale between seedling stands and forests make extrapolations tenuous. For this reason, ongoing research must attempt to determine how and to what extent tree physiology differs as a function of stand scale.

Effects of CO_2

Bazzaz and McConnaughay (1992) summarized findings from literature on this subject:

o Individually grown plants responded differently to CO_2 compared to plants grown in competition.

o In competitive arrays, CO_2 is seldom the limiting resource.

o Plants have little direct influence on CO_2 acquisition of neighbors.

o Changes in plant morphology growth rates due to CO_2 may allow larger plants to capture more limiting resources than smaller neighbors.

o Different responses to CO_2 may result in competitive advantages for some species, leading to reductions of other species in a community.

o Competitive outcomes between C_3 and C_4 species are difficult to predict.

o CO_2 levels have greater impact on plant-plant interactions when densities are high, competition for light is significant, plant size differences are minimal, impacts on phenological and developmental rates differ greatly, and other resources are not limiting.

Groninger et al. (1993) found no significant difference in relative crowding coefficient in sweetgum nor in loblolly pine

resulting from CO_2 concentration. Total yields were only slightly higher in monocultures of sweetgum and loblolly pine compared to 50:50 mixed stands, regardless of CO_2 concentration (Groninger et al. 1993).

Effects of water

Competitive relationships between loblolly pine and sweetgum are affected by moisture availability (Groninger et al. 1993). Loblolly pine contributed a greater percent to total stand biomass under low-water conditions than in the well-watered treatments. Species-specific changes in root: shoot ratio resulting from competition for soil moisture may also have significant effects on competitive outcomes (Kolb and Steiner 1990). Mixed stands of greenleaf manzanita (*Arctostaphylos patula*) and ponderosa pine (*P. ponderosa*) had drier soil than pine monocultures, indicating that manzanita was outcompeting pine for soil moisture; consequently, pine productivity on mixed stands was significantly lower than productivity in pine monocultures (Shainsky and Radosevich 1986).

Interactions of CO_2 and water

Bazzaz and Carleson (1984) showed that *Polygonum pensylanicum* (C_3) increased its contribution to total community

biomass relative to *Amaranthus retroflexus* (C_4) under elevated CO_2 at two soil moisture levels. The response of *Polygonum* was especially pronounced as CO_2 and soil moisture increased, suggesting an interaction between water and CO_2 availability due to species-specific differences in WUE and carbon-fixation pathways.

In well-watered treatments, loblolly pine response to CO_2 level was greater in monocultures than in mixed stands (Groninger et al. 1993). In water-stressed treatments, loblolly pine response to CO_2 level was reversed: greater in mixed stands than in monoculture. Sweetgum exhibited trends opposite those of loblolly pine: response to CO_2 in well-watered treatments was greater in monocultures, while volume responded more to CO_2 within water-stressed, mixed stands. Although most of the data presented by Groninger et al. (1993) are not statistically significant, the results do suggest that under elevated CO_2 pine may continue to outcompete sweetgum on dry sites, while sweetgum may still dominate on wetter sites; in addition, the effects of CO_2 and moisture appear to be differ between monocultures and mixed stands. Jifon et al. (1995) concluded that below-ground competition between loblolly pine and sweetgum

would increase under elevated CO_2 conditions when water and nutrients are non-limiting.

MATERIALS AND METHODS

Seedling culture and growth conditions

This experiment was conducted at the U.S.D.A. Forest Service Center for Forest Environmental Studies, Dry Branch, GA. Seeds of loblolly pine and sweetgum were gathered in native stands at Rapides Parish, LA (Louisiana Forest Seed Co.). All seeds were soaked in water overnight, drained, and chilled at approximately 3°C for 14 days. Following this stratification, seeds were planted in plastic containers (approximately 59 cm^3) in a greenhouse. Seedlings were fertilized once per week after the cotyledons emerged from the seed coats. One teaspoon of Miracle-Gro 15-30-15 (respective percentages N, P_2O_4, K_2O) was mixed to a gallon of water. The soil was wet with tap water, fertilizer solution applied until it drained from the bottoms of the containers, and the foliage was rinsed. At age 95 days (April 6, 1994) the seedlings were transplanted at 7.6-cm spacings into wooden boxes measuring 0.76 m per side and 1.22 m deep. Three stand types were planted: monocultures of loblolly pine or sweetgum and 50:50 replacement mixtures of these two species. The inner 5x5 seedlings served as the measurement plot, surrounded by buffer of two buffer rows of seedlings along each

edge. Each box was plastic-lined with a drain at the bottom. Boxes contained approximately 10 cm of 2.5-cm diameter gravel at the bottom and were filled to the top with soil. The soil was gathered from a forested site on the Coastal Plain (Orangeburg series: fine-loamy, siliceous, thermic Typic Kandiudults); this soil was amended with approximately 20% coarse sand to maintain soil texture and drainage properties.

At each watering, well-watered treatments received eight liters of water per box; water-stressed treatments received four liters—approximately equivalent to 4.2 cm and 2.1 cm per week of rainfall, respectively. During the first growing season, all seedlings were watered three times per week. During the winter, seedlings were watered once or twice per week. Due to increased seedling size, seedlings were watered more frequently, as needed, during the second growing season.

Aluminum-framed OTCs, 4.6 m in diameter and 3.5 m tall, were covered with clear polyvinyl chloride (PVC). A large fan, approximately 1.5 m in diameter, forced air through a 1.5 m diameter PVC tube into the double-layered plenum at the bottom of each chamber. Complete air exchange in the chambers occurred approximately twice per minute. CO_2 gas, stored in a centralized tank as liquid, was vaporized, piped to each elevated-CO_2 chamber, and released into the PVC tube between the fan and the plenum. Holes (3 cm in diameter) located on the inside layer of the plenum distributed the CO_2 treatment evenly around the base of the

chamber. Mean CO_2 concentrations in the ambient- and elevated-CO_2 chambers were 430 ppm and 840 ppm during June, 1994. Concentrations for other months were unavailable but are likely similar to levels measured when CER data were collected (Table 1). A frustrum and canopy prevented rain from entering the OTCs. The interior and exterior of the PVC coverings of the OTCs were scrubbed in September 1994 to reduce light attenuation by dirt.

On August 14-16, 1995, all seedlings were destructively harvested. Roots were separated at the root collar and washed. Foliage was removed from stems. All tissue samples were placed in labeled paper bags and oven-dried.

Measurements

Leaf CER was measured approximately once per month between August 1994 and August 1995 using the LI-6200 portable photosynthesis system (Li-Cor, Inc., Lincoln, NB). CER was measured with a 1/4-liter cuvette. CO_2 draw-down inside the cuvette was monitored during a 20-second sampling period. Measurements were taken on foliage in the upper third of the canopy for all dates except August and September 1994 and August 1995 when gas exchange was measured in both the upper and lower third of the canopy. Two fascicles of pine from the same seedling or one sweetgum leaf was measured from the inner 5 x 5 array in each treatment. 1995 foliage was used beginning in March for sweetgum and in June for loblolly

Table 1. Means and standard deviations (S.D.) of CO_2 concentration in ambient- and elevated-CO_2 chambers, temperature (Temp), and relative humidity (RH). Data were measured with a Li-Cor 6200 inside a 1/4-liter leaf cuvette. Monthly means are based on measurements in upper-canopy foliage averaged across all treatments.

