

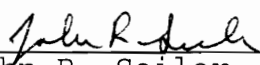
STAND DYNAMICS AND GAS EXCHANGE IN LOBLOLLY PINE AND
HARDWOOD SEEDLING STANDS: IMPACT OF ELEVATED CARBON
DIOXIDE, WATER STRESS AND NUTRIENT STATUS

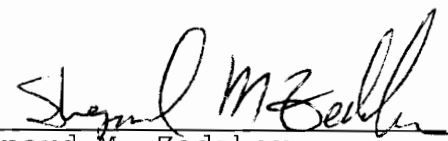
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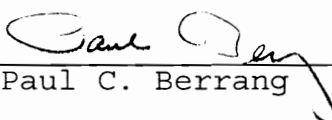
John William Groninger

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Virginia Polytechnic Institute and State University
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of
DOCTOR OF PHILOSOPHY
in
Forestry

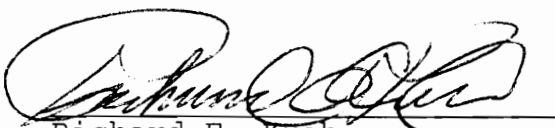
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[ABSTRACT]

Loblolly pine (*Pinus taeda*) occurs in mixed stands with hardwood species including red maple (*Acer rubrum*) and sweetgum (*Liquidambar styraciflua*) across much of the southern United States. Rising atmospheric CO₂ concentrations over the next several decades could influence competitive interactions between these species. This research examined the effects of increased atmospheric CO₂ concentration in combination with the availability of other resources on growth and gas exchange characteristics of these species grown in direct competition in miniature stands and compared characteristics of miniature stands with field-grown stands of similar composition.

In a greenhouse study, loblolly pine and red maple were grown in monoculture and 50:50 replacement mixtures at a 2.54 x 2.54 cm spacing for two growing cycles under ambient (408 ppm) or elevated (806 ppm) CO₂ concentrations and well-watered or droughted (0.5x well-watered) conditions. Loblolly pine dominated all mixed stands and

was proportionally larger while red maple was smaller in mixtures versus monocultures. This pattern was also observed in weed-free field-grown stands after five growing seasons.

Biomass data from loblolly pine and red maple grown in monocultures and 50:50 replacement mixtures at 2.54, 5.08 and 7.62 cm² initial spacing suggest that relative dominance of species in miniature stands is not dependent on initial spacing. Dominance of red maple over loblolly pine in all mixed stands in this experiment suggests that soil medium is important in determining relative growth of these species.

Photosynthesis rates and response to elevated CO₂ differed between whole stands and individual seedlings from these stands. Individual seedlings tended to be more responsive to elevated CO₂ compared to whole stands suggesting reduced responsiveness of lower canopy leaves may dampen the effect of elevated CO₂ on canopy photosynthesis rates.

Growth under elevated CO₂, alone or in combination with water did not affect relative sizes of these species. These results suggest that competitive interactions will not change between these species in response to growth in high CO₂ environments.

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CHAPTER I

INTRODUCTION

Rising atmospheric carbon dioxide (CO_2) concentration has recently become an issue of concern among the scientific community as well as the general public. Data taken in northern Europe has concluded that atmospheric CO_2 levels have been increasing from pre-industrial revolution concentrations between 270 and 280 ppm to current levels of approximately 360 ppm (Eamus and Jarvis 1989). CO_2 concentration is increasing at a rate of 1.2 ppm per year from present-day levels of approximately 350 ppm (Conway et al. 1988) and is expected to be 700 ppm by mid to late 21st century (Clark et al. 1982). Concern has also arisen that elevated CO_2 may also be accompanied by an increase in mean global temperature (Dickinson 1982) and changes in regional moisture regimes (Manabe et al. 1981).

While elevated CO_2 levels are generally associated with increased plant growth, plant species have been shown to vary greatly in their response to CO_2 enrichment (Kaushal et al. 1989; Poorter 1993; Ceulemans and Mousseau 1994). Based on data obtained from plants grown individually under higher than ambient CO_2 concentrations, researchers have hypothesized that differential responses to CO_2 enrichment may alter the outcome of competitive interactions between plant species and ultimately influence the composition of

some plant communities (Tolley and Strain 1985; Poorter 1993; Johnson et al. 1993). Growth chamber experiments involving the culture of two or more different herbaceous plant species in competitive mixtures have shown that competitive outcomes can be dependent on CO₂ concentration (Wray and Strain 1987; Bazzaz and Garbutt 1988; Reekie and Bazzaz 1989). Availability of other resources needed for plant growth will likely influence individual and community response to ambient CO₂ concentration (Hunt et al. 1991).

In the southeastern United States, loblolly pine (Pinus taeda) is widely managed for wood products, wildlife and aesthetic benefits. On many sites, loblolly pine growth is reduced through negative interactions with hardwood tree species including sweetgum (Liquidambar styraciflua) and red maple (Acer rubrum) (Miller et al. 1991; Glover and Zutter 1993). The increasing ingrowth of hardwood species in pine stands throughout the South during recent years has resulted in increased competition between pines and hardwoods (Boyce and Knight 1980). This, coupled with increased public interest in mixed pine-hardwood stands, will likely result in more mixed pine-hardwood forests in the future. Management strategies for these stand types under future atmospheric conditions are nonexistent since changes in stand dynamics under potentially altered growth environments are not known. The ongoing changes in ambient CO₂ concentration will likely impact the

growth and physiology of these species confounding the development of management strategies.

Other factors that influence growth of both pines and hardwoods are water stress, nutrient status and light availability. Interactions of these factors, with increased atmospheric CO₂, on the stand dynamics of hardwoods and pines grown in monoculture and mixtures have not been evaluated. In many cases, the physiological basis for responses to these environmental factors alone is also poorly understood. Optimum management of these forest types will require a more thorough knowledge of physiological response to interacting environmental factors as they relate to tree growth and yield. Global carbon modelers also need to better understand potential changes in carbon inputs and outputs in these forests to more accurately ascertain potential changes in global carbon cycling (Amthor 1994).

Ideally, these questions would be addressed through large scale in situ CO₂ fumigation experiments under a wide array of resource availabilities (Hendrey et al. 1993). The high cost associated with these experiments limits the applicability of this method. Miniature scale forest stands have shown potential for use in modeling effects of resource availabilities, including atmospheric CO₂ concentration, on forest stand dynamics (Williams et al 1986; Reekie and Bazzaz 1989; Fredericksen et al. 1993;

Ceulemans and Mousseau 1994). Compared to *in situ* studies, the small scale of these experiments reduces the amount of CO₂ needed for fumigation and shortens the time needed for competitive interactions to occur.

The primary objectives of this research were to determine the effects of ambient CO₂ concentrations on growth and gas exchange in miniature stands of loblolly pine grown in monoculture or mixture with sweetgum or red maple and under varying levels of resource availability. The role of intra- versus interspecific competition in determining species response to elevated CO₂ was evaluated. Observations were made to determine the extent to which miniature stands reflect stand development and gas exchange characteristics of loblolly pine and red maple stands planted in the field.

OBJECTIVES

1. To assess the physiological responses, allometry, resource use efficiency and relative yield responses between pure and mixed stands of loblolly pine (Pinus taeda) and each of two hardwood species, sweetgum (Liquidambar styraciflua) and red maple (Acer rubrum), in response to elevated CO₂, water stress and nutrient availability.
2. To determine the utility of greenhouse-grown mixtures and monocultures of loblolly pine and red maple in modeling growth, yield, allometric and physiological relationships in field-grown stands.
3. To determine the extent to which the outcome of competition loblolly pine-red maple mixtures is dependent upon stand density.
4. To measure growth and physiology of loblolly pine, red maple, white pine (Pinus strobus) and yellow-poplar (Liriodendron tulipifera) grown under different light environments.

CHAPTER II

LITERATURE REVIEW

COMPETITION FOR RESOURCES

Plant growth depends upon the availability of certain resources including light, water and nutrients. Some ecologists have hypothesized that competitive success is linked to resource uptake and internal use characteristics (Tilman 1982: Canham and Marks 1985: Grime 1979). This portion of the literature review summarizes current information regarding resource use characteristics of conifers and hardwoods as they relate to competitive interactions under varying levels of resource availability.

Light

The outcomes of competition for light are readily observable in plant communities but underlying processes remain poorly understood. The observation that species of trees have different abilities to survive and grow under reduced light environments led foresters to the development of the concept of shade tolerance. Shade tolerance is very difficult to quantify and its biological foundation has been hotly debated among forest researchers for many

decades (Toumey and Korstian 1937; Shirley 1943; Daniel et al. 1979). This debate centers on the relative importance of aboveground (competition for light) versus belowground factors (primarily competition for water and nutrients). This discussion focuses on the aboveground aspects of tolerance.

Hardwoods, in general, and particularly sweetgum and red maple, are considered to be more shade tolerant than loblolly pine (Baker and Longdon 1990; Kormanik 1990; Walters and Yawney 1990). Characteristics associated with shade tolerance include more leaf area, higher photosynthetic efficiency, and lower respiration in the understory (Loach 1967; Teskey and Shestha 1985; Walters and Field 1987). Early studies in which the photosynthetic rates of loblolly pine and Piedmont hardwood species were compared under varying light intensities indicated that pine has lower rates of net photosynthesis under low light and higher photosynthesis under high light conditions relative to the hardwood species (Kramer and Decker 1944; Kozlowski 1949). These studies suggested that low photosynthetic rates in loblolly pine under shaded conditions resulted in an inability to allocate enough carbon to roots, resulting in desiccation and death during periods of drought. Low photosynthetic rates of pine seedlings under shaded conditions have been attributed to a

higher degree of mutual shading of pine leaves relative to hardwoods (Kramer and Clark 1947).

Shade tolerance cannot be determined from the results of the aforementioned studies alone since net photosynthesis measurements were instantaneous and did not take into account the whole plant carbon budget (Walters et al. 1993). To determine whole plant carbon budget, total leaf area needs to be determined when making net photosynthesis calculations (Teskey et al. 1987). Studies that attempt to quantify shade tolerance, but ignore dark respiration and reallocation of carbon to non-photosynthetic tissue, underestimate whole plant light compensation point (Givnish 1988). Since light per unit area is a finite resource, canopy architecture and leaf area at the individual tree and stand levels may influence competitive abilities and stand structure. Trees with thick, many-layered crowns intercept available light more effectively and reduce the potential for growth of plants beneath them, further reducing negative interference from below.

Water

Water availability is an important factor limiting plant distribution, seedling establishment and growth throughout much of the world (Kozlowski et al. 1991). Diameter growth

of loblolly pine in Arkansas was found to be highly correlated with the amount and seasonal availability of soil moisture (Bassett 1964; Shoulders and Tiarks 1980). Plants reduce water loss under conditions of low water availability by closing stomata. Stomatal closure in loblolly pine was observed when water potentials reached -0.9 to -1.8 MPa while hardwood stomates remained open until potentials reached -1.9 to -2.5 MPa (Teskey and Hinckley 1986).

Hardwood species possess a number of mechanisms contributing to their success on dry sites. One mechanism thought to be responsible for the superior performance of some hardwoods relative to loblolly pine under dry conditions is a higher water absorption capacity in hardwoods because of a larger root system (Kozlowski 1949). Hardwoods were able to outcompete pines on the North Carolina Piedmont due seemingly to greater depth of rooting (Coile 1937). Sweetgum and broomsedge (Andropogon virginicus) depleted soil moisture below 14 cm and increased predawn xylem water potential of loblolly pine during their first growing season (Mitchell et al. 1993). In another study, the impact of weeds on loblolly pine water use decreased by the end of the second growing season (Morris et al. 1993).

Dougherty and Hennessey (1986) suggested that less water is lost by hardwoods on a per stand basis as a result

of having less leaf area and shorter leaf area duration. However, Zahner (1955) found little difference in evapotranspiration rates between pure pine and mixed pine/upland oak stand over the length of a growing season. Despite the evidence suggesting greater drought tolerance of hardwoods, loblolly pine is often able to outcompete hardwoods on dry upland sites (Gjerstad and Barber 1987) suggesting the importance of other factors. The importance of water availability in limiting tree growth and competition tends to decrease over time as nutrients become the more important limiting factor (Nambiar and Sands 1993).

Nitrogen

Nitrogen deficiencies limit loblolly pine growth in both the Coastal Plain and Piedmont physiographic provinces (Burger and Kluender 1982; Allen et al. 1990). Much less is known about the nutrient requirements of southern hardwood species but nitrogen deficiencies likely limit their growth as well. Following the reasoning of Vitousek (1982), conifers should be more successful on nutrient poor sites than deciduous trees because of their ability to produce more dry matter per unit available nitrogen. Growth reductions have been associated with application of nitrogen fertilizer under weeded conditions in white pine

(Pinus strobus) (Brand 1990) and red pine (Pinus resinosa) (Elliott and White 1993). Trees that are well-matched to soil nutrient status will likely be successful competitors. In this way, nutrient status can influence competitive interactions and outcomes.

Nitrogen is essential for the production of protein, chlorophyll and a number of other compounds. Photosynthetic capacity has been correlated with leaf nitrogen content in several species (Walters and Field 1987; Ellsworth and Reich 1992). Nutrient availability can also influence carbon allocation in conifers. In a long-term fertilization study, Scots pine (Pinus sylvestris) and Norway spruce (Picea abies) responded to sub-optimal nutrient levels by allocating a larger portion of photosynthates toward fine-root production resulting in decreased stem and leaf growth and reduced ability to produce photosynthates (Axelsson and Axelsson 1986). However, increased nitrogen availability did not change below-ground partitioning of photosynthates in a Wisconsin deciduous forest (Nadelhoffer et al. 1985).

PHYSIOLOGICAL RESPONSES TO ELEVATED CO₂

The resource use patterns described in the previous sections are underlain by several interrelated physiological processes. A number of studies have been

conducted to determine how elevated atmospheric CO₂ affects these processes. An important distinction to be made among these studies is the CO₂ environment in which experimental plant material was grown and physiological processes measured. Following the terminology of Eamus and Jarvis (1989), plants grown at ambient CO₂, but measured at elevated CO₂ levels, are referred to as "non-acclimated" while those both grown and measured at some elevated CO₂ concentration are defined as "acclimating." This distinction is necessary because physiological responses to a sudden increase in CO₂ may not accurately represent long term responses. For example, in crop plants, short-term (non-acclimated) CO₂ assimilation was higher compared to longer term assimilation rates (Cure and Acock 1986). Measurements made on acclimating seedlings are likely to be more representative of plants in future environments where CO₂ concentration will remain consistently higher than present levels. Predicting responses of plants in future environments is further complicated by the observations that acclimation may require months or even generations (Woodward 1987). Furthermore, individual trees are likely to change their response to elevated CO₂ as a function of age (Eamus and Jarvis 1989). Because of the complications associated with non-acclimated plant studies, only acclimating plant studies are cited in this review.

Stomatal Conductance

Plants obtain CO₂ through stomata. Since water loss accompanies CO₂ gain, plants appear to regulate stomatal opening so that an adequate supply of CO₂ is available for photosynthesis while a minimum amount of water is lost. Studies conducted with forest tree seedlings show that species vary in their stomatal response to elevated CO₂ (Eamus and Jarvis 1989). Tolley and Strain (1985) found sweetgum seedlings grown under both high and low light conditions reduce stomatal conductance in response to elevated CO₂ while loblolly pine seedlings showed unchanged stomatal conductance under high light and reduced conductance in response to high CO₂ under low light conditions. Stomatal conductance increased under elevated CO₂ concentrations in yellow-poplar (Liriodendron tulipifera) (Norby and O'Neill 1991) and Douglas-fir (Pseudotsuga menziesii) (Hollinger 1987). Relative conductance varied diurnally in ponderosa pine (Pinus ponderosa) grown under elevated CO₂ conditions in open-top chambers, a pattern not observed under ambient CO₂ concentrations (Surano et al. 1986). Stomatal conductance decreased in response to elevated CO₂ in P-deficient Monterey pine (Pinus radiata) but not in seedlings in which other nutrients were not limiting (Conroy et al. 1988). Lower conductance under elevated CO₂ may be a result of

reduced stomatal density and reduced stomatal opening (Woodward and Bazzaz 1988; Ceulemans and Mousseau 1994).

CO₂ concentration can affect transpiration rate so that leaf temperature regulation is altered. Transpiration increases proportionally with stomatal conductance assuming leaf surface temperature and relative humidity remain constant. However, decreased transpiration under high CO₂ environments reduces evaporative cooling resulting in increased leaf surface temperature. This could lead to heat injury in hot environments. Under these circumstances, transpiration does not decrease as rapidly as stomatal conductance due to higher internal vapor pressure (Pearcy and Bjorkman 1983). Surano et al. (1986) reported the incidence of heat injury in Ponderosa pine grown in open-top chambers under an elevated CO₂ environment. Decreased stomatal conductance and transpiration has been shown to contribute to increased water use efficiency in tree species grown at elevated CO₂ including Monterey pine (Conroy et al. 1988), white oak (Quercus alba) (Norby et al. 1986a), yellow-poplar (Norby and O'Neill 1991) red spruce (Picea rubens) (Samuelson and Seiler 1994) and sweetgum (Tolley and Strain 1985). Increased water use efficiency occurs at the leaf level in response to decreased stomatal conductance and transpiration as well as through stimulation of photosynthesis by elevated CO₂ (Tyree and Alexander 1993).

However, other morphological changes were reported to be more important contributors toward increased water use efficiency on the whole plant level. In yellow-poplar seedlings, increased fine root to leaf area (water absorbing to water losing organ) ratios under increased CO₂ concentrations were associated with increased plant water use efficiency. Plants with higher water use efficiency were also found to have higher stomatal conductance (Norby and O'Neill 1991). However, these results are based on measurements from single leaves which may be an unreliable indicator of whole tree response to CO₂ enrichment (Norby and O'Neill (1991).

Increased water use efficiency may reduce water consumption on a per unit leaf area basis decreasing the likelihood of drought damage in plants in which leaf area is not increased by elevated CO₂. However, total leaf area often increases in response to CO₂ enrichment, possibly negating the benefit of increased water use efficiency as measured on a per unit leaf area basis (Eamus and Jarvis 1989). A possible benefit of CO₂ enrichment is the continuation of growth further into a drought than otherwise possible since the onset of drought is delayed and reduced in severity by increased atmospheric CO₂ levels (Eamus and Jarvis 1989).

Plant water status is affected by a change in transpiration and an increase in osmotically active

compounds in leaves. Plants respond to increased CO₂ by reducing transpiration, thereby lowering the water potential gradient and reducing the driving force for water from the soil and through the plant (Pearcy and Bjorkman 1983). However, increased photosynthesis could cause an increased concentration of osmotically-active compounds in leaves. Osmotic potential decreased in wheat plants and turgor was maintained at lower water potentials. As a result, plants were thought to be better adapted to drought under elevated CO₂ (Sionit et al. 1980). Tolley and Strain (1984a) reported that CO₂ enrichment ameliorated growth reduction in water stressed environments in sweetgum and, to a lesser extent, in loblolly pine. Effects of water stress on gas exchange were delayed for sweetgum seedlings at elevated CO₂ (Tolley and Strain 1985).

Photosynthesis

Photosynthetic rates are generally initially higher in trees grown in elevated CO₂ environments relative to those in ambient CO₂. Both water-stressed and unstressed loblolly pine and sweetgum grown at high light (1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD) responded to elevated CO₂ with slightly higher net photosynthetic rates. Both species maintained higher net photosynthetic rates in response to drought stress when

grown under high CO₂ concentrations (Tolley and Strain 1985).

Photosynthetic response to elevated CO₂ can be affected by nutrient status. Monterey pine growing in elevated CO₂ increased photosynthetic rates only when phosphorus was not deficient (Conroy et al. 1986) and photosynthesis in two-year old loblolly pine seedlings responded to elevated CO₂ only when supplemental nitrogen was provided (Tissue et al. 1993; Griffin et al. 1993).

Mechanisms for increased photosynthetic responses under elevated CO₂ conditions include higher substrate availability for Rubisco, higher Rubisco activation, higher quantum yield and decreased photorespiration (Pearcy and Bjorkman 1983). Drought stress may have been delayed in Monterey pine seedlings through a maintenance of electron flow subsequent to photosystem II occurring only in seedlings grown under high CO₂ conditions (Conroy et al. 1986). These authors also attribute reduced photosynthesis in phosphorus deficient seedlings at high CO₂ to structural changes in the chloroplast thylakoid membrane resulting in reduced energy transfer in photon-harvesting proteins.

Photosynthetic acclimation, or reduced photosynthesis rates over time in seedlings grown under elevated CO₂ is a widely observed phenomenon. Differences in long-term plant response to elevated CO₂ may be a consequence of differential CO₂ acclimation between species. Fetcher et

al. (1988) reported photosynthetic acclimation in sweetgum, but not in loblolly pine, following 15 months exposure to elevated CO₂. Acclimation can result from decreased chlorophyll content and is thought to be caused by a feedback inhibition in which starches accumulate in leaves due to decreased sink strength (Bowes 1991; Farrar and Williams 1991; Stitt 1991). Acclimation can be accompanied by chlorosis (Wulff and Strain 1982; Oberbauer et al. 1985) and reduced chlorophyll a:b ratio as a result of decreased chlorophyll a content (Cave et al. 1981). High starch concentration may reduce RuBP/P regeneration capacities and disrupt chloroplasts thereby reducing photosynthetic capacities (Wulff and Strain 1982; Bowes 1991; Tissue et al. 1993). Starch accumulation was believed to cause reduction in specific leaf area in tropical tree species Ochroma lagopus and Pentaclethra macroloba (Oberbauer et al. 1985). Maintenance of high photosynthetic rates depends on the presence of active carbon sinks (Koch et al. 1986; Bowes 1991). Pot grown seedlings may exhibit photosynthetic reduction because of limited soil volume and nutrient availability (Arp 1991; Thomas and Strain 1991). Acclimation occurred in sweet chestnut (Castanea sativa) seedlings not supplied with supplemental nitrogen while acclimation did not occur in fertilized seedlings (El Kohen and Mousseau 1994). However, net photosynthesis changes in red spruce in response to growth under high CO₂ was

unaffected by pot size (Samuelson and Seiler 1994). While widely reported in greenhouse studies, photosynthetic acclimation has not been observed in field grown tree species and may be an artifact of experimental conditions (Gunderson et al. 1993; Garcia et al. 1994).

Respiration

In C_3 plants, large amounts of fixed carbon are lost through photorespiration. Although evidence is limited, increasing ambient CO_2 appears to result in decreased whole plant respiration (Farrar and Williams 1991). Decreases in photorespiration occur through an increase in the competitive ability of CO_2 versus O_2 on Rubisco reaction sites. Whole plant dark respiration in sweet chestnut seedlings was reduced under elevated CO_2 concentrations (Mousseau 1993). Wullshleger et al. (1992) found dark respiration decreased in yellow-poplar and white oak exposed to elevated CO_2 . These authors caution that the implications of these data are unclear within the context of future environmental conditions. Potential increases in temperature, combined with contradictory results with agronomic crops (Farrar and Williams 1991), further complicated the inferences drawn from these data.

Respiratory patterns in tree organs have not been measured even though such information would be more

meaningful than whole plant data toward understanding the nature of dry weight accumulation in response to environmental changes (Farrar and Williams 1991). Research with agricultural crops has shown response of leaf and root respiration to elevated CO₂ to be species dependent (Gifford et al. 1985; Farrar and Williams 1991).

Growth

Most studies involving long-term exposure to elevated CO₂ have resulted in increased growth compared to ambient controls (Eamus and Jarvis 1989; Ceulemans and Mousseau 1994).

Sweetgum grown at elevated CO₂ (675 ppm) and high light (1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$) showed increased height, leaf area, basal stem diameter and total dry weight compared to controls (Tolley and Strain 1984b). Sweetgum grown under high CO₂ and low light (250 $\mu\text{mol m}^{-2} \text{s}^{-1}$) showed the same tendencies but to a lesser extent. Loblolly pine growth in the same study was largely unresponsive to elevated CO₂. Growth enhancement was not observed in an open top chamber study with the same species (Rogers et al. 1983).

Other studies have shown that elevated CO₂ can ameliorate growth reductions associated with droughted conditions (Morison 1993). Seedlings grown under elevated CO₂ and droughted conditions grew as large or

larger than well-watered seedlings grown under ambient CO₂ concentrations in loblolly pine (Tschaplinski et al. 1993) and sweetgum (Tolley and Strain 1984a). Growth of droughted cotton plants was more responsive to elevated CO₂ compared to well-watered plants (Kimball et al. 1993).

Red maple seedlings grown from seed for one growing season responded to growth under elevated CO₂ under most factorial combinations of light and nitrogen (Bazzaz and Miao 1993). Seedlings were especially responsive under lower levels of availability of these resources. However, red maple response to elevated CO₂ appears to be slow; seedling height, diameter and leaf area had not responded to elevated CO₂ after 60 days of growth from seed (Bazzaz et al. 1990).

While relative growth increases at elevated CO₂ can be affected by nutrient status (Brown and Higginbotham 1986), growth responses have been observed in white oak seedlings (Norby et al. 1986a,b) and cotton (Kimball et al. 1993) despite severe nitrogen deficiency. Loblolly pine showed a positive growth response to elevated CO₂ only when fertilized with nitrogen (Griffin et al. 1993).

Photosynthetic acclimation associated with elevated CO₂ in some species can be manifested in reduced growth rates. Under experimental conditions restricted rooting can reduce growth increases associated with elevated CO₂ (Idso and Kimball 1994). Increase in sweetgum dry weight over the

course of a 113-day CO₂ enrichment study occurred primarily during the earlier stages of the study. Larger portions of available photosynthate were allocated toward the maintenance of larger seedlings during the latter portions of the study (Tolley and Strain 1984b). The same response was observed to a lesser extent in loblolly pine. These authors suggested that these results support the hypothesis that increased atmospheric CO₂ will accelerate the rate of biomass accumulation rather than increase the total amount of biomass present.

Root:Shoot Ratio

Root:shoot ratio in tree seedlings varies greatly in response to growth under elevated CO₂ (Tyree and Alexander 1993). Most species studied show no significant change in root:shoot ratio. These include red maple, sugar maple (Acer saccharum), white pine (Bazzaz et al. (1990), Austrian pine (Pinus nigra) (Kaushal et al. 1989), Douglas-fir and Monterey pine (Hollinger 1987). Significant decreases in root:shoot ratio were found in American beech (Fagus grandifolia) (Bazzaz et al. 1990). Increased root:shoot ratios in several CO₂ enrichment studies (Norby et al. 1986a; Luxmoore et al. 1986; Norby et al. 1987) was thought to be a result of low soil fertility (Eamus and Jarvis 1989). In these studies, nutrient stress

resulting from CO₂-enhanced growth resulted in a higher proportion of carbon allocated to fine root production (Luxmoore et al. 1986; Eamus and Jarvis 1989). However, Higginbotham and others (1985) working with lodgepole pine (Pinus contorta) and Mousseau and Enoch (1989) using sweet chestnut (Castanea sativa) found root:shoot ratio increased despite apparently adequate soil nutrient status (Eamus and Jarvis 1989). Root:shoot ratio may be sensitive to experimental conditions that were not controlled in CO₂ enrichment studies. In sweetgum and loblolly pine, increased (Rogers et al. 1983), decreased (Tolley and Strain 1984a) and unchanged (Sionit et al. 1985) root:shoot ratios have been attributed to CO₂ enrichment. The ambiguity of these results suggests the importance of some factor other than CO₂ concentration. Variability of root:shoot ratios may result from varietal differences, length of CO₂ exposure, plant age, nutrient status, root zone restriction, or other unfavorable growth environment (Enoch and Zieslin 1988).

EFFECTS OF ELEVATED CO₂ ON COMPETITION

Trees in natural settings rarely grow in the absence of competition. Studies attempting to measure the effects of CO₂ on inter- and intraspecific competition represent a step

beyond individual seedlings studies toward understanding community changes under future environmental conditions.

Some attempts have been made to predict competition in future environments by measuring relative yields of two or more species grown together in high CO₂ environments. These studies have adopted both indirect and direct approaches in addressing this problem. The indirect approach involves growing plants of two or more species individually and making inferences regarding competitive success based on relative yield (Tolley and Strain 1984b; Wray and Strain 1986). Other studies have measured competition effects directly by growing plants together in interspecific or inter- and intraspecific mixtures (Wray and Strain 1987; Bazzaz and Garbutt 1988; Rochefort and Bazzaz 1992).

Accelerated growth under elevated CO₂ can directly affect stand dynamics. Self-thinning occurred more rapidly in pure stands of the C₃ annual Abutilon grown under elevated CO₂ resulting in more homogeneous stand structure (Bazzaz and McConnaughay 1992). A number of studies have grown C₃ and C₄ plants together in competitive mixtures. Invariably, species with a C₃ metabolism have a competitive advantage at higher CO₂ levels. In North Carolina old fields, Aster pilosus, a C₃ plant is frequently replaced by the C₄ broomsedge Andropogon virginicus. Based on a study, where the two species were grown at elevated CO₂, Wray and Strain (1986,1987) suggested that succession may be delayed

under these circumstances in future environmental conditions. Increased drought tolerance under high CO₂ was thought to be the mechanism responsible for the success of the Aster. Similarly, improved drought tolerance and higher growth rates of sweetgum relative to loblolly pine under high CO₂ may be a mechanism allowing sweetgum to colonize dryer sites currently more favorable for the establishment of loblolly pine. Tolley and Strain (1984a) and Sionit et al. (1985) arrived at these conclusions based on data collected from seedlings grown individually in pots.

Several studies have shown that individual plant response to elevated CO₂ can depend on the availability of other resources such as light, nutrients and water. Growing seedlings as individuals, versus under competition, can also affect response to CO₂ concentration. Zangerl and Bazzaz (1984) found allocation to seed, reproductive success and shoot biomass changed in response to increased CO₂ in a six species mixture of annual plants. Community response to CO₂ enrichment was found to be light and nutrient dependent. However, response to CO₂ enrichment was more dependent upon light and nutrients in individuals versus communities. In a serpentine grass community grown on native soils, individuals showed a significant response to CO₂ enrichment in two of six species tested (Williams et al. 1988). No significant responses to CO₂ were observed in

any species when grown in competitive mixture. These authors suggested that CO₂ response may have been further dampened by adaptation to low resource availability in these species.