| | CO₂ CONCENTRATION | | | | TEMP (°C) | | RH (%) | |
| | AMBIENT | | ELEVATED | | | | | |
Date	mean	S.D.	mean	S.D.	mean	S.D.	mean	S.D.
8/3/94	360	19	720	28	36.9	2.8	48.3	9.9
9/29/94	363	7	722	13	36.4	3.9	40.1	7.3
11/18/94	401	23	700	39	27.7	4.3	49.1	7.8
12/20/94	383	10	734	54	23.2	3.9	29.9	4.3
1/20/95	406	5	741	25	18.3	1.8	29.5	2.5
2/27/95	392	4	742	24	25.8	2.7	49.0	7.0
3/27/95	420	22	798	31	24.6	1.4	51.0	6.3
5/1/95	398	63	759	57	33.8	2.7	41.2	9.2
6/2/95	351	7	726	27	30.7	1.7	60.5	6.1
7/6/95	398	73	728	73	36.9	2.9	50.0	6.2
8/15/95	397	27	768	35	37.8	3.1	51.1	7.4
MEAN	388	24	740	37	30.2	2.8	45.0	6.7

pine. Ambient light levels were used except in June 1995 when ambient light was supplemented with a QBEAM 2001 (Quantum Devices, Inc., Barneveld, WI) set at 700 μE m^{-2} s^{-1} for several chambers due to cloud cover. Branch respiration was measured on sweetgum from December 1994 to February 1995 by inserting 3.4 cm of a branch into the same cuvette. Mean branch diameter was 1.3 mm.

Mean air temperature inside the photosynthesis cuvette at measurement times varied between 18.3°C in January and 37.8°C in August 1995 (Table 1). Mean RH inside the cuvette ranged from 29.5% in January to 60.5% in June 1995 (Table 1). Mean PAR above the canopy ranged from 240.9 μE m^{-2} s^{-1} in March, 1995, to 758.3 μE m^{-2} s^{-1} in July, 1995.

In addition to these standard monthly measures, photosynthetic acclimation was estimated on three occasions. In August 1994, gas exchange was measured at high-CO_2 cuvette concentrations in the low-CO_2 chambers by injecting CO_2 into the Li-Cor cuvette and measured at low-CO_2 cuvette concentrations in the high-CO_2 chambers by scrubbing the CO_2 concentrations down with soda lime. In July 1995, gas exchange of excised foliage from all pure stands was measured outside the chambers at ambient CO_2 levels. In August 1995, excised foliage from elevated-CO_2, pure-stand treatments was again measured outside the chambers at ambient CO_2 levels and compared with measurements from foliage grown and measured at ambient-CO_2 levels in monoculture. This

change in protocol was done to eliminate errors associated with leaks resulting from differences in CO_2 concentration inside and outside the cuvette.

Following all gas exchange measurements, foliage used in CER measures was placed in labeled, plastic bags and stored in an ice-chest during transport to Virginia Polytechnic Institute and State University. At the laboratory, foliage was stored in a cold chamber at 4°C. Loblolly pine total needle surface areas were calculated using methods described by Ginn et al. (1991). Sweetgum leaf areas were measured as the average of three measurements using area meters: LI-3050A (August 1994—February 1995) and LI-3100 (March 1995—August 1995) (Li-Cor, Inc., Lincoln, NB). For sweetgum twig measurements, branch diameter was measured with digital calipers, and branch surface area was calculated using the formula of a cylinder. Foliage and twig gas exchange data were calculated as μmol CO_2 exchanged per cm^2 tissue surface area per second.

Soil respiration was measured monthly with a specially-constructed soil cuvette using the Li-Cor 6200 portable photosynthesis system. Measurements from August 1994 through July 1995 were taken with a cuvette having a soil-surface sample area of 4 cm^2 and a total volume of 175 cm^3. Subsampling was repeated at three locations in each box. In August 1995, a larger cuvette with a sample area of 18.4 cm^2 and a total volume of 216.5 cm^3 was used, and only two subsamples were measured per box. For each subsample, the cuvette was inserted slightly into the soil within

the 5x5 inner array of seedlings. The CO_2 level inside the cuvette was initially scrubbed below the ambient chamber concentration. Three respiration rates were measured at ten second intervals: one below ambient CO_2 concentration, one near ambient CO_2, and one above ambient CO_2. For each subsample, a mean respiration rate was calculated from the three measurements at the three CO_2 levels. Then a mean soil respiration rate for the box was calculated by averaging the respiration rates from the two or three subsamples.

PAR was measured during the growing seasons using a Li-Cor LI-185B Quantum/Radiometer/Photometer. During the first growing season, PAR above the canopy was measured once above the canopy, then at five haphazardly selected locations at soil level, and once more above the canopy. During the second growing season, PAR was measured above and below the canopy as before, with additional light levels measured at five locations mid-way between the top of the canopy and the bottom of the live crown. Average PAR at each canopy level was calculated, and light extinctions to the mid-canopy and ground level were calculated as a percentage of the light above the canopy.

Seedling height and root-collar diameter of all twenty-five sample seedlings per box were measured in November 1994 and April and August 1995 by U.S.F.S. personnel. Data from each month were analyzed separately in order to demonstrate effects of treatments over time. For live seedlings only, stem volume was estimated as the product of seedling height and the square of the

38

diameter. Total stand stem volume of each species in each box was summed in order to compare total yields under various experimental conditions (e.g. CO_2, water, stand type).

Dry weights of roots, stems, and foliage were measured for each species per box. Shoot biomass was calculated as the sum of foliar and stem weights, total biomass as the sum of roots and shoots. Root: shoot ratio was also calculated. Relative crowding coefficients for each species (RCCP and RCCS for loblolly pine and sweetgum, respectively) and relative yield total (RYT) for stand stem volume and biomass data were calculated (Harper 1977).

Immediately prior to final harvest, water potential was measured on upper-canopy foliage from one seedling of each species per box using a pressure chamber (PMS Instruments Inc., Corvallis, OR).

Experimental design and analyses

The experiment was designed as a completely randomized, split-plot with CO_2 level (ambient and ambient + 400 ppm) as the main plot with four replications. Six boxes were placed in each of the eight OTCs. The factorial combinations of water (2 levels) x stand type (3 types) served as the subplots. Stand types consisted of monocultures (loblolly pine and sweetgum) and 50:50 replacement mixtures.

Analysis of variance was performed with SAS (SAS Institute Inc., Cary, NC) statistical software. When significant interactions

were found, analyses were repeated separately by each treatment. For gas exchange data, any diurnal variation was removed from the analyses by using time as a blocking variable; data were collected from one ambient-CO_2 chamber and one elevated-CO_2 chamber in close succession and together considered one block. Duncan's mean separations (Ott 1993) were used to evaluate differences between stand composition effects on soil respiration. T-tests were used to compare differences in RCCP, RCCS, or RYT between treatment levels. Yields of a single species in mixed stand were doubled when compared with yield in monoculture in order to account for differences in sample size.

RESULTS

Physiology

<u>Water potential</u>

Water potential was measured only once - at the final harvest. At this time, water potentials in both species were significantly lower in drought-stressed treatment (Table 2). For loblolly pine, water potential was also significantly more negative in boxes grown in ambient-CO_2 concentration. There were no other significant main effects nor significant interactions on water potential for either species. The water stress treatments did successfully induce stress based on biomass reductions as discussed below.

40

Table 2. Water potential measurements of loblolly pine and sweetgum upper-canopy foliage immediately prior to final harvest. Means within species and treatment followed by different letter are significantly different ($p < 0.05$).

| | | WATER POTENTIAL | |
| | | Loblolly pine | Sweetgum |
Treatment	Level	(MPa)	(MPa)
CO_2	ambient	-1.43 A	-1.03 A
	elevated	-1.06 B	-0.77 A
Water	low	-1.44 A	-1.19 A
	high	-1.05 B	-0.60 B
Stand	monoculture	-1.34 A	-0.84 A
	mixture	-1.15 A	-0.96 A

Above-ground CER

Only CO_2 main effects on CER were consistently significant for either species on a monthly basis (fig. 1). CER was consistently higher in seedlings grown in elevated-CO_2 chambers and significantly higher on four of eleven measurement dates for loblolly pine and on three of eleven dates for sweetgum. Loblolly pine maintained a positive mean CER at all treatment levels throughout the study except on the first two measurement dates when CER of loblolly pine at ambient CO_2 was slightly negative (fig. 1). No interactions were consistently significant.