Results from studies where other resources presumably did not limit growth varied with respect to projected competitive outcomes. A community of five tropical tree seedlings showed species-dependent changes in canopy architecture under high CO₂ concentrations (Reekie and Bazzaz 1989). Both relative canopy heights and leaf distribution patterns changed. Trichospermum and Cecropia developed crowns that were both taller and wider near the top relative to Senna which displayed no increase in crown height growth as well as a more compact crown. While competitive outcomes were not determined, the results of this study suggested that competitive outcomes under high CO₂ would be determined by a species ability to capture light.

Williams et al. (1986) established simulated upland and bottomland forest communities consisting of three species mixtures of one-year-old tree seedlings under high and low light conditions and three levels of CO₂. No significant CO₂ main effects were observed in terms of growth in either community. Light level significantly affected the growth of sycamore (Platanus occidentalis) relative to silver maple (Acer saccharinum) and green ash

(Fraxinus pennsylvanica). Similarly, in the upland community, growth of yellow-poplar increased relative to hickory (Carya ovata) and red oak (Quercus rubra).

Growing plants in inter- and intraspecific mixtures allows comparison between the relative importance of each of these types of competition. A study where annual plant species were grown in one, two, three and four species mixtures resulted in increased competitive success of C_3 versus C_4 species (Bazzaz and Garbutt 1988). No other patterns associated with CO_2 concentration were observed. Four species of birches grown in inter- and intraspecific pairs under ambient and elevated CO_2 showed a growth response effect associated with neighboring species that was not influenced by CO_2 environment (Rocheftort and Bazzaz 1992). Wray and Strain (1987) found leaf area and biomass per plant were greater in 50:50 mixtures versus monocultures for the C_3 aster and the opposite was shown in the C_4 broomsedge. Total community productivity was greater in 50:50 mixtures of the two species after 5 weeks in high CO_2 treatments. This response is reversed by 9 weeks at which time mixed yield was less than monoculture yields.

While increased relative drought tolerance associated with elevated CO_2 is expected to favor some species, the importance of increased water use efficiency remains unclear. Bazzaz and Carlson (1984) suggest that increased water use efficiency in Polygonum pensylvanicum allowed the

species to partially displace Amaranthus retroflexus in simulated communities. However, Reekie and Bazzaz (1989) suggested that elevated CO₂ would favor the species with a high water requirement (low water use efficiency) under conditions of water stress.

EXPERIMENTAL APPROACHES FOR ASSESSING COMPETITIVE INTERACTIONS IN A HIGH CO₂ ENVIRONMENT

Ideally, the effects of atmospheric CO₂ increase on forest stands could be determined through long-term fumigation experiments in stands of various ages and composition. Unfortunately, the cost of CO₂ over a sufficient length of time usually prohibits wide spread implementation of these types of studies. For this reason, researchers have most often conducted CO₂ exposure studies under greenhouse conditions. However, temporal, spatial and physiological differences between greenhouse and field-grown plants need to be considered before extrapolating experimental results.

Greenhouse versus Field-Grown Plants

Little research has been conducted to determine how greenhouse grown plants differ physiologically from those grown under field conditions. Physiological differences could have a profound impact on species interactions.

Leaves of Populus clones grown in controlled environments had less cuticular wax than field-grown counterparts. Also, occlusion of stomata were observed on the abaxial surface of leaves in field-grown plants (Pallardy and Kozlowski 1980). Differences in light intensity and relative humidity are thought to be responsible for these differences. Both physiological differences are thought to reduce water loss in the field grown leaves through the reduction of minimal leaf diffusive resistance and result in delayed fatal desiccation during droughts (Pallardy and Kozlowski 1980).

Geneticists working with loblolly pine seedlings have devised a methodology for predicting future seedling growth in the field based on early growth of greenhouse-raised seedlings. Waxler and van Bouteren (1981) grew loblolly pine seedlings from West Gulf Coast sources under a range of moisture stress conditions. Shoot weight and root:shoot ratio were found to be the growth variables most highly correlated with later success in the field. Seedlings grown under unstressed conditions in the greenhouse were found to be the best predictor of family superiority when outplanted across a range of site conditions. Li et al. (1991) working with loblolly pine from coastal plain North Carolina and Virginia seed sources found shoot weight to be poorly correlated with future performance. Cyclic elongation, number of growth cycles, and number of stem

units were found to be most highly correlated with 12th year height. Seedlings grown in the greenhouse under nitrogen concentrations similar to those found under field conditions provided the best prediction of future height growth.

Competition Experiments Under Greenhouse and Field Conditions

Studies have been conducted where plant species were grown under competitive conditions in both greenhouse and field environments. Unfortunately, comparison between the greenhouse and field components of each experiment is limited by differences in experimental design (eg. Perez and Masiunas 1990). Fredericksen et al.(1993a,b) grew loblolly pine seedlings with each of two hardwood species, red maple and black locust, under field and greenhouse conditions. In the field, loblolly pine was dominant while hardwoods were dominant in the greenhouse. Fredericksen (1991) suggested a number of possible factors that may have been responsible for the differences in competitive outcomes. These include reduced resource use efficiency by loblolly pine in the greenhouse due to suboptimal light availability for this shade-intolerant species. Differences in developmental phenology between the two species may have produced density-dependent

competition outcomes. Loblolly pine may require a longer initial developmental period free from competition in order to later become the dominant species. Perhaps the high planting density in the greenhouse resulted in the two species initiating competitive interactions prior to the completion of the establishment period in the pine (Fredericksen 1991). Top-clipping of the hardwoods in the greenhouse experiment may have produced a more favorable root-shoot ratio responsible for the superior performance of these species.

In a study where two varieties of potato (Solanum tuberosum) and two weeds, redroot pigweed (Amaranthus retroflexus) and barnyard grass (Echinochloa crus-galli) were grown in two-species competitive mixtures with one potato and one weed species in each, competitive outcomes differed between the two experimental environments (Vangessel and Renner 1990). Barnyard grass was more competitive under greenhouse conditions while pigweed was the dominant weed in the field. Competitive differences between the two species was thought to result from differences in soil moisture between field and greenhouse conditions. High moisture availability in the greenhouse favored the growth of barnyard grass leading these researchers to conclude that competitive outcomes were dependent upon resource levels (cf. Grime 1979). Another study using wild oats (Avena fatua) and barley (Hordeum

vulgare) in similarly designed field and greenhouse replacement series concluded oats to be the superior competitor regardless of environmental conditions (Dunan and Zimdahl 1991).

Differences in root:shoot ratios commonly confound controlled pine and hardwood competition studies. All of the studies mentioned here involve trees established as seedlings or from seed at the beginning of the study. However, on recently harvested forest land, competitive hardwoods are usually stump sprouts or root suckers. These individuals are capable of more rapid initial growth and are probably more successful competitors for light, nutrients and water compared to newly-established seedlings because of starch reserves and a more extensive root system. The outcome of competition studies may also be impacted by the timing of planting. All species are generally sown or planted at the same time, potentially resulting in artificial timing of emergence compared to natural settings. Timing of emergence can greatly impact three-year-old seedling height in yellow-poplar as shown by Trimble and Tryon (1969).

Competition studies are often plagued by the difficulty associated with finding homogeneous sites for studies. Competitive outcomes are influenced by site-related factors. Studies where plants were grown at

several densities can have confounding site or block-related interactions.

Design of Competition Experiments

A number of experimental schemes have been developed to assess competitive interactions between two plant species. These have included substitutive designs, replacement, complete additive, additive series, and partial additive designs (Harper 1977). Additive designs hold the density of the crop species constant while weed species density is varied. The applicability of this method is limited because simultaneous variation of proportion and density confound some interpretations of results. In the replacement design, total plant density is held constant while the proportion of individual species is varied. The nature of competitive interactions is then determined by comparing the yield of species in mixtures with those in monoculture (i.e. whether interspecific interactions are negative (competition), neutral or positive (synergistic) or any of a number of other permutations outlined by Burkholder (1952)). These experiments are based on the assumption that plants are grown to the point of constant final yield (de Wit 1960). The disadvantage of the replacement design is that outcomes of interspecific competition experiments can depend upon planting density

(Marshall and Jain 1969). This is most easily overcome by repeating replacement-type designs over a range of densities as recommended by Rejmanek et al. 1988 and Roush et al. (1989). Rejmanek et al. (1988) found the complete additive design where densities of both species are varied in all possible combinations to provide the best model of overall competitiveness between barnyard grass and tomato (Lycopersicon esculentum).

Controlled competition experiments have traditionally used total plant biomass or merchantable yield as the response variable. This seems to be appropriate for agricultural field crops where experiments can be conducted for the duration of the plant's lifecycle. In contrast, experiments with tree species are conducted for only a small fraction of the lifespan and terminate long before a merchantable product is obtained. Forestry competition experiments have traditionally used stem biomass (Fredericksen 1993b) or estimated stem volume (Cole and Newton 1987; Fredericksen et al. 1993a; Shainsky and Radosevich 1991). Tree height or crown position may be a more appropriate response variable in these experiments since future success is a more important consideration than present yield. In an experiment where potato and two common weed species were grown in competition, belowground biomass for both crop and weed species was suggested as a more accurate predictor of interference (Vangessel and

Renner 1990). A series of replacement experiments with wild oats and barley used classical growth analysis variables including relative growth rate, net assimilation rate, leaf area ratio, and absolute growth rate in addition to total leaf area and biomass per plant. Dry weight was found to be the most sensitive indicator of competition (Dunan and Zimdahl 1991).

The best predictor of future success could conceivably vary in response to environmental conditions. For example, belowground biomass as it relates to water and nutrient uptake may be the most appropriate response variable in environments where these resources are limiting. Where light is a limiting factor, leaf biomass or crown volume may be the best determinant of future success. Jolliffe et al. (1984) suggested the use of leaf area or dry matter partitioning as additional response variables to explain the physiological basis of yield variation between mixed and monoculture stands. In the absence of data determining the best response variable under a given set of conditions, stem volume or biomass will probably continue to be used since both of these variables integrate other physiological functions and allometric relationships.

Studies evaluating the impact of increased atmospheric CO₂ on competitive interactions must operate within the temporal and spatial constraints associated with most research programs? Bazzaz and McConnaughay (1992) suggest

that plant-plant interactions can be maximized under elevated CO₂ by creating experimental conditions where the following conditions are provided: 1. Plant densities are high, 2. Competition for light is intense, 3. Interspecific size differences are small, 4. Response of growth to CO₂ is great, 5. Other resources do not limit growth.

DYNAMICS OF PINE-HARDWOOD MIXTURES

In recent years, public pressure has stimulated an interest in the management of pine-hardwood forests in the southeast. Mixed stands are more diverse biologically in terms of wildflower, tree and wildlife populations and therefore have greater aesthetic appeal. Mixed stands can also provide a low cost management alternative for landowners unwilling to invest large amounts of capital in their forestland (Phillips and Abercrombie 1987: Cooper 1989). Mixed stand management is generally believed to be less profitable than monoculture management but even this is debated (Cooper 1989: Franklin 1989).

Silvicultural strategies for mixed stands remain poorly developed. In a South Carolina Piedmont hardwood stand, openings were cut one-third and one-tenth acre in size with and without herbicidal control of hardwood vegetation. Survival of planted loblolly pine was good in all treatments (Waldrop 1990). Further data collected from

this study should prove useful in the development of unevenaged pine-hardwood management strategies.

Two studies where pine-hardwood mixtures were developed resulted in very different conclusions regarding the effects of season of harvest on stand composition. In a 50-year-old mixed oak stand on the Virginia Piedmont, loblolly pine seedlings were planted in conjunction with clearcutting and an array of herbicide treatments. Harvests were carried out during the dormant and growing season. Following five years of stand development, the pine component was found to be larger in response to harvesting during the growing season (Zedaker et al. 1989). However, McMinn (1989) found the pine component to be greater in association with dormant season harvesting in naturally regenerated pine-hardwood stands on the Georgia Piedmont. The variability of results underscores the need to develop management strategies for pine-hardwood stands on a localized, site quality-specific basis (McGee 1989).

Most research in the area of pine-hardwood stand management has been in the form of case studies where the primary objective was the evaluation of silvicultural strategies. Very few studies have employed systematic designs to study interspecific interactions in forest systems. Shainsky and Radosevich (1986) used a modified replacement series design to evaluate competitive interactions in a Ponderosa pine-manzanita system in the

Pacific Northwest. Growth with manzanita was found to reduce water potentials and productivity of pine compared to monoculture stands. Fredericksen et al. (1993a,b) studied pine-hardwood interactions on the Virginia Piedmont and in greenhouse stands using a replacement series design. Loblolly pine was grown in monoculture and in competitive mixture with red maple and black locust (Robinia pseudoacacia) under total herbaceous control or with a tall fescue (Festuca arundinacea) ground cover. Loblolly pine dominated in all competitive mixtures with hardwoods. This response was stronger under the herbaceous control treatment. The success of loblolly pine was attributed to efficient use of water and nutrients. Allometric relationships including root:shoot ratio, crown dimensions and specific leaf area varied between competitive regimes.

In two competition experiments conducted on the coastal plain of Alabama, loblolly pine growth was negatively impacted by sweetgum and broomsedge during the first growing season (Perry et al. 1993; Morris et al. 1993). Growth suppression of pine was correlated with density in the addition series experiment (Perry et al. 1993).

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CHAPTER III

EFFECTS OF ELEVATED CARBON DIOXIDE, WATER STRESS AND NITROGEN LEVEL ON COMPETITIVE INTERACTIONS OF SIMULATED LOBLOLLY PINE AND SWEETGUM STANDS

INTRODUCTION

Atmospheric concentration of carbon dioxide has been increasing since the onset of the industrial revolution. These increases are projected to continue until sometime near the middle of the 21st century resulting in nearly double present day levels (Clark et al. 1982). Studies with forest tree species have shown early growth responses to CO₂ to vary between species. Loblolly pine (Pinus taeda L.) and sweetgum (Liquidambar styraciflua L.) are widely co-occurring tree species of biological and economic importance throughout southern United States.

Understanding the impact of increasing atmospheric CO₂ concentrations on the growth characteristics and competitive interactions of these species will help forest managers of the region prepare for possible changes in forest dynamics.

Several studies have evaluated the response of loblolly pine and sweetgum to a range of atmospheric CO₂ concentrations at various levels of resource availability. Loblolly pine and sweetgum seedlings grown under high CO₂ were larger than controls grown under ambient CO₂ (Tolley

and Strain 1984b; Sionit et al. 1985). The availability of water and nutrients can also affect tree growth response to elevated CO₂. Loblolly pine seedlings grown under drought stress and elevated CO₂ had the same total, root and shoot biomass as well-watered plants grown under present day CO₂ concentrations (Tschaplinski et al. 1993). Drought stressed seedlings of both species grown under high CO₂ were found to maintain growth further into a drought than low CO₂ controls. This response was stronger in sweetgum than in loblolly pine prompting the researchers to conclude that sweetgum under a future, high CO₂ environment may replace loblolly pine on dry sites (Tolley and Strain 1984a). Nutrient availability may also mediate growth response to elevated CO₂. Loblolly pine grown in an infertile artificial soil medium showed a positive growth response to elevated CO₂ only when nitrogen fertilizer was supplied (Griffin et al. 1993).

Studies attempting to predict forest response to elevated CO₂ concentrations have typically used individually-grown seedlings (Tolley and Strain 1984a,b; Sionit et al. 1985). However, research with annual species has suggested that the development of natural stands in a high CO₂ environment differs from that of individual plants (Zangerl and Bazzaz 1984; Williams et al. 1988; Bazzaz and McConnaughay 1992). In these studies, competition dampened the elevated CO₂-induced positive growth response.

To date, all studies using simulated forest stands in CO₂ studies have grown mixtures of several species (Reekie and Bazzaz 1989: Williams et al. 1986). Since trees grown in stands interact with individuals of the same as well as those of other species, our understanding of stand dynamics under elevated CO₂ would benefit from the use of simulated monocultures and mixed stands. Inherent interspecific variation in the rate of resource capture under different levels of resource availability may result in stand yield and growth characteristics dependent on the availability of several resources as well as stand composition.

The objectives of this study were to determine the interaction of CO₂ enrichment, water availability, nitrogen status, and stand composition on yield and stand biomass allocation. Seedlings were grown for two accelerated growing cycles to better mimic characteristics of field grown plants. A narrow initial spacing was used to hasten interactions between seedlings. While this study and others of similar design do not necessarily predict the exact outcome of competition under field conditions (Vangessel and Renner 1990: Fredericksen et al.1993), they may be useful in determining relative competitive success between species under various levels of resource availability.

METHODS

The study was conducted at the Center for Forest Environmental Studies (U. S. D. A. Forest Service) in Dry Branch, Georgia. The experimental stands were grown for two growing cycles over the course of a ten month period.

Plant Culture and Growth Environment

Plastic pots 30 cm in diameter and 37 cm deep were filled with a Cowarts series (fine loamy, silicious, thermic, Typic Kanhapludult) forest soil. Prior to potting, soil was sifted through a 64 mm (one-quarter inch) hardware cloth screen, amended with 200 kg K/ha, 100 kg P/ha and 50 kg Ca/ha and mixed with coarse, washed white sand at a 5:1 ratio to insure adequate drainage. Stratified loblolly pine and sweetgum seed collected from open pollinated trees (Rapides Parish, La.) were planted in pots at a 2.54 by 2.54 cm spacing both as pure stands of each species and in 50:50 replacement series mixtures.

Following seedling establishment, pots were placed in Continuous Stirred Tank Reactors (CSTRs) maintained at one of two CO₂ concentrations: One treatment was maintained at ambient CO₂ concentrations, averaging 408 ppm with a range of 363 to 459 ppm. The elevated CO₂ treatment attempted to add 400 ppm CO₂ to ambient concentrations and averaged 806

ppm with a range of 759 to 857 ppm.

CSTRs were enclosed in a greenhouse and exposed to full sunlight. Supplemental lighting was provided by 1000 watt metal halide lights to maintain a 16-hour photoperiod. After ten weeks of growth, photoperiods were reduced to eight hours per day and air temperature was gradually reduced to induce dormancy. During the first growing cycle, temperature and relative humidity averaged 21°C and 65% respectively. During the shortened photoperiod, temperature was gradually lowered from 21°C to approximately 10°C over a one month period. Temperature and relative humidity averaged 11°C and 80% respectively during the final four weeks of the shortened photoperiod. Eight weeks of cold storage in a cold room at 2°C were used to fulfill chilling requirements. Plastic bags were placed over stands to prevent desiccation during chilling. Second growing cycle temperature and relative humidity averaged 22°C and 46% respectively.

All pots were initially well-watered with deionized water for one month. Water stress treatments commenced one month after establishment. Well-watered treatments initially received approximately 2.5 cm of water per week. The amount of water applied to the pots during the eight hour photoperiod was gradually reduced to approximately one cm per week as temperatures decreased. During the second growing cycle, as plants became larger, water was increased

to approximately 4 cm per week. Pots in the low water treatment always received half the amount of water given to well-watered pots.

N-deficient treatments received the equivalent of 20 kg N/ha (based on the surface area and taper of the pots) with irrigation water as NH_4NO_3 five weeks following germination. N-sufficient treatments received 20 kg N/ha at two weeks, 34 kg N/ha at one month, 21 kg N/ha at two months, 35 kg N/ha at six months, and 105 kg N/ha nine months after germination.

Measurements and Analysis

Stands were destructively harvested during the second growing cycle, 42 weeks after planting. Immediately prior to harvest, the innermost five by five block of seedlings (stand) was delineated and percent survival by species determined. Stands were surrounded on all sides by a buffer consisting of at least two rows of seedlings from the sides of the pots. Leaf, stem and root biomass were determined following oven drying to a constant weight.

The study used a split-plot design in which CO_2 concentration was the main plot and the factorial combination water, nitrogen availability and stand type were the split-plots. All possible CO_2 , water, nutrient treatments and stand type combinations were replicated four

times. Analysis of variance was used to determine significance of main effects and interactions. Biomass values from mixed stands were corrected to account for differences in the number of trees initially established per stand relative to monocultures. Data were transformed to minimize unequal variance when appropriate (Gomez and Gomez 1984). Total biomass was tested as a covariate in analysis of variance for root:shoot ratio data but was not found to be statistically significant and was not used in the analysis presented here. Competitive interactions between stand composition and CO₂ concentration were analyzed by comparing relative yield total (RYT) and Relative Crowding Coefficient (RCCP and RCCS for pine and sweetgum respectively) (Harper 1977). A t-test was used to detect differences in RYT, RCCP and RCCS between levels of a treatment. Statistical differences of $p < 0.05$ were considered significant throughout the study.

RESULTS

High nitrogen stands had higher sweetgum mortality than low nitrogen stands (Table 3.1). No other significant main effects or interactions were observed for survival in either species. Loblolly pine total biomass and shoot biomass response to carbon dioxide, water and stand type main effects were significant while sweetgum showed

significant responses to carbon dioxide, water and nitrogen (Tables 3.1 and 3.2). Elevated CO₂ increased pine biomass 22% and sweetgum biomass 31% per unit land area across all other treatments (Table 3.3). Root biomass showed a significant response to water, nitrogen and stand type main effects in loblolly pine and to CO₂ and water in sweetgum (Table 2). Sweetgum root:shoot ratio exhibited water, nitrogen and stand type main effects while loblolly pine exhibited nitrogen effects only. Increased root:shoot ratio were typical for seedlings grown under low water and low nutrient availabilities. Sweetgum grown in mixture with pine had a higher root:shoot ratio than monoculture-grown seedlings.

Total, root and shoot biomass of sweetgum was greater under the higher levels of carbon dioxide, water and nitrogen availability while loblolly pine showed a positive growth response to increased carbon dioxide only (Tables 3.1 and 3.2). In loblolly pine, a negative growth response was observed in total root biomass for the higher level of nitrogen availability. The average biomass of individual loblolly pine in monocultures were greater than those grown in mixtures. A significant water x stand type response was present for total, shoot and root biomass (Tables 3.1 and 3.2). The magnitude of these interactions follows similar trends for shoot, root and total biomass (Figure 2.1). Monocultures of both species and mixed stands produced

similar quantities of total biomass (Figure 2.1). In mixed stands, water availability determined the proportion of total biomass each species contributed to the stand. Under well-watered conditions, sweetgum was dominant while stands under droughted conditions contained nearly equal proportions of loblolly pine and sweetgum. Significant changes in relative crowding coefficients for the two species between wet and dry conditions reflect the environmentally-induced competitive differences between these species (Figure 3.1).

No interactions between CO₂ and any of the other main effects were detected for any of the biomass variables, survival or root:shoot ratio with the exception of a CO₂ x water interaction for root biomass in loblolly pine.

DISCUSSION

Loblolly pine and sweetgum biomass increases under elevated CO₂ are consistent with the results of previous studies using these two species (Rogers et al. 1983: Tolley and Strain 1984b: Sionit et al. 1985). However, availability of water and nitrogen did not significantly mediate the response to changes in ambient CO₂ concentration. Loblolly pine and sweetgum in mixed stands responded to water availability according to their recognized silvicultural characteristics: Loblolly pine is dominant on dry sites,

sweetgum is favored on moist sites.

Sweetgum relative crowding coefficients varied between levels of water availability to a greater magnitude than did those for loblolly pine (Figure 3.1). This suggests that sweetgum grown under high water availability is able to take advantage of abundant resources to a greater extent than loblolly pine, especially through root growth under interspecific competition. Relative Yield Total values did not differ significantly, suggesting that the nature of interspecific interactions does not differ in response to water availability.

Root:shoot ratio did not change as a result of exposure to elevated CO_2 . Reports of root:shoot ratio changes in these species when exposed to elevated CO_2 have shown a wide range of responses. Root:shoot ratios in this study have been consistently lower than those reported by Tolley and Strain (1984a) despite having similar total biomass (0.71 g and 1.47 g mean total oven dry weight for loblolly pine and sweetgum respectively in the present study). While the seedlings in the present study were considerably older and other factors may affect root:shoot ratio, intense competition for light in these miniature stands likely produced allocation shifts toward the above-ground portions of the trees. During harvest, roots did not occupy much of the available soil volume and seldom extended to the bottom of the pot suggesting that pot

binding, and accompanying shifts in allocation did not occur. Root biomass data reported here is based on whole seedling harvests and is not consistent with data obtained from soil core measurements taken from the same stands (Jifon et al. 1994). Differences in root recovery have been reported between whole plant and core sampling methods (Friend et al. 1991)

In a previous study where loblolly pine and sweetgum were grown as individual plants, mean biomass increment was significantly greater in sweetgum following drought stress when grown at 675 ppm CO₂ concentrations compared to seedlings grown under present-day levels (Tolley and Strain 1984a). Loblolly pine showed a positive but non-significant response under the same conditions. The differential response to drought shown by the two species led those authors to suggest that sweetgum may be able to occupy drier sites presently dominated by loblolly pine. Data from monoculture stands in the present study concur with these findings. Under low water availability and high CO₂, sweetgum stands showed a 48% increase in growth compared to low CO₂ controls while pine shows a 5% growth increase (Fig. 2). However, data obtained from mixed stands show that growth of neither species is affected by elevated CO₂ under drought conditions. Although the CO₂ x water x stand interaction was not significant, this comparison was presented to underscore the importance of

growing species in competitive mixtures when attempting to predict the effects of resource availability on interspecific competition. Growing species in mixtures integrates the ability of a species to capture a finite resource with its influence on the operational environment of other species (Bazzaz and McConnaughay 1992).

In this study, competitive interactions in mixed stands of loblolly pine and sweetgum were determined by the level of water availability at both present ambient and projected future CO₂ concentrations. These results suggest that water availability would continue to be the primary determinant of competitive outcomes for loblolly pine and sweetgum under these growth conditions: sweetgum would continue to dominate wet sites and loblolly pine would remain dominant on dry sites.

Extrapolating data from miniature stands grown in greenhouses should be done with caution. The use of miniature stands to model the effects of global change on forest tree systems is still in its early stages. Questions remain regarding the validity of comparing stands grown in chambers at very high densities for short periods of time to natural stands. The greatest value of this method seems to be in the evaluation of stand dynamics in very young stands where eventual competitive success may be determined. Differences in time and spacial scale could alter the outcomes of interspecific competition

(Fredericksen et al. 1993). Timing of seed germination was shown to alter the response of a simulated two species mixture of annual plants to CO₂ enrichment (Wray and Strain 1987a,b). Given these limitations, mixed species miniature stands are probably most useful for the comparison of the relative response of species to a range of environmental conditions rather than to predict the exact outcome of competitive interactions.

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Table 3.1. Analysis of variance for seedling survival and total biomass per species for loblolly pine and sweetgum grown in miniature stands after two growing cycles.

Source	df	SURVIVAL				TOTAL BIOMASS			
		Loblolly Pine		Sweetgum		Loblolly Pine		Sweetgum	
		F-value	pr > F	F-value	pr > F	F-value	pr > F	F-value	pr > F
Block	3	1.28	0.4219	7.21	0.0695	8.05	0.0603	0.17	0.9094
CO ₂	1	0.65	0.4776	3.46	0.1599	13.28	0.0356	14.38	0.0322
CO ₂ x Block	3	2.25	0.0963	0.44	0.7275	0.53	0.6654	0.86	0.4716
Water	1	0.02	0.8933	0.80	0.3763	7.80	0.0078	35.87	0.0001
CO ₂ x Water	1	3.08	0.0862	0.05	0.8242	1.88	0.1772	0.27	0.6090
Nitrogen	1	2.20	0.1451	32.49	0.0001	1.00	0.3234	16.31	0.0002
CO ₂ x Nitrogen	1	0.46	0.5035	0.31	0.5792	0.00	0.9854	2.62	0.1132
Water x Nitrogen	1	1.48	0.2313	1.25	0.2700	1.63	0.2001	0.45	0.5081
CO ₂ x Water x Nitrogen	1	0.46	0.5035	2.45	0.1251	1.64	0.2080	0.83	0.3664
Stand	1	1.48	0.2313	1.51	0.2257	47.79	0.0001	0.60	0.4447
CO ₂ x Stand	1	0.89	0.3502	1.01	0.3202	0.18	0.6751	0.05	0.8591
Water x Stand	1	0.16	0.6876	1.80	0.1871	20.83	0.0001	21.57	0.0001
CO ₂ x Water x Stand	1	0.02	0.8933	0.05	0.8242	0.00	0.9711	1.72	0.1974
Nitrogen x Stand	1	0.02	0.8933	0.61	0.4384	3.65	0.0631	2.08	0.1562
CO ₂ x Nitrogen x Stand	1	0.16	0.6876	0.11	0.7391	0.55	0.4638	0.00	0.9661
Water x Nitrogen x Stand	1	0.46	0.5035	4.05	0.0507	1.19	0.2825	0.84	0.3650
CO ₂ x Water x Nitrogen x Stand	1	0.46	0.5035	0.45	0.5061	1.25	0.2691	0.14	0.7063

Table 3.2. Analysis of variance for shoot and root biomass per species per unit land area and root:shoot ratio of miniature stands of loblolly pine and sweetgum after two growing cycles.

Source	df	SHOOT BIOMASS				ROOT BIOMASS				ROOT:SHOOT RATIO			
		Loblolly Pine		Sweetgum		Loblolly Pine		Sweetgum		Loblolly Pine		Sweetgum	
		F-value	pr > F	F-value	pr > F	F-value	pr > F	F-value	pr > F	F-value	pr > F	F-value	pr > F
Block	3	10.84	0.0406	0.07	0.9739	4.99	0.1099	0.54	0.6893	1.12	0.4638	1.15	0.4564
CO ₂	1	32.49	0.0107	15.09	0.0302	2.22	0.2332	11.09	0.0447	0.01	0.9136	0.03	0.8750
CO ₂ x Block	3	0.22	0.8840	0.80	0.5033	1.14	0.3422	0.90	0.4486	1.16	0.3351	1.20	0.3218
Water	1	6.16	0.0171	50.40	0.0001	5.75	0.0210	10.69	0.0022	0.15	0.7021	24.81	0.0001
CO ₂ x Water	1	0.34	0.5612	0.10	0.7538	5.57	0.0230	0.73	0.3975	2.96	0.0928	1.40	0.2437
Nitrogen	1	0.06	0.8086	28.29	0.0001	7.83	0.0077	1.82	0.1848	8.22	0.0065	35.11	0.0001
CO ₂ x Nitrogen	1	0.21	0.6459	2.92	0.0949	0.41	0.5253	1.91	0.1737	1.17	0.2848	0.55	0.4642
Water x Nitrogen	1	1.35	0.2519	1.54	0.2219	0.84	0.3655	0.36	0.5512	0.13	0.7210	9.85	0.0031
CO ₂ x Water x Nitrogen	1	0.55	0.4627	0.60	0.4448	3.41	0.0718	1.25	0.2685	0.97	0.3300	0.59	0.4461
Stand	1	37.98	0.0001	0.00	0.9944	29.78	0.0001	3.83	0.0569	0.05	0.8185	21.26	0.0001
CO ₂ x Stand	1	0.54	0.4670	0.01	0.9360	0.00	0.9449	0.42	0.5200	0.67	0.4192	2.44	0.1262
Water x Stand	1	17.28	0.0002	22.41	0.0001	12.60	0.0010	17.21	0.0002	0.30	0.5860	0.61	0.4385
CO ₂ x Water x Stand	1	0.02	0.8827	1.74	0.1946	0.21	0.6454	1.54	0.2212	0.01	0.9045	0.05	0.8294
Nitrogen x Stand	1	5.06	0.0298	3.56	0.0661	0.57	0.4539	0.38	0.5422	1.04	0.3137	8.47	0.0058
CO ₂ x Nitrogen x Stand	1	0.15	0.7026	0.00	0.9723	0.70	0.4079	0.01	0.9425	0.79	0.3795	0.01	0.9262
Water x Nitrogen x Stand	1	1.13	0.2935	1.38	0.2472	0.50	0.4847	0.08	0.7780	0.01	0.9048	2.11	0.1537
CO ₂ x Water x Nitrogen x Stand	1	0.43	0.5160	0.32	0.5724	1.53	0.2226	0.00	0.9891	1.24	0.2722	1.36	0.2496

Table 3.3. Seedling biomass response to CO₂, water, nitrogen and stand type main effects of loblolly pine and sweetgum grown in miniature stands after two growing cycles. Stand type biomass values for mixed stands were corrected for statistical analysis to account for the fact that mixed stands contained half as many trees as pure stands.