On a seasonal basis, CO_2 main effects were significant for both species during both growing seasons (Table 3). Loblolly pine CER averaged 55% and 149% higher in elevated-CO_2 chambers during the summers of 1994 and 1995, respectively. For sweetgum, the respective increases were 40% and 76%. During the winter (December 1994—February 1995), mean CER of loblolly pine averaged across all treatments was 2.92 μmol m^{-2} s^{-1}, approximately 83% the rate of either summer (fig. 1). Pine winter CER was significantly higher in elevated-CO_2 stands (158%) or well-watered conditions (52%) (Table 3). Sweetgum twig CER was negative for all three winter months and averaged -2.51 μmol m^{-2} s^{-1} (fig. 1). Sweetgum winter twig respiration was approximately twice as great in monoculture as in mixed stands (Table 3). There were no other seasonal main effects or interactions for either species.
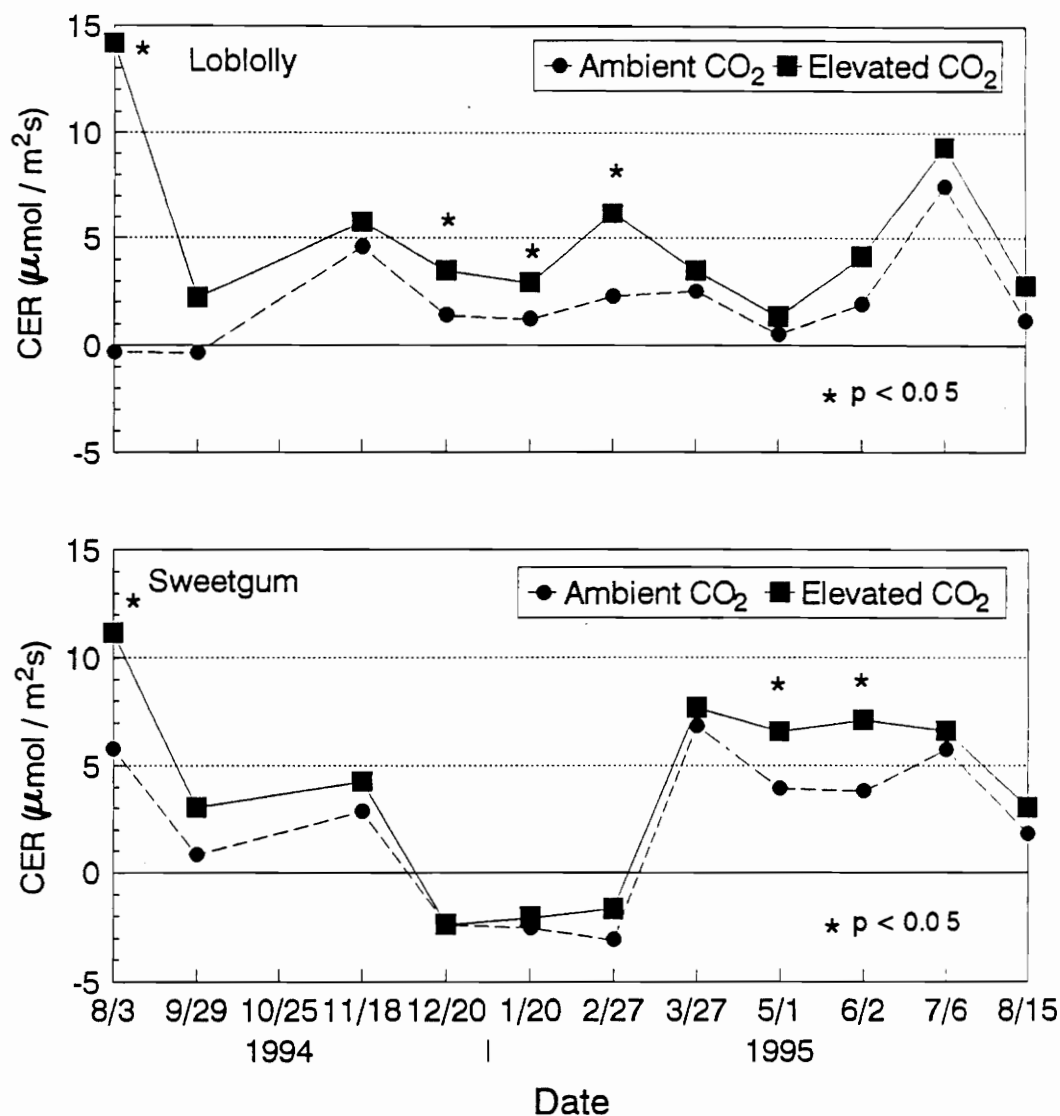
Figure 1. Monthly mean carbon exchange rates (CER) for loblolly pine and sweetgum grown in open-top chambers at ambient- or elevated-CO_2 concentrations for two growing seasons. Measurements were taken on upper-canopy foliage except for sweetgum during the winter when CER was measured on branches. Mean CER between CO_2 concentrations within species and measurement date marked by an asterisk are significantly different ($p < 0.05$).

Table 3. Seasonal mean carbon exchange rates (CER) for loblolly pine and sweetgum. Measurements were made on upper-canopy foliage except for sweetgum winter CER which was measured on twigs. Means within species, season, and treatment followed by different letters are significantly different ($p < 0.05$).

CARBON EXCHANGE RATE (μmol m^{-2} s^{-1})

Treatment	Level	Loblolly pine			Sweetgum		
		summer '94[1]	winter '94-'95	summer '95	summer '94	winter '94-'95	summer '95
CO$_2$	ambient	2.712 A	1.629 A	2.035 A	4.428 A	-2.675 A	2.923 A
	elevated	4.212 B	4.201 B	5.072 B	6.195 B	-2.344 A	3.856 B
Water	low	3.441 A	2.317 A	3.516 A	5.152 A	-2.500 A	2.923 A
	high	3.482 A	3.513 B	3.591 A	5.445 A	-2.515 A	3.129 A
Stand	monoculture	3.631 A	2.470 A	3.519 A	5.199 A	-3.364 A	2.838 A
	mixture	3.292 A	3.360 A	3.588 A	5.402 A	-1.633 B	3.215 A

1 Summer averages included the months of August, September, and November in 1994, and February, May, June, July, and August 1995. Winter average included December 1994, and January and February 1995.

44

Significant downward acclimation of CER was measured in sweetgum upper-canopy foliage only in July 1995. At this time, CER of sweetgum seedlings grown in elevated-CO_2 chambers and measured at low-CO_2 concentration was 54% lower than CER of seedlings grown and measured in low CO_2. There was never significant acclimation in sweetgum lower-canopy foliage. Loblolly pine did not demonstrate significant acclimation, regardless of measurement date or canopy position. When expressed on a leaf-weight basis, acclimation in the upper canopy only was significant for sweetgum at all three measurement dates and for loblolly pine in August 1994 (data not shown).

Canopy-position effects

Loblolly pine CER was significantly affected by canopy position interactions at all three dates measured. In August 1994, position x CO_2 x water level was significant (Table 4). In the upper canopy, positive CER response to increased CO_2 was one order of magnitude larger in drought-stressed seedlings than in well-watered seedlings. In the lower canopy, the positive response to elevated CO_2 was not dependent on water availability (Table 4). In September 1994 and August 1995, loblolly pine CER was significantly affected by a canopy position x CO_2 interaction (Table 5). At both dates, lower-canopy leaf CER was lower in elevated CO_2 treatments than in ambient-CO_2, while the pattern was reversed in the upper canopy. In September 1994, differences in CER were significant at the $p < 0.07$ level between canopy positions in low-CO_2 treatments and between CO_2-treatments

Table 4. Loblolly pine mean carbon exchange rate (CER) from August, 1994. Canopy position x water x CO2 interaction was significant at $p < 0.05$. Means within canopy position and CO_2 treatment level followed by different upper-case letters are significantly different ($p < 0.05$). Means within canopy position and water treatment followed by different lower-letters are significantly different at the same level.

		CARBON ECHANGE RATE (μmol m^{-2} s^{-1})			
		LOWER CANOPY		UPPER CANOPY	
Date 8/94	$\underline{CO_2\ Level}$	Drought stressed	Well watered	Drought stressed	Well watered
	ambient	-2.604 Aa (227)[1]	-2.063 Aa (216)	-0.931 Aa (582)	0.259 Aa (609)
	elevated	6.440 Ab (378)	7.428 Ab (281)	19.870 Ab (646)	8.455 Bb (501)

1 Photosynthetic active radiation (μE m^{-2} s^{-1}) shown below each corresponding CER measurement.

46

Table 5. Loblolly pine mean carbon exchange rate (CER) from September, 1994, and August, 1995. Canopy position x CO_2 interaction was significant at $p < 0.05$. Means within canopy position or CO_2 level were never significantly different.

		CARBON ECHANGE RATE (μmol m^{-2} s^{-1})	
Date	CO_2 Level	Lower canopy	Upper canopy
9/94	ambient	2.2446	-0.3619
		(197)[1]	(201)
	elevated	1.4938	2.2129
		(212)	(251)
8/95	ambient	1.1248	1.1769
		(60)	(429)
	elevated	0.1984	2.7737
		(123)	(411)

1 Photosynthetic active radiation (μE m^{-2} s^{-1}) shown below each corresponding CER mean.

in the upper canopy. In August 1995, CER differences between canopy positions were significant at the $p < 0.001$ level in elevated-CO_2. There were no other significant interactions involving canopy position for loblolly pine CER.

Sweetgum CER was significantly affected by canopy position in August 1994 and August 1995. At both these dates, CER was approximately 70% lower in the lower canopy than in the upper canopy. Sweetgum CER demonstrated no significant interactions involving canopy position at any date.

Soil respiration

Only CO_2 treatments consistently had significant effects on monthly soil respiration rates (fig. 2). Soil respiration rates were significantly higher in elevated-CO_2 chambers on four of eleven measurement dates. Soil respiration was greatest during the first growing season. There was smaller peak in May of the second growing season when CO_2 main effect was significant. When averaged across the year, soil respiration was significantly increased (70%) in elevated-CO_2 chambers relative to low-CO_2 chambers (Table 6). There were no other significant main effects or interactions.

BIOMASS

Total, shoot, and root biomass

For total biomass, CO_2 x stand type interaction was significant for sweetgum ($p = 0.032$) and for loblolly pine ($p = 0.096$) (Table 7).

48
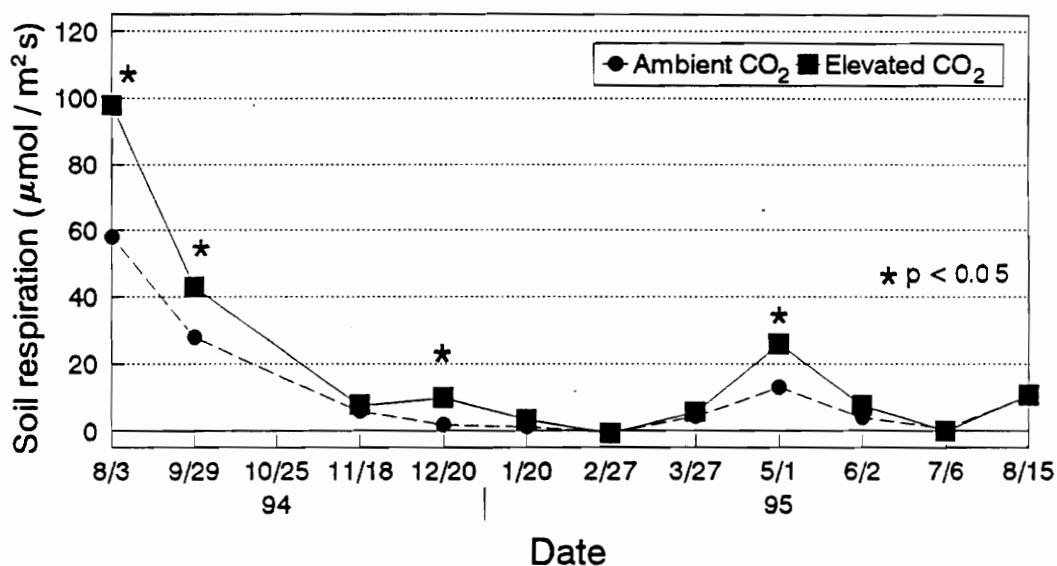
Figure 2. Monthly mean soil respiration rates from boxes (0.6 m² x 1.22 m tall) of forest soil with loblolly pine and/or sweetgum seedlings grown in open-top chambers of ambient- or elevated-CO_2 concentrations. Soil respiration is expressed as μmol CO_2 efflux per m² land area per second. Mean soil respiration rates between CO_2 concentrations within measurement date marked by an asterisk are significantly different ($p < 0.05$).

Table 6. Mean annual soil respiration rates expressed as μmol CO_2 efflux per m^2 soil area per second. Means within treatments followed by different letter are significantly different ($p < 0.05$).

Treatment	Level	Soil respiration (μmol CO_2 m^{-2} soil s^{-1})
CO_2	ambient	6.708 A
	elevated	11.374 B
Water	low	7.907 A
	high	10.145 A
Stand	loblolly monoculture	8.543 A
	mixture	8.856 A
	sweetgum monoculture	9.697 A

Table 7. Analysis of variance for total biomass per m^2 soil area of miniature stands of loblolly pine and sweetgum after two growing seasons. Biomasses of each species in mixed stands were doubled to account for different sample sizes.

| | | TOTAL BIOMASS | | | |
| | | Loblolly pine | | Sweetgum | |
Source	d F	F-value	$p > F$	F-value	$p > F$
CO_2	1	39.86	< 0.0005	15.53	< 0.01
Water	1	11.76	0.0030	74.36	0.0001
CO_2 x water	1	0.10	0.7542	0.01	0.9326
Stand	1	31.43	0.0001	5.52	0.0304
CO_2 x stand	1	3.09	0.0960	5.39	0.0322
Water x stand	1	29.34	0.0001	5.22	0.0347
CO_2 x water x stand	1	0.15	0.6988	0.27	0.6085

Total biomass of seedlings grown in elevated-CO_2 was approximately 25% greater in monoculture than in mixture for both sweetgum and pine (fig. 3). Loblolly pine and sweetgum total biomass also demonstrated a significant water x stand type interaction, but the pattern of this interaction was species-dependent (Table 7, fig. 4). In mixture, loblolly pine biomass was 13% lower in well-watered stands; in monoculture, biomass increased by 57% in response to increased water availability. Sweetgum biomass response to increased water was 24% greater in mixture than in monoculture, indicating that sweetgum competes better, especially against loblolly pine, under well-watered conditions.