		Biomass (g/m ²)	
		Loblolly Pine	Sweetgum
CO ₂	408 ppm	866 A	1082 A
	806 ppm	763 B	824 B
Water	Well-watered	823 A	1118 A
	Droughted	805 B	788 B
Nitrogen	20 kg N/ha	817 A	1092 A
	215 kg N/ha	811 A	814 B
Stand Type	Pure	1198 A	1205 A
	Mixed	430 B	701 A

NOTE. Pairs of means followed by the same letter are not significantly different ($p < 0.05$).

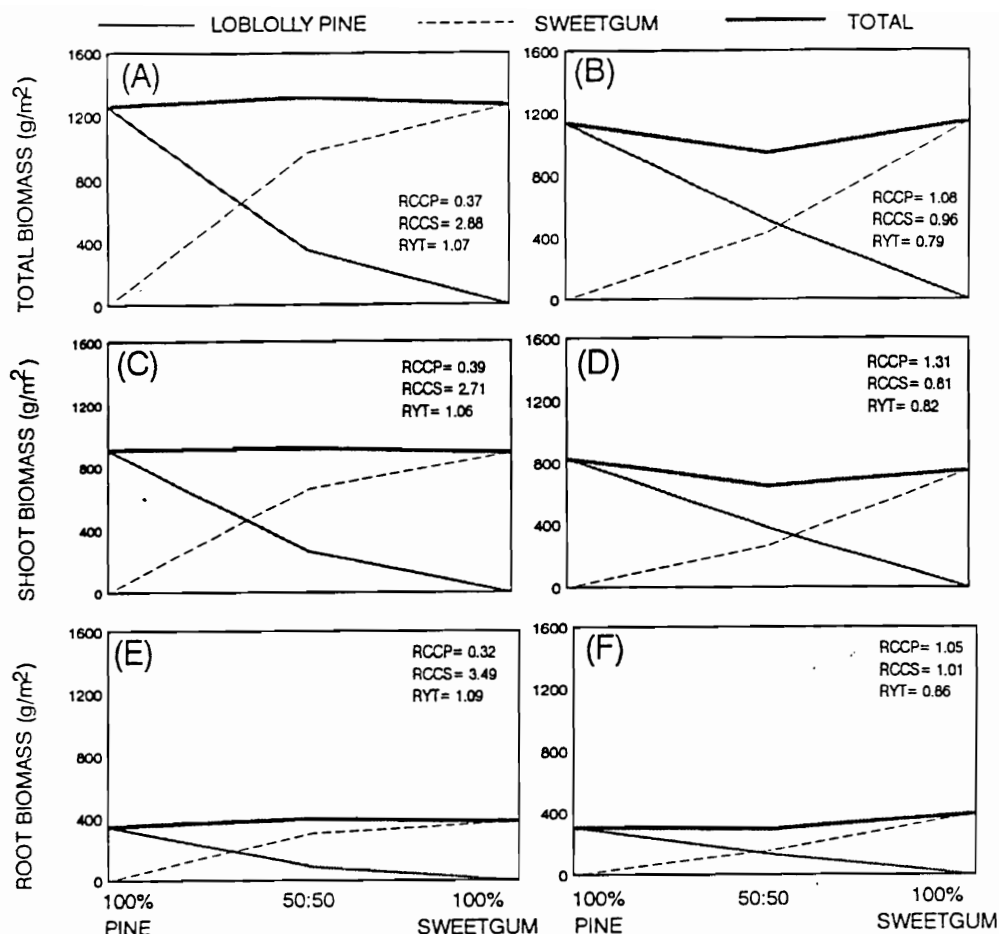


Figure 3.1. Relative yield diagrams for pure and 50:50 mixed loblolly pine and sweetgum miniature stands grown under well-watered and droughted conditions. (A) Total biomass, well-watered, (B) total biomass, droughted, (C) aboveground biomass, well-watered, (D) aboveground biomass, droughted, (E) belowground biomass, well-watered, (F) belowground biomass, droughted. Relative yield totals (RYT) and relative crowding coefficients for loblolly pine (RCCP) and sweetgum (RCCS) are presented. Differences in relative crowding coefficients within a species were detected between well-watered and droughted conditions at $p < 0.5$ for total, aboveground and belowground biomass. Relative yield totals were not different at that level.

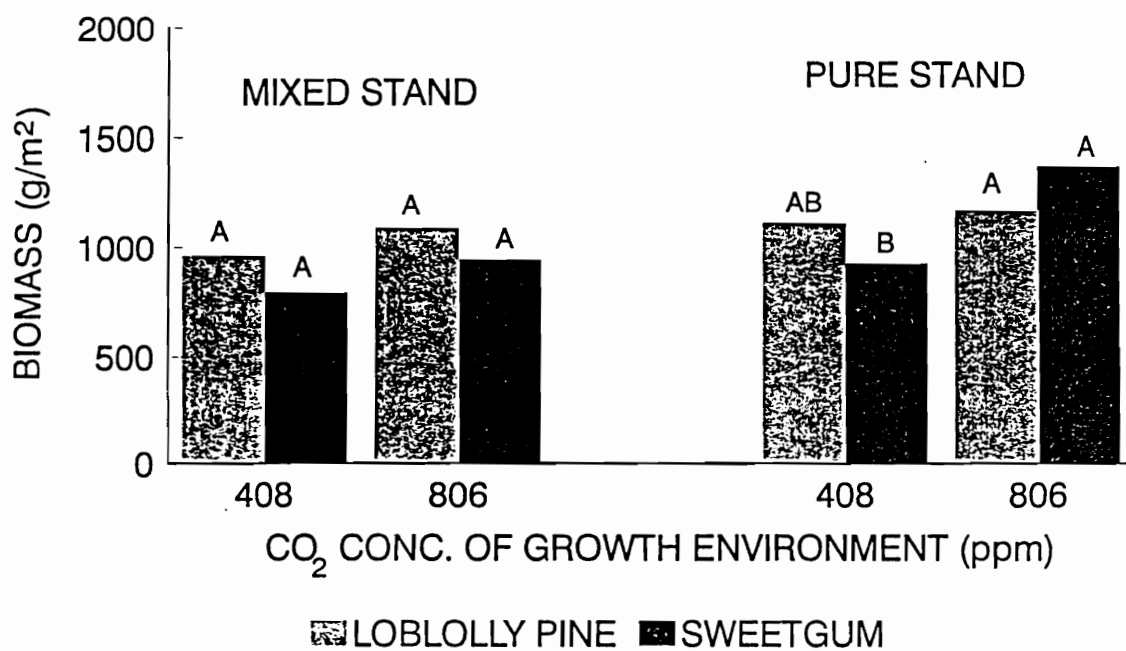


Figure 3.2. Biomass of loblolly pine and sweetgum grown under droughted conditions in monoculture and mixed stands under ambient and elevated CO₂ concentrations. Means within a stand type marked with the same letter are not significantly different at the $p < 0.05$ level.

CHAPTER IV

EFFECTS OF ELEVATED CARBON DIOXIDE, WATER STRESS AND NITROGEN LEVEL ON PHOTOSYNTHESIS IN GREENHOUSE-GROWN MINIATURE STANDS OF LOBLOLLY PINE AND SWEETGUM

INTRODUCTION

Most tree species grown under experimental conditions where atmospheric carbon dioxide (CO_2) was elevated to projected mid-21st century levels (Clark et al. 1982) have responded with changes in photosynthetic rates. Photosynthetic variation in response to atmospheric CO_2 concentration among tree species and interaction among other environmental factors could alter tree growth rate and, ultimately, forest composition (Eamus and Jarvis 1989; Tolley and Strain 1985). Two species that have received much attention concerning their response to increasing atmospheric CO_2 concentration are loblolly pine (Pinus taeda) and sweetgum (Liquidambar styraciflua). These species co-occur throughout much of the southeastern United States and are important to the economic and ecological integrity of the region. Understanding how these species will respond to future atmospheric CO_2 concentrations will allow foresters to adopt management strategies appropriate for a changing environment.

Results of a previous study where loblolly pine and sweetgum individuals were grown for several months under present and projected future CO_2 concentrations found

loblolly pine photosynthetic rates to increase and sweetgum to decrease slightly in response to elevated CO₂ (Fetcher et al. 1988). However, another study of shorter duration found both species maintained higher photosynthetic rates under elevated CO₂ (Tolley and Strain 1985).

Increasing atmospheric CO₂ concentrations may be accompanied by changes in precipitation patterns which have the potential to increase the frequency and severity of drought (Clark 1982). Growth under elevated CO₂ is thought to improve the water use efficiency of plants permitting positive photosynthetic rates farther into a drought compared to plants grown under present CO₂ concentrations (Eamus and Jarvis 1989). Both loblolly pine and sweetgum maintained higher net photosynthetic rates in response to drought stress when grown under elevated CO₂ concentrations (Tolley and Strain 1985; Lenham 1994).

Availability of nutrients has also been found to affect photosynthetic response to elevated CO₂. Two-year-old loblolly pine seedlings exposed to elevated CO₂ for their second growing season showed a positive photosynthetic response only when supplemental nitrogen (N) was provided (Tissue et al. 1993). Maintenance of adequate nutrition is thought to prevent the downward adjustment of photosynthesis (acclimation) observed in several CO₂ exposure studies (eg. Fletcher et al. 1988; Tissue and Oechel 1987; Tissue et al. 1993; Sage et al. 1989).

Previous CO₂ exposure studies with loblolly pine and sweetgum have used seedlings or saplings grown individually, in a non-competitive environment. Gas exchange characteristics of plants grown in stands may respond to elevated CO₂ concentrations differently from those grown as individuals (Bazzaz and McConnaughay 1992). Most gas exchange studies conducted with tree seedlings have employed single leaf gas exchange measurements. Little work has been done to assess the viability of predicting stand or whole individual-level photosynthesis from single leaf measurements despite potential problems associated with making these comparisons (Norby and O'Neill 1991).

The objective of this study was to compare the photosynthetic response of individual leaves and whole canopies of intact miniature seedling stands of sweetgum and loblolly pine. Photosynthetic growth responses to CO₂ enrichment, water availability, nutrient status, and stand composition (monoculture vs mixture) were also evaluated.

METHODS

This study was conducted in a greenhouse at the U. S. D. A. Forest Service Center for Forest Environmental Studies in Dry Branch, Georgia.

Stand culture

Plastic pots 30 cm in diameter and 37 cm deep were filled with a Cowarts series (fine loamy, silicious, thermic, Typic Kanhapludults) forest soil. Prior to potting, soil was sifted through a 64 mm (one-quarter inch) hardware cloth screen, amended with 200 kg K/ha, 100 kg P/ha and 50 kg Ca/ha and mixed with washed, coarse white sand at a 5:1 ratio to insure adequate drainage. Stratified loblolly pine and sweetgum seed from open-pollinated trees (Rapides Parish, La.) were planted in pots at a 2.54 by 2.54 cm spacing both as pure stands of each species and in 50:50 replacement series mixtures.

Following seedling establishment, pots were placed in Continuously Stirred Tank Reactors (CSTRs) maintained at one of two CO₂ concentrations: one treatment was maintained at ambient CO₂ concentrations, averaging 408 ppm with a range of 363 to 459 ppm. The elevated CO₂ treatment added 400 ppm CO₂ to ambient concentrations and averaged 806 ppm with a range of 759 to 857 ppm.

Supplemental lighting in CSTRs was provided by 1000 watt metal halide lights to maintain a 16-hour photoperiod. Seedlings were subjected to two growing cycles to simulate two growing seasons rather than expose seedlings to a single, artificially extended growing season (Samuelson and Seiler 1994). After ten weeks of growth, photoperiods were

reduced to eight hours per day and air temperature was gradually reduced to induce dormancy. During the first growing cycle, temperature and relative humidity averaged 21°C and 65% respectively. During the shortened photoperiod, temperature was gradually lowered from 21° C to approximately 10°C over a one month period. Temperature and relative humidity averaged 11°C and 80% respectively during the final four weeks of the shortened photoperiod. Eight weeks of cold storage in a cold room at 2°C were used to fulfill chilling requirements. Stands were covered with plastic bags to prevent desiccation during chilling. Second growing cycle temperature and relative humidity averaged 22°C and 46% respectively.

All pots were initially well-watered with deionized water for one month. Water stress treatments commenced one month after establishment. Well-watered treatments initially received approximately 2.5 cm of water per week. The amount of water applied to the pots during the eight hour photoperiod was gradually reduced to approximately one cm per week as temperatures decreased. During the second growing cycle, as plants became larger, water was increased to approximately 4 cm per week in the high water treatment. Pots in the low water treatment always received half the amount of water given to well-watered pots.

N-deficient treatments received the equivalent of 20 kg N/ha (based on the surface area and taper of the pots)

with irrigation water as NH_4NO_3 five weeks following germination. N-sufficient treatments received 20 kg N/ha two weeks, 34 kg N/ha one month, 21 kg N/ha two months, 35 kg N/ha six months, and 105 kg N/ha nine months after germination.