Shoot biomass of loblolly pine and sweetgum were both significantly affected by CO_2 x stand type and water x stand type interactions (Table 8). A water x stand type interaction was significant for loblolly pine root biomass (Table 8). The patterns of these interactions on shoots or roots were similar to those of total biomass (figs. 3 and 4). Sweetgum root biomass was significantly affected only by main effects with responses very similar to those of sweetgum total biomass. Pine and sweetgum root biomass increased by 38% and 29%, respectively in response to elevated CO_2.

Root:shoot ratio of loblolly pine was significantly lower (7%) in monocultures than in mixture with shoot biomass increase greater than that of roots (Table 8). Sweetgum root:shoot ratio was significantly greater (20%) due to elevated-CO_2 (Table 8). The sweetgum root:shoot ratio was significantly affected by a water x
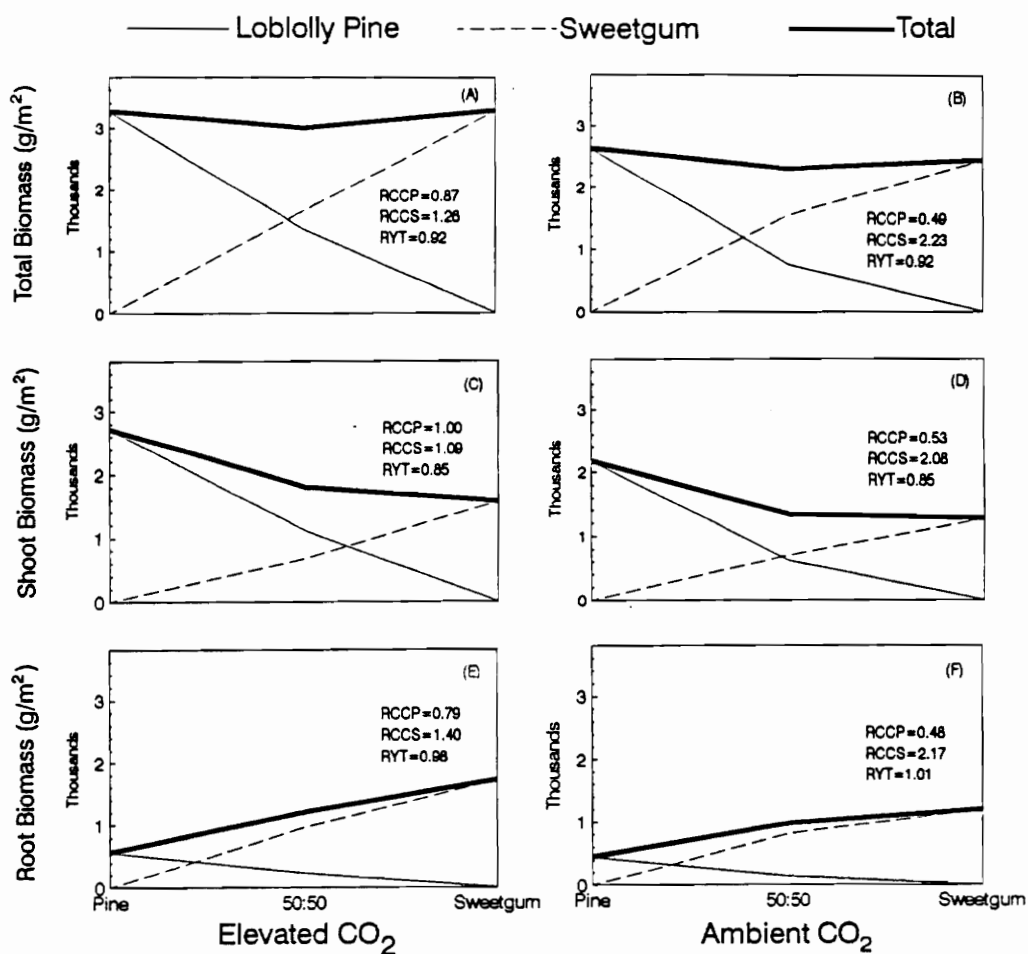
Figure 3. Relative yield diagrams of total, root, and shoot biomass for monoculture and 50:50 mixed loblolly pine—sweetgum miniature stands grown under elevated-CO_2 and ambient-CO_2 conditions. Stand biomasses are expressed per m^2 soil area. Relative yield totals (RYT) and relative crowding coefficients for loblolly pine (RCCP) and sweetgum (RCCS) are presented. There were no significant differences between elevated- and ambient-CO_2 conditions for RCCP, RCCS, or RYT ($p < 0.05$).

Loblolly Pine   - - - - - Sweetgum   Total

(A)

Total Biomass (g/m²)

Thousands

3

2

1

0

RCCP=0.47
RCCG=2.20
RYT=0.87

(B)

Thousands

3

2

1

0

RCCP=0.99
RCCG=1.03
RYT=0.99

(C)

Shoot Biomass (g/m²)

Thousands

3

2

1

0

RCCP=0.50
RCCG=2.05
RYT=0.81

(D)

Thousands

3

2

1

0

RCCP=1.19
RCCG=0.87
RYT=0.91

(E)

Root Biomass (g/m²)

Thousands

3

2

1

0
Pine   50:50   Sweetgum

RCCP=0.47
RCCG=2.25
RYT=0.93

(F)

Thousands

3

2

1

0
Pine   50:50   Sweetgum

RCCP=0.87
RCCG=1.16
RYT=1.08

Well-watered

Drought-stressed

Figure 4. Relative yield diagrams of total, root, and shoot biomass for monoculture and 50:50 mixed loblolly pine—sweetgum miniature stands grown under well-watered and drought-stressed conditions. Stand biomasses are expressed per m² soil area. Relative yield totals (RYT) and relative crowding coefficients for loblolly pine (RCCP) and sweetgum (RCCS) are presented. There were no significant differences between well-watered and drought-stressed conditions for RCCP, RCCS, or RYT ($p < 0.05$).

Table 8. Analysis of variance for shoot (stem plus foliage) and root biomass per m^2 soil area and for root:shoot ratio of miniature stands of loblolly pine and sweetgum after two growing seasons. Biomasses for each species in mixed stands were doubled to account for different sample sizes.

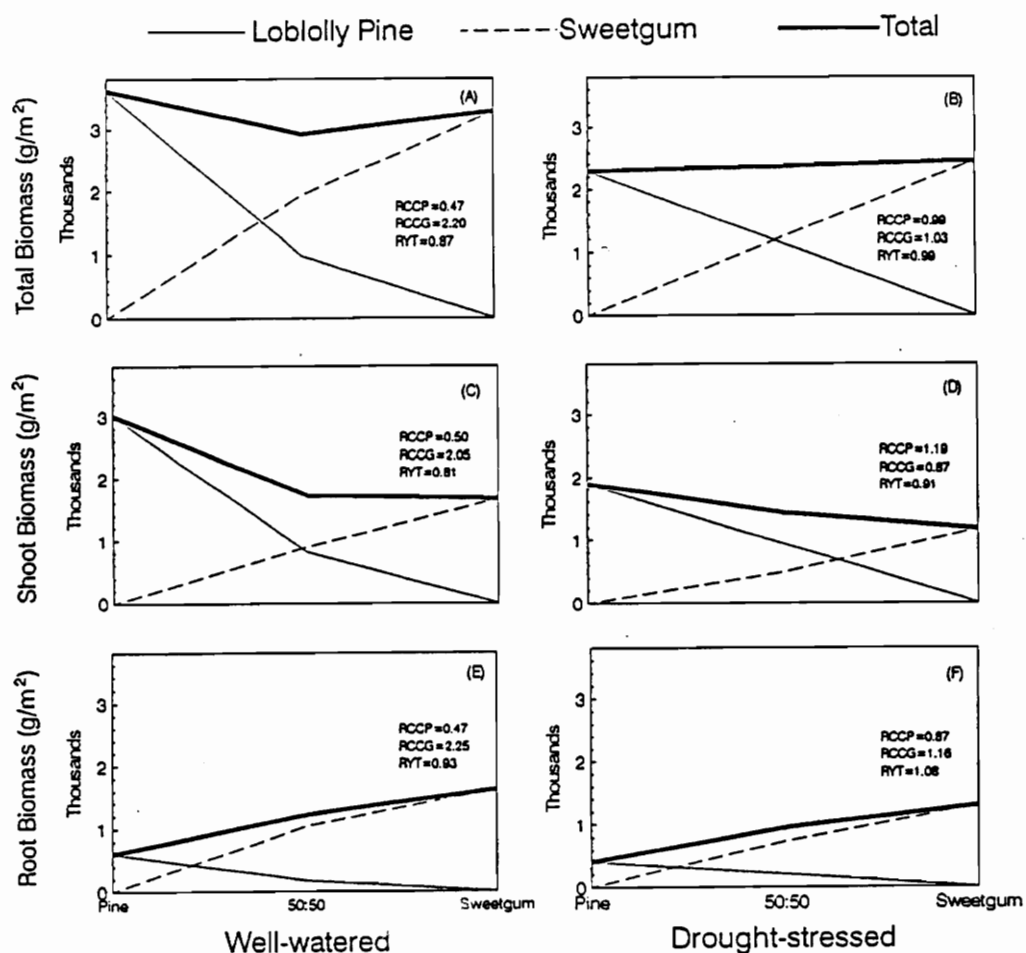| Source	dF	SHOOT BIOMASS				ROOT BIOMASS				ROOT: SHOOT RATIO			
		Loblolly pine		Sweetgum		Loblolly pine		Sweetgum		Loblolly pine		Sweetgum	
		F-value	$p>F$	F-value	$p>F$	F-value	$p>F$	F-value	$p>F$	F-value	$p>F$	F-value	$p>F$
CO_2	1	35.10	< 0.005	2.36	> 0.10	30.54	< 0.005	30.34	< 0.005	1.17	> 0.25	14.84	< 0.01
Water	1	12.57	0.0023	112.94	0.0001	7.23	0.0150	37.02	0.0001	2.26	0.1505	36.02	0.0001
CO_2 x water	1	0.05	0.8280	0.01	0.9372	0.58	0.4564	0.04	0.8361	2.33	0.1446	0.31	0.5852
Stand	1	32.45	0.0001	0.13	0.7185	23.22	0.0001	18.35	0.0004	4.66	0.0446	66.76	0.0001
CO_2 x stand	1	3.37	0.0830	8.84	0.0081	1.65	0.2152	2.39	0.1392	2.52	0.1299	1.23	0.2882
Water x stand	1	29.96	0.0001	7.77	0.0121	23.47	0.0001	2.67	0.1197	0.47	0.5021	10.22	0.0050
CO_2 x water x stand	1	0.23	0.6391	1.88	0.1876	0.00	0.9802	0.05	0.8300	1.39	0.2545	2.14	0.1608

stand type interaction. In both stand types, increased water availability resulted in a lower root:shoot ratio; the percent decrease was 13% greater in monoculture than in mixture. This interaction was driven by a larger biomass response to water in shoots than in roots, regardless of stand type.

Stem volumes

Across all treatments, loblolly pine volume increased throughout the study and remarkably doubled between November, 1994, and April, 1995 (figs. 5, 6). This increase in stand volume was due to increases in stem diameter during winter months. By August 1995, pine volumes had increased by an additional 50%. Loblolly pine response to elevated CO_2 also increased throughout the study with pine volumes 55% greater in elevated-CO_2 chambers by August 1995 (fig. 5). Loblolly pine response to water availability was greater in monoculture than in mixture (Table 9, fig. 6). This interaction was significant for diameters, heights, and stand volumes in November 1994 and in April and August 1995. Loblolly pine stand volumes in well-watered, monocultures averaged 107% greater than volumes in drought-stressed, mixed stands.