Photosynthesis measurements

Leaf gas exchange was measured with a Li-Cor 6250 portable photosynthesis system (Li-Cor Inc., Lincoln, NE) on one seedling per species in each stand. Seedlings used in gas exchange measurements were arbitrarily selected from the second row from the outside edge of the pot. Single seedling photosynthesis measurements were taken once during the first growing cycle (8 weeks following germination) and twice during the second growing cycle (37 and 42 weeks following germination). The nature of leaf material used for photosynthesis measurements varied with sampling period due to changes in seedling size over the course of this study. First growing cycle measurements were made using all foliage. During the second growing cycle, measurements were made on a single, fully expanded leaf near the apical meristem for sweetgum and several fully expanded fascicles for loblolly pine. Seedlings were clipped at groundline and measurement foliage was immediately placed in a .25l cuvette while still attached to the stem. Photosynthesis

was unaffected by clipping for the duration of the gas exchange measurement. Efforts were made to minimize self-shading of leaf material in the cuvette. Gas exchange was measured under ambient (360 ppm), then elevated (706 ppm) CO₂ concentrations for each seedling. Elevated CO₂ concentrations were established in the cuvette by injecting a small amount of pure CO₂ gas immediately prior to the elevated CO₂ measurement. Single seedling photosynthesis measurements were calculated on a dry weight basis for leaf material in the cuvette during measurement. Saturating light levels were maintained during measurements with an incandescent light (120V, General Electric PAR white flood light). Average relative humidity and leaf temperature were 29% and 27°C respectively. Whole stand gas exchange was measured during the second growing cycle, 42 weeks following germination using an open photosynthesis system. A plexiglass cuvette, measuring 83 cm high and 11 cm on a side was placed over the innermost five by five array of seedlings. Air with CO₂ concentrations averaging 408 or 806 ppm was pumped into the top of the cuvette above the canopy of the seedling stand at a rate of 10 l min⁻¹. Reference air was drawn just prior to entry into the cuvette. Sample air was drawn 5 cm above the soil surface and well below the bottom of the foliage canopy. Reference and sample air was drawn at a flow rate of 1.5 l min⁻¹. Air mixture was provided by a small fan near the top of the

cuvette and a high flow rate. Excess air forced out the bottom of the cuvette prevented CO₂ from soil respiration from interfering with measurements. CO₂ concentration and temperature were measured using a Li-Cor 6262 CO₂/H₂O analyzer. The data used for photosynthesis measurements represented a mean of 12 CO₂ concentration measurements, taken at 3 second intervals, beginning immediately after stand photosynthesis reached equilibrium (approximately 5 minutes). Temperature and light availability averaged 32°C and 730 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at the top of the plant canopy.

Stands were harvested immediately following whole stand gas exchange measurements. Leaves, stems and roots were separated by stand, oven dried, and weighed. Whole stand gas exchange measurements were calculated on a total leaf dry weight basis and a total land area basis. All data discussed here were taken 42 weeks following establishment of this study unless noted otherwise.

The study used a split-plot design in which CO₂ concentration was the main plot and the factorial combination of water, nitrogen and stand type were the split-plots. All possible CO₂, water, nitrogen and stand type combinations were replicated four times. Analysis of variance was used to determine significance of main effects and interactions. Analysis of single seedling gas exchange data included shoot weight of the seedling used in these measurements as a covariate to account for canopy status

effects on photosynthetic rate. Photosynthesis data were log transformed when necessary to minimize unequal variance. Presence or absence of photosynthetic acclimation due to growth under elevated CO₂ was determined by comparing photosynthetic rates measured under ambient CO₂ concentrations for individuals or stands grown under elevated versus ambient CO₂ concentrations. Differences in means of $p < 0.05$ were considered to be statistically significant.

RESULTS

Photosynthetic rates and responsiveness to elevated CO₂ often differed between individual seedlings and whole stand canopies. Photosynthesis rates expressed on a per unit leaf weight basis were higher in individually-measured seedlings than in whole stands irrespective of measurement and growth environment CO₂ concentrations (Figure 1). Sweetgum individuals were more responsive to elevated cuvette CO₂ concentrations compared to sweetgum monoculture stands (Figure 1). Photosynthetic rates averaged across growth environment CO₂ concentrations increased 40% more in sweetgum individuals compared to stands. In contrast, the magnitude of loblolly pine response to cuvette CO₂ concentration was almost identical (1% difference) for individuals and stands.

Increases in photosynthetic rates due to measurement under elevated CO_2 were greater in sweetgum individuals compared to sweetgum monoculture stands. Individuals grown and measured under elevated CO_2 had photosynthetic rates 170% higher than those grown and measured under ambient CO_2 concentrations. Sweetgum stands showed only a 110% increase under the same conditions (Figure 1). In contrast, loblolly pine photosynthetic rates increased more in monoculture stands (125%) compared to individuals (85%) in response to elevated CO_2 .

Photosynthetic rates expressed on a land area versus a leaf weight basis showed a more dramatic response to measurement under elevated CO_2 in stands with a sweetgum component (Figures 2 and 3). Sweetgum monoculture photosynthetic rates averaged across water treatments were 39% higher in monocultures and 66% higher in mixed stands when expressed on a land area versus a leaf weight basis. Loblolly pine photosynthetic rates were only 4% higher on a land area versus a leaf weight basis.

Sweetgum, but not loblolly pine, grown under elevated CO_2 showed downward photosynthetic acclimation when measured on both an individual seedling and a whole stand basis. Acclimation was not detected for either species during previous individual seedling gas exchange measurements (data not shown).

Photosynthetic rates of loblolly pine and sweetgum

individuals grown in mixed and pure stands measured at the CO_2 concentration under which they were grown usually showed significant differences due to CO_2 , water and nitrogen main effects (Tables 1 and 2). Photosynthetic rates were greater at the higher level of availability for each resource except for nitrogen in loblolly pine (Table 2). Photosynthesis rates for monoculture stands of both species showed a significant main effect for CO_2 growth environment when expressed on either a total leaf weight or land area basis (Tables 1 and 2). The only other significant effect was a water main effect for loblolly pine monoculture stands.

Significant interactions between CO_2 and water were observed for loblolly pine individual seedlings and sweetgum photosynthesis expressed on a land area basis (Table 1). Factorial combinations of CO_2 and water suggest that whole stand photosynthesis for monocultures of both species is more responsive to elevated CO_2 under the lower level of water availability (Figures 2 and 3). Single seedling photosynthetic response to elevated CO_2 was less dependent on water availability compared to whole stand measurements (Figure 4). No other significant interaction was observed between CO_2 and any other resource (Table 1).

Single seedling conductance for individuals of either species grown in monoculture or mixture did not show a significant response to growth or measurement CO_2

concentration during any measurement period.

DISCUSSION

Lower whole stand versus individual seedling photosynthetic rates may have resulted from a smaller photosynthetic contribution and larger respirational contribution of lower canopy leaves in stands relative to the upper canopy leaves used in single seedling measurements. Low light availability in the lower canopy may have been responsible for lower whole stand photosynthesis rates. Differences between individual and whole stand photosynthetic rates are likely to be underestimated in this study since the CO_2 concentrations were lower and the differential between ambient and elevated concentrations smaller during individual seedling versus whole stand measurements.

Species-dependence of individual versus canopy response may have been related to canopy architecture differences. Although total canopy extinction of photosynthetically-active light was nearly identical across stand types (94% in pure sweetgum and mixed stands and 92% in pure pine stands), light extinction probably occurred nearer the top of the canopy when sweetgum was present due to the broad form and horizontal orientation of these leaves. Although mid-canopy light extinction was not measured, a larger proportion of lower canopy sweetgum

leaves were probably exposed to a light environment below their light compensation point compared to pine stands. Superficially, pine stands appeared to be more open and light better able to penetrate deeper into the canopy which probably contributed to the similarity of individual seedling and miniature stand photosynthetic response to elevated CO₂. Crown architectural configurations preventing self-shading are potentially better able to take advantage of increased leaf biomass typically associated with growth under elevated CO₂ concentrations (cf. Garcia et al. 1994).

Previous studies have suggested that leaf response to elevated CO₂ may be dependent on light availability. Individual sweetgum seedlings, when grown under elevated CO₂, were able to maintain significantly higher photosynthetic rates through a drought only when grown under high (1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$) versus low (250 $\mu\text{mol m}^{-2} \text{s}^{-1}$) light availabilities (Tolley and Strain 1985). Similarly, bigtooth aspen (Populus grandidentata), seedlings responded to elevated CO₂ only when incident light levels were above approximately 300 and 700 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Curtis and Teeri 1992). Decreased availability of CO₂ due to diffusion limitations in dense canopies may also reduce the impact of elevated CO₂ in stands versus individuals (Bazzaz and McConnaughay 1992; Reicosky 1989). However, this did not appear to be the case since CO₂ depletion in air passed through the canopy was never greater than 56 ppm with an

average depletion of only 17 ppm.

A larger photosynthetic response to elevated CO₂ in stands with a sweetgum component when photosynthesis is expressed on a land area versus a leaf weight basis suggests a large portion of leaves were unresponsive to elevated CO₂. Higher leaf area indices in sweetgum grown under high versus low levels of water availability may have caused these canopies to be less responsive to elevated CO₂. This underscores the importance to distinguish between leaf weight and land area basis when modelling climate change effects on forest canopy gas exchange dynamics.

The presence of acclimation in sweetgum, but not loblolly pine, is consistent with the findings of another relatively long-term study where both species were grown as individuals for 15 months (Fetcher et al. 1988). Acclimation may be attributable to a number of mesophyll limitations (Bowes 1991; Stitt 1991) and could reduce carbon fixation, ultimately producing changes in competitive abilities if species are differentially susceptible to acclimation. Despite photosynthetic acclimation in sweetgum, but not loblolly pine, sweetgum dominated all mixed stands in this study (chapter III). The influence of competitive interactions on photosynthetic acclimation is not known.

The interactive effect of elevated CO₂ and water availability as observed in this study indicates that

growth in elevated CO₂ may compensate for low water availability by increasing leaf photosynthesis rates under elevated CO₂. In other studies with these species, high CO₂ allowed individually-grown plants grown under low water to attain sizes exceeding those of low CO₂, well-watered plants (Tscharplinski et al. 1993; Tolley and Strain 1984). Greater relative increases in photosynthetic rate under droughted versus well-watered conditions has been a widely reported response to growth under elevated CO₂ and is thought to be due to increased water use efficiency under elevated CO₂ (Conroy et al. 1986; Bowes 1993). However, in the present study, final whole stand biomass did not reflect a compensatory effect of elevated CO₂ for low water (chapter III)..

The magnitude of photosynthetic increase due to growth and measurement under elevated CO₂ is much greater than those observed by Fetcher et al. (1988) and Tissue et al. (1993). Previous work with loblolly pine reported increased photosynthetic rates only when supplemental nitrogen was provided in conjunction with growth in an elevated CO₂ environment (Griffin et al. 1993; Tissue et al. 1993). In the present study, photosynthesis response of single leaves to elevated CO₂ was not dependent on nitrogen availability, possibly because intense competition for light in miniature stands prevented complete exploitation of belowground resources.

Differences in photosynthetic rates between individual leaves and whole stands, may have important implications for the parameterization of carbon budget models. Discrepancies between the photosynthetic response of individual leaves and whole canopies could result in vastly different estimates of the carbon sink capacity of forests under future atmospheric CO₂ concentrations.

As with all studies where seedlings are grown in controlled environments, results of this study should be extrapolated to field situations with extreme caution. These species may respond to treatments differently depending on seasonal and life stage phenology, planting density, canopy density and resource availability. Miniature stands do provide a competition component which appears to dampen plant response to changes in resource availability. By mimicking natural systems where plant-plant interactions play an important role in individual plant and ecosystem development, studies of this nature may represent an improvement over the traditional, single seedling approach to global change research.

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Table 4.1. Analysis of variance for photosynthesis rates of individual seedlings and whole stands of loblolly pine and sweetgum measured under growth environment CO₂ concentrations. Whole stands data used measurements from monoculture stands only. Shoot dry weight of measurement seedlings was a covariate in individual seedling measurements.

Source	df	INDIVIDUALLY-MEASURED SEEDLING PHOTOSYNTHESIS										WHOLE STAND PHOTOSYNTHESIS									
		LEAF WEIGHT BASIS					LEAF WEIGHT BASIS					LEAF WEIGHT BASIS					LAND AREA BASIS				
		Loblolly Pine		Sweetgum			Loblolly Pine		Sweetgum			Loblolly Pine		Sweetgum			Loblolly Pine		Sweetgum		
		F-value	pr > F	F-value	pr > F	pr > F	F-value	pr > F	F-value	pr > F	pr > F	F-value	pr > F	F-value	pr > F	pr > F	F-value	pr > F	F-value	pr > F	pr > F
Block	3	4.37	0.1286	1.62	0.3503		2.95	0.1988	0.99	0.5019		23.30	0.0140	2.18	0.2696						
CO ₂	1	54.21	0.0052	12.90	0.0370		137.49	0.0013	16.14	0.0277		807.40	0.0001	82.25	0.0028						
CO ₂ x Block	3	1.61	0.2026	1.72	0.1769		0.44	0.7243	0.55	0.6524		0.10	0.9588	0.40	0.7551						
Water	1	42.55	0.0001	4.01	0.0518		6.51	0.0207	0.48	0.4972		14.09	0.0016	1.50	0.2367						
CO ₂ x Water	1	6.45	0.0150	0.26	0.6128		0.58	0.4564	1.03	0.3235		1.41	0.2510	5.34	0.0329						
Nitrogen (N)	1	8.49	0.0058	4.19	0.0472		0.32	0.5814	0.10	0.7527		1.81	0.1957	0.08	0.7759						
CO ₂ x N	1	0.00	0.9920	1.16	0.2885		3.00	0.1016	0.31	0.5872		1.60	0.0748	0.04	0.8516						
Water x N	1	0.23	0.6372	3.25	0.0789		0.04	0.8391	0.54	0.4715		0.00	0.9544	0.02	0.9008						
CO ₂ x Water x N	1	0.24	0.6243	1.65	0.2055		0.01	0.9060	0.12	0.7295		0.11	0.7419	0.14	0.7125						
Stand	1	0.16	0.6905	2.11	0.1536																
CO ₂ x Stand	1	3.51	0.0683	0.30	0.5882																
Water x Stand	1	0.67	0.4182	0.52	0.4754																
CO ₂ x Water x Stand	1	1.66	0.2051	0.02	0.8864																
N x Stand	1	8.83	0.0049	0.00	0.9561																
CO ₂ x N x Stand	1	1.36	0.2508	1.66	0.2052																
Water x N x Stand	1	1.03	0.3163	0.40	0.5305																
CO ₂ x Water x N x Stand	1	0.20	0.6609	0.00	0.9722																
Shoot biomass	1	0.56	0.4586	7.65	0.0085																

NOTE. shoot biomass of the seedling from which single leaf photosynthesis was measured was used as a covariate in this analysis.

Table 4.2. Mean photosynthesis rates by main effects of individual seedling and whole stand gas exchange for loblolly pine and sweetgum measured under growth environment CO₂ concentrations. Whole stands data used measurements from monoculture stands only.

		Individual Seedling		Whole Stand			
		Leaf Area Basis ($\mu\text{mol/g s}$)		Leaf Area Basis ($\mu\text{mol/g s}$)		Land Area Basis ($\mu\text{mol/m}^2\text{s}$)	
		Loblolly Pine	Sweetgum	Loblolly Pine	Sweetgum	Loblolly Pine	Sweetgum
CO ₂	Elevated	0.0808 A	0.1038 A	0.0166 A	0.0110 A	0.1815 A	0.0812 A
	Ambient	0.0380 B	0.0420 B	0.0074 B	0.0052 B	0.0767 B	0.0321 B
Water	Well-watered	0.0744 A	0.0785 A	0.0138 A	0.0089 A	0.1555 A	0.0608 A
	Droughted	0.0444 B	0.0673 B	0.0105 B	0.0074 A	0.1076 B	0.0524 A
Nitrogen	High	0.0526 B	0.0878 A	0.0118 A	0.0080 A	0.1374 A	0.0598 A
	Low	0.0662 A	0.0580 A	0.0125 A	0.0083 A	0.1245 A	0.0535 A
Stand Type	Monoculture	0.0602 A	0.0628 A				
	Mixture	0.0586 A	0.0830 A				

NOTE: Pairs of means within a species marked with a different letter are significantly different at $\alpha < 0.05$.