In contrast, sweetgum volumes decreased slightly in all treatment levels during the winter due to consistent decreases in stem diameter. Sweetgum volumes were significantly greater in well-watered stands than in droughted conditions at all three measurement dates with 96% greater volumes by August 1995 (fig. 6). Although sweetgum volumes were consistently lower in
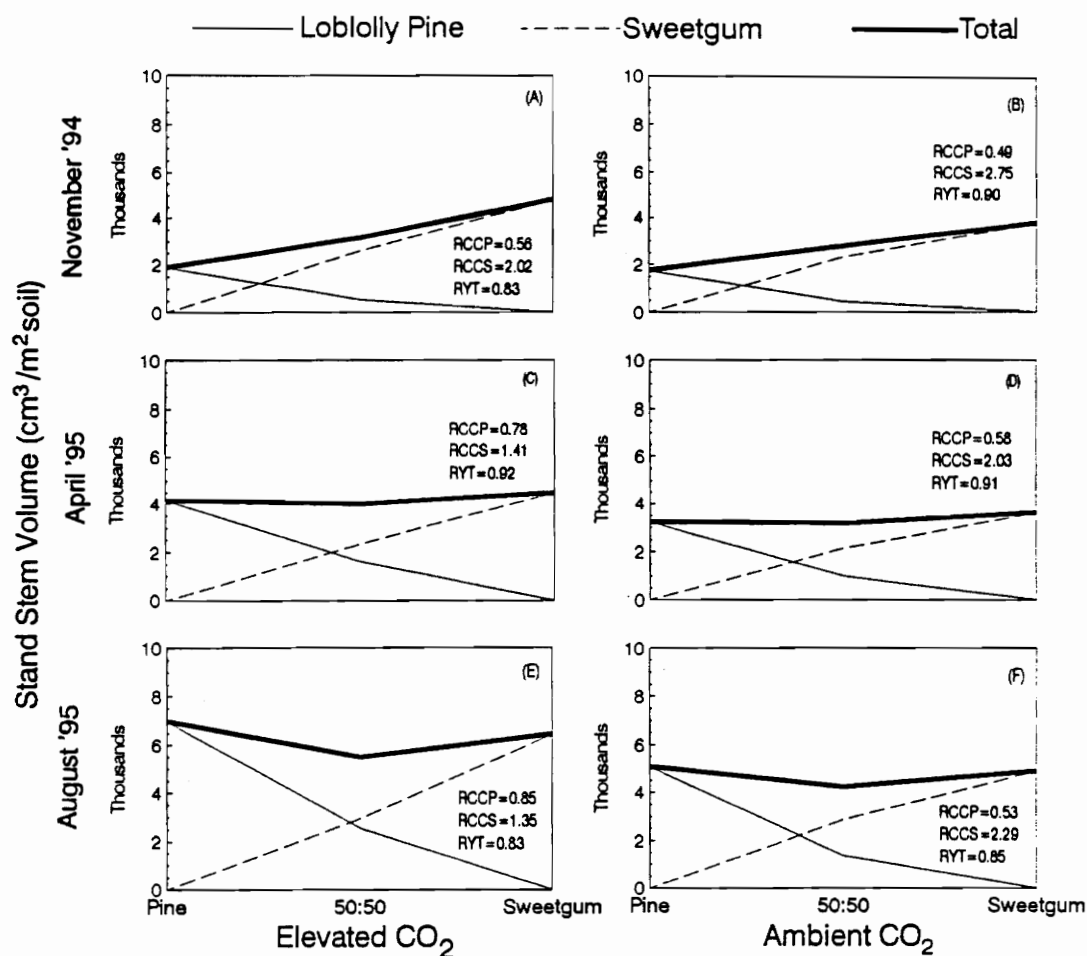
Figure 5. Relative yield diagrams of stand stem volumes for monoculture and 50:50 mixed loblolly pine—sweetgum miniature stands grown under elevated-CO_2 and ambient-CO_2 conditions. Stand volumes are expressed per m^2 soil area. Relative yield totals (RYT) and relative crowding coefficients for loblolly pine (RCCP) and sweetgum (RCCS) are presented. There were no significant differences between elevated- and ambient-CO_2 conditions for RCCP, RCCS, or RYT ($p < 0.05$).
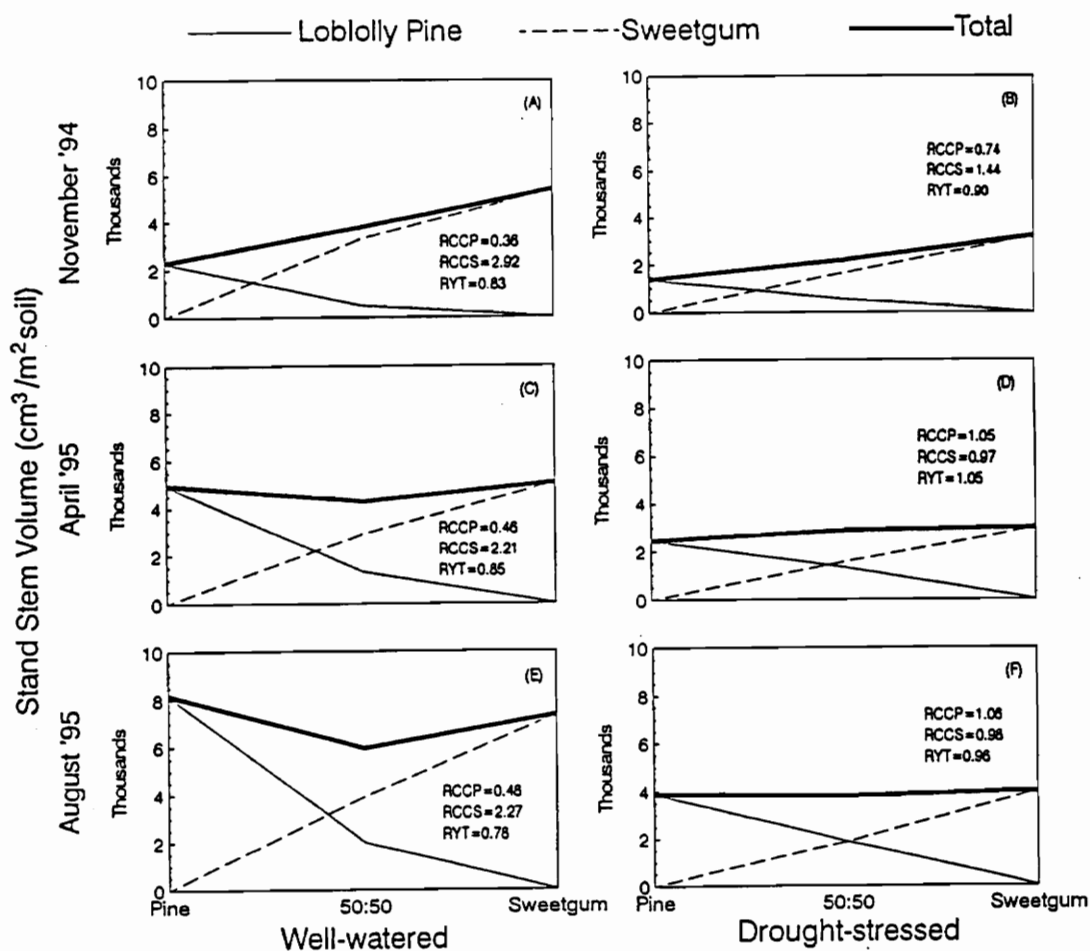
Figure 6. Relative yield diagrams of stand stem volumes for monoculture and 50:50 mixed loblolly pine—sweetgum miniature stands grown under well-watered and drought-stressed conditions. Stand volumes are expressed per m^2 soil area. Relative yield totals (RYT) and relative crowding coefficients for loblolly pine (RCCP) and sweetgum (RCCS) are presented. There were no significant differences between well-watered and drought-stressed conditions for RCCP, RCCS, or RYT ($p < 0.05$).

Table 9. Mean stem heights, mean stem diameters, stand stem volumes, and percent changes as affected by stand type x water availability interaction. Data are from November 1994, April 1995, and August 1995. Data within measurement basis, date, and stand type followed by different upper-case letter are significantly different ($p < 0.05$). Data within measurement basis, date, and water availability followed by different lower-case letter are significantly different at the same level.

	HEIGHTS (cm)			DIAMETERS (mm)			VOLUMES (cm³/m² soil area)		
	Drought-stressed	Well-watered	% change	Drought-stressed	Well-watered	% change	Drought-stressed	Well-watered	% change
11/94									
mixture	28.57 Aa	28.14 Aa	-1.5	4.23 Aa	4.05 Aa	-4.3	1033.54 Aa	974.24 Aa	-5.7
monoculture	31.64 Aa	40.47 Bb	27.9	4.74 Aa	5.51 Bb	16.2	1366.66 Ab	2264.27 Bb	65.7
% change	10.8	43.8		12.1	36.0		32.2	132.4	
4/95									
mixture	48.17 Aa	49.39 Aa	2.5	5.21 Aa	5.06 Aa	-2.9	2616.59 Aa	2637.11 Aa	0.8
monoculture	44.83 Aa	60.45 Bb	34.9	5.29 Aa	6.59 Bb	24.6	2446.23 Aa	4929.13 Bb	101.5
% change	-6.9	22.4		1.7	30.4		-6.5	86.9	
8/95									
mixture	58.66 Aa	60.07 Aa	36.7	5.94 Aa	5.84 Aa	-1.8	3799.28 Aa	4023.59 Aa	5.9
monoculture	61.74 Aa	80.15 Bb	29.8	5.98 Aa	7.50 Bb	25.4	3862.52 Aa	8160.72 Bb	111.3
% change	5.3	33.4		0.6	28.5		1.7	102.8	

59

monoculture than in mixture (due to decreased diameters), this decrease was significant only in April 1995 (13%). There were no other significant main effects or interactions on sweetgum volumes.

Competitive interactions

RCCS was greater than RCCP for root, shoot, and total biomass at both levels of CO_2 or water availability except for shoots in drought-stressed treatments (figs. 3 and 4). However, RCCP of root, shoot, and total biomasses increased in elevated-CO_2 conditions, while RCCS decreased and RYT remained uniform (fig. 3). Increased water resulted in greater RCCS; RCCP and RYT both decreased (fig. 4). The strong water x stand type interaction resulted largely from decreased pine volume and increased sweetgum volume in well-watered, mixed stands.

On a stand-volume basis, loblolly pine growth during winter months allowed pine in mixed stands to increase its competitiveness relative to sweetgum, especially in elevated-CO_2 chambers where RCCP increased from 0.56 to 0.78 while RCCS decreased from 2.02 to 1.41 during the study. By August 1995 and in both levels of CO_2, sweetgum had a greater proportion of mixed stand volume than did loblolly pine, even though pine monoculture stand volumes were slightly greater than those of sweetgum (fig. 5). At each measurement date, RCCP increased and RCCS decreased as a result of drought treatment (fig. 6). In drought-stressed stands, was greater than RCCS by April 1995. By August 1995, average stand stem volume of loblolly pine in mixture was greater than that of

sweetgum in drought-stressed treatments. In well-watered conditions, pine volume in mixed stands never reached that of sweetgum even though pine monoculture volume exceeded that of sweetgum (fig. 6).