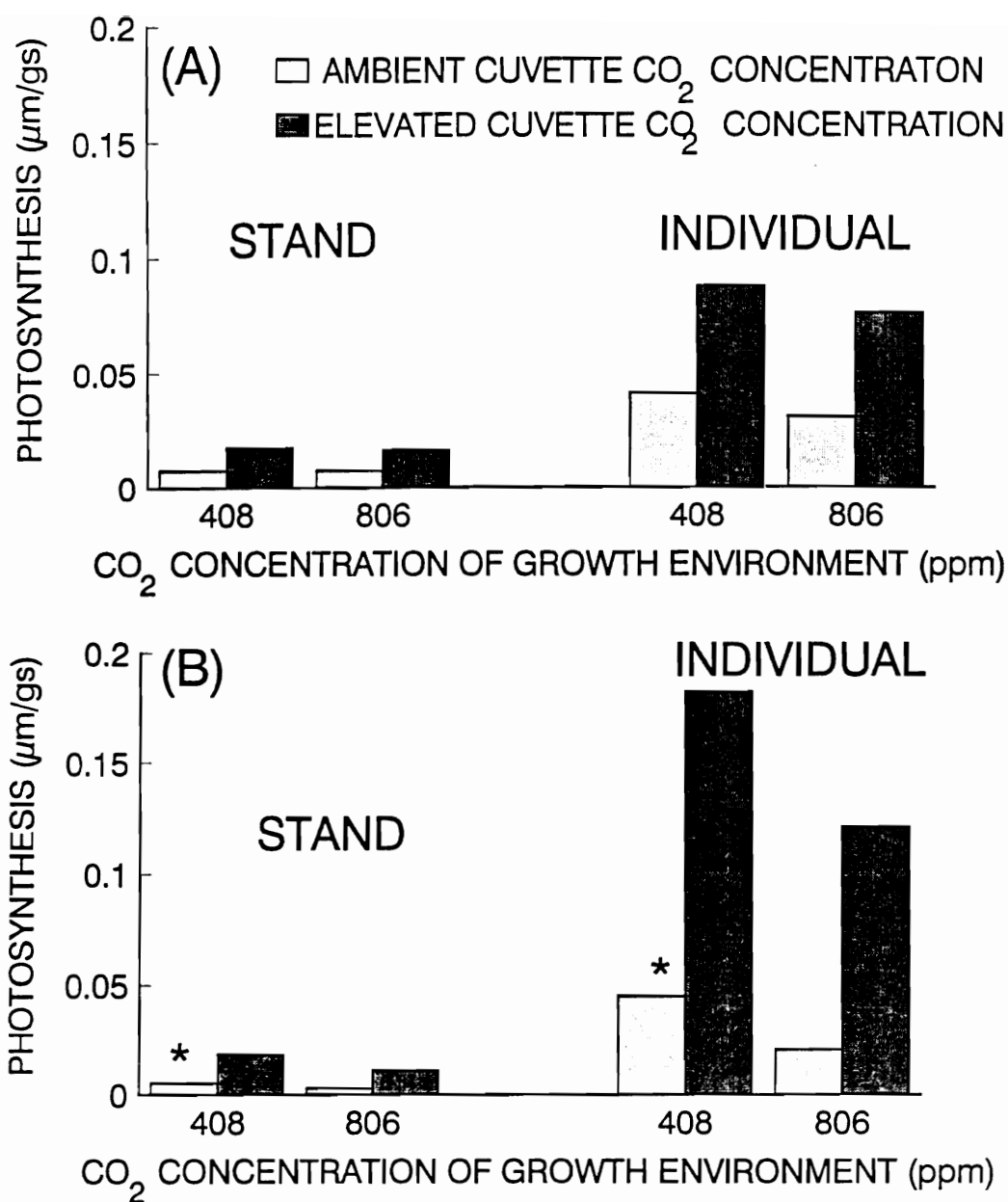


Figure 4.1. Photosynthesis rates in whole miniature stands and individual seedlings from these stands for loblolly pine (a) and sweetgum (b) grown under ambient (360) and elevated (750?) ppm CO₂ concentrations. Photosynthesis was measured under both ambient and elevated CO₂ concentrations. Significant differences in photosynthesis rates between measurement within measurement CO₂ concentrations within stand and individual measurements for a species are marked with an asterisk.

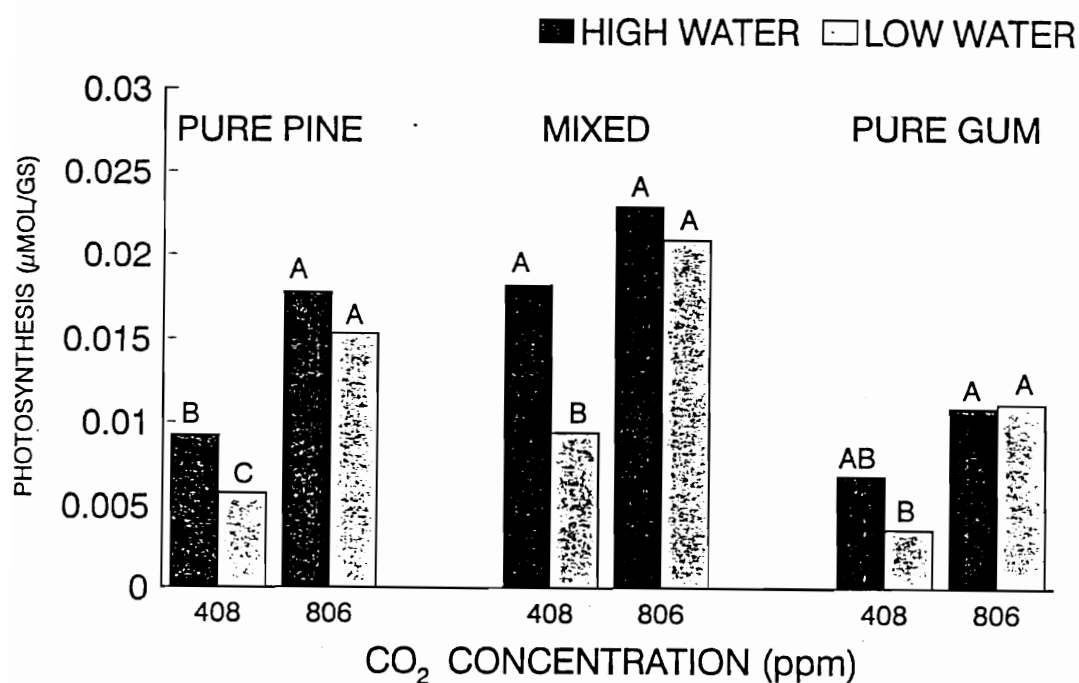


Figure 4.2. Stand photosynthesis per unit leaf weight for miniature stands of loblolly pine and sweetgum monocultures and 50:50 replacement mixtures (mixed) as influenced by CO₂ concentration and water availability. Photosynthesis rates were measured under growth environment CO₂ concentrations. Factorial combinations of CO₂ concentration and water availability within a stand type labelled with the same letter are not significantly different at the $p < 0.05$ level.

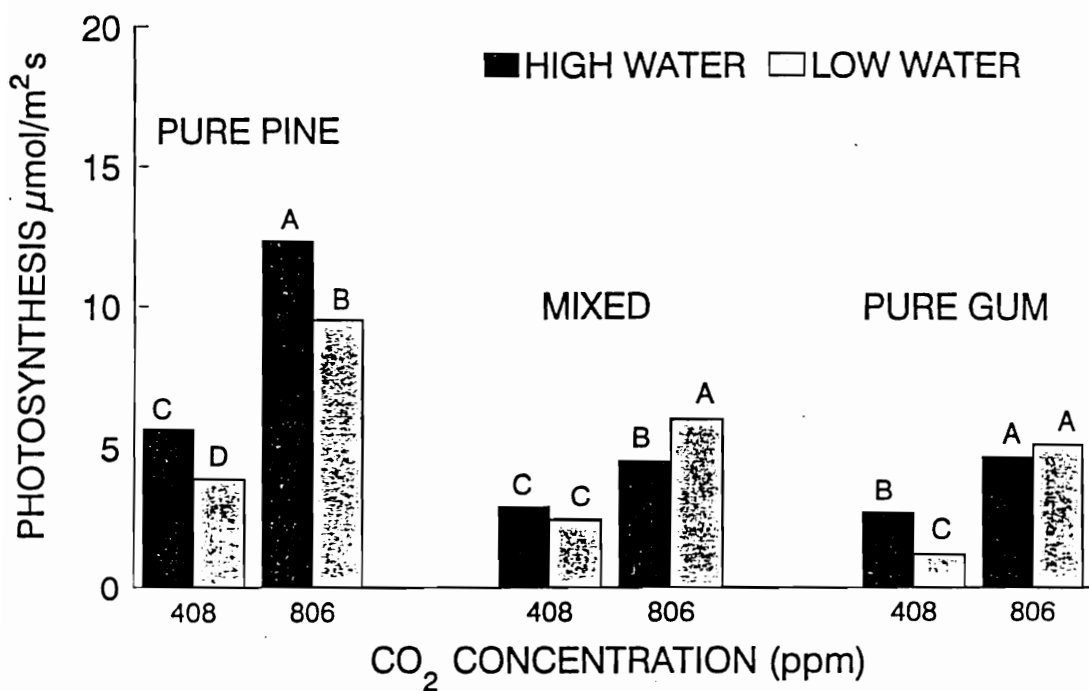


Figure 4.3. Stand photosynthesis per unit land area for miniature stands of loblolly pine and sweetgum monocultures and 50:50 replacement mixtures (mixed) as influenced by CO_2 concentration and water availability. Photosynthesis rates were measured under growth environment CO_2 concentrations. Factorial combinations of CO_2 concentration and water availability within a stand type labelled with the same letter are not significantly different at the $p < 0.05$ level.

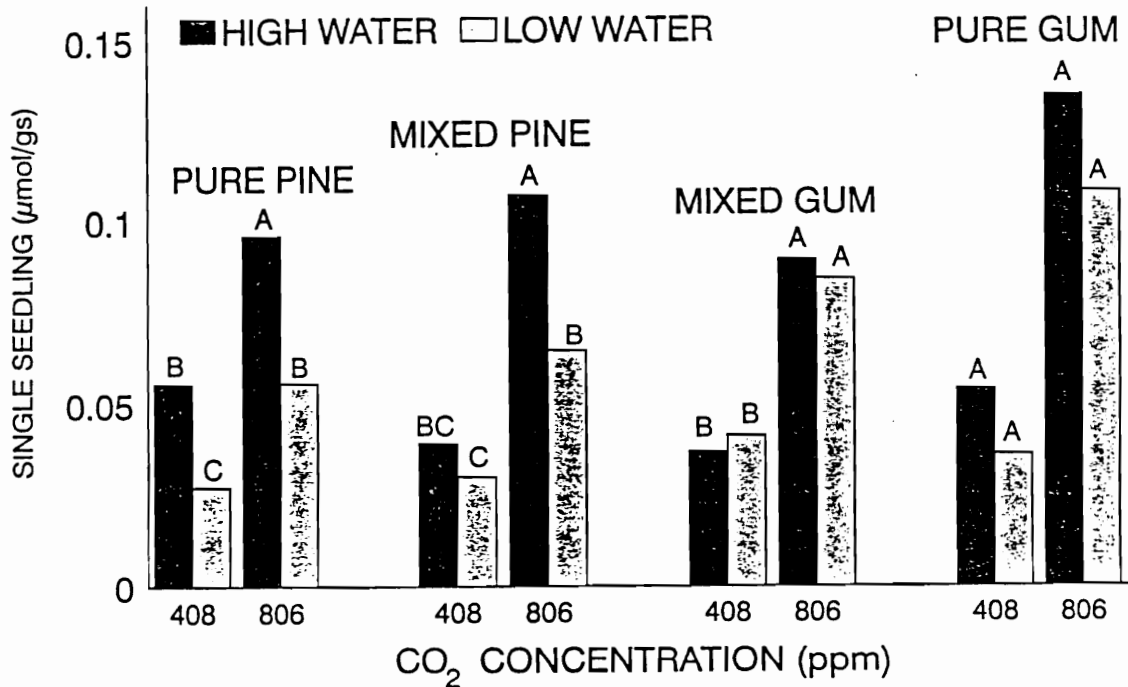


Figure 4.4. Photosynthesis rates for single seedlings from miniature stands of loblolly pine and sweetgum monocultures and 50:50 replacement mixtures (mixed) for factorial combinations of CO_2 concentration and water availability. Photosynthesis in seedlings grown under ambient (408 ppm) CO_2 concentrations were measured at 360 ppm cuvette CO_2 concentration. Seedlings grown under the elevated (806 ppm) CO_2 concentrations were measured under a cuvette CO_2 concentration of 706 ppm. Factorial combinations of CO_2 concentration and water availability within a species and stand type labelled with the same letter are not significantly different at the $p < 0.05$ level.

CHAPTER V

GROWTH AND PHYSIOLOGICAL CHARACTERISTICS OF PLANTED LOBLOLLY PINE AND RED MAPLE GROWN IN PURE AND MIXED STANDS IN THE FIELD.

INTRODUCTION

Recently, interest has increased in the management of pine-hardwood forests in the southeast. Mixed stands are more diverse biologically in terms of wildflower, tree and wildlife populations and considered by some to have greater aesthetic appeal compared to single-species, intensively managed loblolly pine stands (Cooper 1989). Mixed stands also provide a low cost management alternative for landowners unwilling to invest large amounts of capital in their forestland (Phillips and Abercrombie 1987; Cooper 1989). Mixed stand management is generally believed to be less profitable than monoculture management but even this is debated (Cooper 1989; Franklin 1989). Under some circumstances, establishment of mixed stands may be a viable strategy allowing land managers to meet multiple land use objectives. Planting pine-hardwood mixtures require knowledge of proper vegetation management strategies and the compatibility of growing particular species together.

The objectives of this study are to characterize the effects of herbaceous vegetation and forest stand composition on physiology and growth of loblolly pine and

red maple for the first five years following establishment from 1-0 seedlings. Also, the use of height-diameter ratio and live crown ratio as an index for between-stand comparisons of competitive status in young stands is evaluated.

METHODS

The study was located at Virginia Tech's Reynolds Homestead Forest Resources Research Center in Critz, VA. The study site was an abandoned field and pasture prior to site preparation with glyphosate in Fall 1988. The soil is a Cecil clay loam (clayey, kaolinitic, thermic Typic hapludults). Slope ranges from 2-20%. A number of competitive arrays (stand types) were established during March 1989 in a split-plot design with four replications (Fredericksen et al. 1991, 1993). Split plots consisted of two levels of weed control: weed free or closed ground cover. Weed free conditions were maintained through repeated application of glyphosate and closed ground cover was established by planting Kentucky-31 tall fescue Festuca arundinacea Schreb. at a rate of 28 kg/ha during the August immediately following tree planting. Loblolly pine and red maple (both 1-0 stock) planted both in pure stands and 50:50 mixtures planted at a one by one meter spacing were subplots.