DISCUSSION

During the three winter months when sweetgum lacked foliage (December, 1994, and January and February, 1995), loblolly pine fixed a substantial amount of carbon (fig. 1). Winter photosynthetic rates were quite high, 77% of growing season rates. In fact, winter photosynthesis in loblolly pine grown in elevated CO_2 averaged higher than growing-season rates of pine seedlings grown in ambient CO_2. This winter photosynthesis likely supported the increased pine diameter growth between November 1994 and April 1995. While loblolly increased volume during the winter, sweetgum lost volume, leading to substantial increase in competitiveness of pine. This seasonal competitive gain by pine was particularly evident in elevated-CO_2 (fig. 5) and drought-stressed (fig. 6) mixed stands.

In this study (7.6-cm spacings) and that of Groninger et al. (1995) (2.54-cm spacings), decreased water availability increased the yield of pine versus sweetgum (fig. 4). These results contrast with those of Tolley and Strain (1984a) who suggested that sweetgum would be more competitive in a drier, high-CO_2 environment. Although there was no significant CO_2 x water x stand type interaction on volumes or biomass of either species in the

61

current study or that of Groninger et al. (1995), the present data support the contention of Groninger et al. (1995) that loblolly pine will remain more competitive on dry sites, while sweetgum will dominate wetter sites even in a future, elevated-CO_2 environment.

Higher root:shoot ratio of loblolly grown in mixture indicates increased allocation to roots relative to shoots, reinforcing the idea that pine competes more successfully for water. Sweetgum root:shoot ratio on the other hand, decreased in mixed stands. Increased root:shoot ratio in sweetgum but not loblolly pine in elevated-$CO2$ chambers (Table 7) may offset these differences in the future. Pot-binding was not evident during harvest and probably did not account for changes in allocation.

Throughout the study, CER was greater in loblolly pine and sweetgum seedlings grown in elevated CO_2 (fig. 1). The magnitude of CER response to elevated CO_2 was substantially larger than previously reported for loblolly pine (Fetcher et al. 1988, Groninger et al. 1996). Sweetgum CER reported here is greater than that indicated by Fetcher et al. (1988) but one-third as strong as measured by Groninger et al. (1996). Although photosynthetic acclimation was rarely significant in this study, greater acclimation of sweetgum than loblolly pine is consistent with Fetcher et al. (1988) and Groninger et al. (1995). Groninger et al. (1995) suggested that species-specific acclimation (Sage et al. 1989, Gunderson et al. 1993) to elevated CO_2 could lead to changes in interspecific competition. However, growth responses in this study and that of Groninger et al.

(1995) did not support this conclusion for loblolly pine and sweetgum. For acclimation to have any impact on competitive interactions, studies would have to continue for many growing seasons since the effects, even when statistically significant, are subtle.

CER in the lower and upper canopy coincide with photosynthetic rates of loblolly and sweetgum under low (250 μE m^{-2} s^{-1}) and high (1000 μE m^{-2} s^{-1}) light (Tolley and Strain 1985) and in the upper versus lower canopy of loblolly (Higginbotham and Strain 1979). The present study found that loblolly pine CER response to CO_2 was negative in the lower canopy position and positive in the upper (Table 4). These results and those of Tolley and Strain (1985) suggest that there is a significant CO_2 effect on light use efficiency with positive response to CO_2 dependent on higher irradiance levels. Lenham (1994) found no significant changes in quantum yields, light compensation points, or light-saturated photosynthetic rates of loblolly or sweetgum in response to elevated CO_2. Lenham, however, measured only foliage grown in full greenhouse light.

Increased RCCP of shoot biomass in elevated- versus ambient-CO_2 stands (fig. 3) indicates that loblolly in mixed stands was able to compete more successfully with sweetgum for light in a high CO_2 environment. The significantly decreased CER of lower-canopy sweetgum foliage may partially explain the depressed whole-stand CER measured by Groninger et al. (1995). As these authors point out,

the important differences in CER within stands should be accounted for in scaling models from single-leaf measures to the stand level (cf. Cropper and Gholz 1993).

Seedlings of both species grown in drought treatment were smaller than those with increased water availability (figs. 4 and 6), indicating substantial water stress. However, there was no consistent water main effect on CER for either species even though water potentials were significantly higher in elevated CO_2 level for loblolly and in well-watered seedlings of both species (Table 2). Due to scheduling problems, CER was sometimes measured soon after the application of water treatments, decreasing differences in CER between "droughted" and well-watered treatments.

The significantly lower (more positive) branch respiration in sweetgum mixture remains unexplained. However, these data are supported by greater percent decrease in stem volume of sweetgum grown in mixed stands. Decreased light in mixed versus pure sweetgum stands in winter may have lowered temperatures and thus respiration rates. Significant difference in temperature between stand types were not detected while taking respiration measurements. However, measurements taken inside the gas exchange cuvette and on the edge of the stands may not reflect actual twig temperatures.

Soil respiration rates were, on average, slightly higher than rates reported by Cropper et al. (1985) and Kelting et al. (1995). Soil respiration rates measured in August and September, 1994, are

64

approximately one order of magnitude higher than those of other dates in this study (fig. 2). However, the relationship between soil respiration in high- versus low-CO_2 chambers was constant throughout the study. Therefore, even if the mean soil respiration rates in Table 3.5 are high in absolute terms, the statistical comparisons between CO_2 treatment levels remain valid. Significantly higher soil respiration rates in elevated-CO_2 chambers were likely due to increased growth of roots (fig. 3) (Rogers et al. 1992) which account for approximately half of total soil respiration (Ewel et al. 1987, Kelting et al. 1995). Seasonally, the high CO_2 evolution rates in the summer of the first year (fig. 2) may be the result of prolific root growth in seedlings as was reported by Drew and Ledig (1981). The increase in soil respiration in late spring corresponds closely with a seasonal increase in the number of slash pine (*P. elliottii*) fine roots in the A1 horizon observed by Gholz et al. (1985). Drew and Ledig (1981) indicate a seasonal increase in loblolly root respiration in the June of the first growing season and in October of the second year. This October increase might be reflected by a small increase in soil respiration measured in this study during December, 1994. These October rates are in general agreement with those measured by Wallis and Wilde (1969) in a red pine plantation. Per m² soil area, soil respiration is approximately 12% of summer CER for loblolly pine and 30% of summer CER for sweetgum, based on LAI calculations and upper-canopy CER measurements. Respiration may represent a larger percent of whole-stand CER which accounts for

65

depressed lower-canopy CER. Because both soil respiration and foliar CER increased in the elevated-CO_2 stands, it is uncertain how a future climate might shift this carbon balance.

CONCLUSIONS

Significant increases in CER of loblolly pine and sweetgum due to elevated CO_2 occurred on monthly and seasonal measurements. These increases were significant in the upper and lower canopy, although CO_2 effects on CER were diminished in the lower position. Loblolly pine, which maintained positive photosynthesis during the winter, increased its competitiveness during the dormant season. Results suggest that loblolly pine will continue to out-compete sweetgum particularly on dry sites, even in an elevated-CO_2 environment. Significant downward acclimation of CER in sweetgum, but not loblolly pine, occurred only in the upper canopy and was transient. Soil respiration was significantly increased in elevated-CO_2 stands, probably as the result of increased root growth early in the first growing season.

Data from this study closely parallel those of Groninger et al. (1995, 1996) whose miniature stands were grown at 2.54-cm spacings. Although the use of miniature stands for testing stand-level interactions is still a new method, the similar results of the two studies at different scales does lend some validity to the technique.

Results indicate that three important factors - canopy position, stand composition, and soil respiration - have important impacts on

carbon cycling in elevated-CO_2 environments. The presence and implications of acclimation are less clear. Increased study of the roles and possible interactions of all these factors is needed in order to strengthen current stand- and ecosystem-level models of climate change.

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