The outermost row of trees in each stand was removed at

the end of the third growing season and one meter deep trenches lined with plastic sheets were installed the following spring to prevent root interference between adjacent stands. An ice storm following the fourth growing season bent several loblolly pine boles to the extent that temporary staking was necessary. At the end of five growing seasons, survival exceeded 95% for both species regardless of herbaceous cover or stand type.

Annual measurements including root collar diameter, total height and height to live crown were made on a random 25 percent systematic sample of the innermost 48 trees in each stand during the end of the first through third growing season (Fredericksen et al. 1991, 1993) and 100% sampling of the innermost 24 trees following the fourth and fifth growing seasons.

Gas exchange was measured monthly during June, July and August of the fourth and fifth growing season using a Li-Cor 6200 portable photosynthesis system. Midday water potentials were made in conjunction with gas exchange measurements using a PMS pressure chamber. Gas exchange and midday water potential measurements were made on two trees per species, per stand. Measurements were made on trees of representative size and vigor located within a one tree buffer surrounding subplot edges.

Gas exchange was measured on foliage on the south side of the upper one-third of the crown. Measurements were made using two detached fascicles from loblolly pine

held in the same light environment where the needles were growing. Gas exchange in the red maple were made using attached leaves. Midday water potential measurements were made using one upper crown twig from each of the trees used in gas exchange measurements. All physiology measurements were made between 9:00 and 15:00 solar time.

Light extinction estimates were made in weed-free plots using a Li-Cor quantum sensor. Measurements were taken during clear days; twice during the fourth growing season and once during the fifth growing season. Twenty-five sub-canopy measurements were made at arbitrarily selected locations at ground level in each plot. An effort was made to cover equally all portions of the plot within a one tree buffer of the plot edge. Light extinction was expressed as a proportion where the average of the twenty-five sub-canopy measurements was divided by the light level measured in an unshaded location immediately following sub-canopy measurements.

A linear regression equation using natural log ($\ln$) transformed crown volume as the dependent variable and $\ln$ -transformed stem volume index was fitted for each treatment combination (Causton and Venus 1981). An F-test was used to determine significance of differences between slope (relative organ growth rate) and intercept (initial dry matter investment). This analysis eliminates the confounding influence of treatment-induced plant size on allometric relationships.

This study was arranged in a split-plot design where stand types were randomized within the two weed treatment whole plots. Gas exchange and photosynthesis was measured on three replicates using the same replicates, but not necessarily the same individuals, for each measurement period. Differences between means of $p < 0.05$ are considered significant.

RESULTS AND DISCUSSION

Height growth of both loblolly pine and red maple was suppressed by the presence of herbaceous vegetation since the second growing season (Figure 5.1, Table 5.1). Differences in mean tree height due to herbaceous weed control was greatest (52% different) after year three for loblolly pine and after year four (252% different) for red maple. By the end of the fifth growing season, height differences between herbaceous treatments were less. Suppression of pine height and diameter growth due to herbaceous competition was also observed through four growing seasons in loblolly pine on the coastal plain in Alabama (Knowe et al. 1985).

While loblolly pine was dominant in both herbaceous treatments throughout the study, the extent of pine domination over red maple, based on height, peaked in weed-free stands following the third growing season. Even though differences in height between loblolly pine

and red maple have been decreasing, the early growth gained under weed free conditions will continue to be evident in annual growth increment (Britt et al. 1990). Height differences between pine and maple increased in tall fescue plots through the duration of the study (Figure 5.1).

Stem volume was significantly greater in weed-free versus tall fescue stands from the second growing season onward (Fredericksen et al. 1991, 1993). Stem volume was not affected by growth in pure or mixed stands for either species until the fifth growing season (Figure 5.2). Following the fifth growing season, loblolly pine grown in 50:50 replacement mixtures with red maple were 31% larger regardless of herbaceous cover. Larger stem volume in mixed stands is probably due to greater availability of resources for pine since adjacent maples tended to be smaller and less competitive compared to neighboring pines in the pure stands. For red maple, the difference between growth in pure and mixed stands depended upon herbaceous cover during the fifth growing season. Individuals were 82% larger in pure stands than in mixed stands under weed-free conditions. When grown with tall fescue, red maples grown in mixture, although much smaller than trees grown under weed-free conditions, were 75% larger than those grown in pure stands (Table 5.1, Figure 5.2). Apparently, the presence of pine reduced maple growth in the absence of herbaceous weeds.

In tall fescue plots, pines appear to suppress herbaceous vegetation providing a more favorable microenvironment for maples in mixed stands (Fredericksen et al. 1993).

In previous studies, the presence of hardwood vegetation typically reduced pine yield (Glover and Zutter 1993; Miller et al. 1991; Perry et al. 1993). Stem volume index differences between pines with and without control of woody vegetation have been shown to increase for at least three growing seasons following release (Bacon and Zedaker 1987). Comparison between these studies and the present one should be made with caution since hardwood seedlings are less competitive with pine compared with more common stump and seedling sprout-originating hardwoods. The results of this study suggest that competition from planted hardwoods is merely a density dependent response and the presence of planted hardwoods in place of pine can enhance per tree loblolly pine stem volume if total tree density is not increased.

The ratio of tree height to diameter was sensitive to herbaceous vegetation as well as growth in mixed or pure stands (Tables 5.2 and 5.3). Loblolly pine height to diameter ratio was more strongly influenced by growth in pure versus mixed stands than by presence of herbaceous competition. In contrast, red maple was more strongly influenced by herbaceous competition during the second and third growing seasons. This relationship shifted over time with height:diameter ratio of weed-free

stands becoming greater suggesting that competition from trees became more important than herbaceous vegetation by the end of the fifth growing season. Competition in mixed stands became more intense than in pure stands for maples according to this index.

The height:diameter ratio may be a useful index of competitive stress based on the observation that diameter is impacted by competition to a considerably greater extent than height (Lanner 1985; Holbrook and Putz 1989; Knowe 1991; Perry et al. 1993). As competition intensifies during crown closure, greater allocation of resources to height at the expense of diameter may allow an individual to maintain a favorable status for light capture (Holbrook and Putz 1989). This can be observed in maturing pine plantations where trees in unthinned stands have more slender boles than those in thinned stands. Height:diameter ratio has been used to predict responsiveness to release from herbaceous cover in naturally-regenerated loblolly pine less than 6 ft. in height (Cain 1989). Data from the present study suggest that extrapolation of this index may be appropriate for the evaluation of competitive effects in larger trees during and after crown closure.

Shifts in the importance from herbaceous to woody species was also reflected by changes in live crown ratios in loblolly pine (Table 5.4 and 5.5). Loblolly pine grown in weed-free stands maintained higher live

crown ratio during the third growing season. This relationship had shifted during the fifth growing season presumably due to greater lower branch mortality caused by the development of denser canopies in weed-free stands. In contrast, red maple live crown ratio remained higher in weed-free stands from the second growing season onward (Table 5.4). Live crown ratio was significantly higher in mixed versus pine monocultures during the fourth and fifth growing seasons (Table 5.5). In contrast, red maple grown in pure stands had a higher live crown ratio than those from mixed stands during the fifth growing season suggesting greater competitive influence from pine than from itself.

Live crown ratio (LCR) is typically used as an index to determine stand responsiveness to thinning. Trees with larger crowns have been shown to grow more quickly in diameter by maintaining radial growth later into the growing season (Bassett 1966). In practice, trees with LCR greater than 30-40% are expected to have sufficient vigor to respond to thinning (Smith 1986; Cain 1990). Even though the stands reported here had considerably higher LCR's than stands typically considered for thinning, this measure may be appropriate for tracking changes in vigor among a species growing under different competitive regimes.

Height:diameter ratio reflected the shift in importance from herbaceous to woody competition in red

maple but not loblolly pine. In contrast, LCR suggested this change was occurring in loblolly pine but not red maple. Data need to be collected from these species under a number of conditions to determine whether this response is species-specific or merely related to crown class status of these species in this particular study (suppressed to intermediate in red maple, dominant to codominant in loblolly pine). Crown volume:stem volume ratio was not significantly different due to growth in monoculture or mixture for either species in weed-free stands (data not shown).

Data collected during the fourth growing season showed net photosynthesis was significantly higher for loblolly pine in tall fescue plots during the July measurement, but no further significant differences were observed in subsequent measurements (Table 5.6). Red maple photosynthesis was significantly higher on weed-free versus tall fescue plots during the June and July measurement of the fourth growing season but no further significant differences were observed after that time. Overall, average photosynthesis for both loblolly pine and red maple were higher in weed-free plots (3.88 versus 3.68 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for loblolly pine and 5.70 versus 4.83 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for red maple). Photosynthesis was not affected in either species by growth in monoculture or mixture.

Water potential differences between treatments were

small and did not appear to be biologically significant during the fourth and fifth growing season (Table 5.7). In June 1992, decreased net photosynthesis in red maple grown with tall fescue was associated with a trend toward higher water potentials in tall fescue versus weed-free plots. This trend did not accompany photosynthetic differences in either species during the July 1992 measurement. In contrast, herbaceous cover had a significant effect on midday water potentials for both species during the third growing season (Fredericksen et al. 1993). The influence of herbaceous weed control on tree xylem water potential decreases once trees develop root systems able to extract water from greater depths than herbaceous vegetation (Green et al. 1989; Sands and Nambiar 1984). Water potential was not affected in either species by growth in monoculture or mixture.

Mixed stands had consistently lower percent light transmittance compared to pure stands of both species (Figure 5.3). Mixed pine-hardwood stands appear to be more effective in blocking transmittance of light to the forest floor due to differences in crown architecture associated with the two species. In mixed stands, the combination of shade from a dense canopy near the ground contributed by shade tolerant red maple in combination with high shade from the taller pines tend to produce a canopy less light permeable than pure stands of either species. The greater degree of light extinction in mixed

stands could reduce the establishment or growth of herbaceous vegetation in mixed stands relative to monocultures. Canopy suppression of weeds is probably more important in pure maple stands since deep pine litter appeared to suppress virtually all herbaceous volunteers from the fourth growing season onward.

Establishment of mixed stands could also produce more effective visual barriers in landscaping than pure stands of either species.

CONCLUSIONS

While stand dynamics during the first two growing seasons appeared to be governed by herbaceous interference and inherent growth characteristics of the two tree species (Fredericksen et al. 1991), inter and intraspecific competition between trees became more important following the third growing season. Once crown closure occurred, stand tree species composition become increasingly important. Presence or absence of herbaceous vegetation decreased in importance over time but size differences established prior to crown closure continued to be manifested throughout the study. Gas exchange and water relations data failed to explain competitive trends during the fourth and fifth growing seasons.

Changes in the role of woody and herbaceous vegetation in competitive relationships over time are

likely accompanied by a shift in importance from competition for water to competition for nutrients (Nambiar and Sands 1993). Long-term benefits of herbaceous vegetation on nutrient, organic matter and water retention may effect long-term productivity of these sites (Nambiar and Sands 1993: Costantini 1989: Woods et al., 1992). The underlying mechanisms governing changes in competitive status between tree species and the changing role of herbaceous vegetation in this process require further exploration.

The timing and actual nature of competitive interactions discussed here should be applied only to stands where both loblolly pine and red maple are established from seedlings. Typically, red maple is regenerated by stump or seedling sprouts which exhibit much more rapid growth rates and are more strongly competitive than planted 1-0 seedlings used in this study. Initial spacing and the species composition of competing vegetation also plays a role in determining the relative importance of woody and herbaceous vegetation (Cain and Mann 1980: Perry et al. 1993).

MANAGEMENT IMPLICATIONS

Fifth year results of this study strongly suggest that establishment of mixed stands of loblolly pine and red maple from seedlings is possible on Upper Piedmont sites

similar to those described here. Because early growth of red maple is more sensitive to herbaceous vegetation than loblolly pine, the relative dominance of red maple could be regulated through the intensity of herbaceous weed control during early stand development. The persistence of red maple under the planted tall fescue ground cover, especially when grown in mixture with loblolly pine, suggests that this species will become more important as herbaceous cover declines.

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Table 5.1. Analysis of Variance of total height for loblolly pine and red maple grown in pure and mixed stands (Type) under weed-free conditions or tall fescue (Herb) on the Virginia Piedmont.

Year	Source	Loblolly Pine		Red Maple	
		F value	Pr > F	F value	Pr > F
1	Block	4.83	0.04	0.28	0.83
	Herb.	3.97	0.14	0.07	0.81
	Block x Herb.	1.47	0.31	2.48	0.15
	Type	0.27	0.61	0.09	0.76
	Herb x Type	1.60	0.25	0.65	0.45
2	Block	17.85	0.00	1.25	0.37
	Herb.	34.51	0.00	36.53	0.00
	Block x Herb.	4.03	0.06	1.02	0.44
	Type	1.38	0.28	0.15	0.71
	Herb x Type	0.14	0.72	0.86	0.39
3	Block	57.48	0.00	3.94	0.07
	Herb.	194.76	0.00	121.90	0.00
	Block x Herb.	2.17	0.19	2.33	0.17
	Type	4.71	0.07	0.12	0.74
	Herb x Type	3.19	0.12	3.51	0.11
4	Block	66.51	0.00	3.95	0.07
	Herb.	41.87	0.00	104.24	0.00
	Block x Herb.	6.73	0.02	2.73	0.13
	Type	0.80	0.40	0.36	0.57
	Herb x Type	0.01	0.93	3.81	0.09
5	Block	23.08	0.00	3.67	0.08
	Herb.	24.89	0.01	113.16	0.00
	Block x Herb.	5.98	0.03	2.86	0.12
	Type	1.54	0.26	1.25	0.30
	Herb x Type	0.04	0.85	8.36	0.02

Table 5.2. Mean height:diameter ratios for loblolly pine and red maple grown in monoculture and 50:50 replacement mixtures on the Virginia Piedmont for five years. Means within species and year followed by the same letter are not significantly different at $p < 0.05$.

Year	Loblolly Pine		Red Maple	
	Monoculture	Mixed	Monoculture	Mixed
1	0.372 A	0.367 A	0.706 A	0.759 A
2	0.491 A	0.448 A	0.638 A	0.599 A
3	0.550 A	0.505 B	0.710 A	0.694 A
4	0.526 A	0.465 B	0.722 A	0.755 A
5	0.577 A	0.516 B	0.690 B	0.810 A

Table 5.3. Mean height:diameter ratios for loblolly pine and red maple grown under maintained weed-free conditions or with planted tall fescue for five years on the Virginia Piedmont. Means within species and year followed by the same letter are not significantly different at $p < 0.05$.

Year	Loblolly Pine		Red Maple	
	Weed-free	Tall fescue	Weed-free	Tall fescue
1	0.363 A	0.375 A	0.768 A	0.777 A
2	0.430 A	0.500 A	0.560 B	0.677 A
3	0.513 A	0.547 A	0.640 B	0.764 A
4	0.502 A	0.489 A	0.753 A	0.724 A
5	0.555 A	0.538 A	0.785 A	0.709 B

Table 5.4. Mean live crown ratios for loblolly pine and red maple grown for five years under maintained weed-free conditions or with planted tall fescue on the Virginia Piedmont. Means within species and year followed by the same letter are not significantly different at $p < 0.05$.

Year	Loblolly Pine		Red Maple	
	Weed-free	Tall fescue	Weed-free	Tall fescue
2	0.868 A	0.814 A	0.799 A	0.623 B
3	0.914 A	0.876 B	0.805 A	0.707 B
4	0.803 A	0.848 A	0.895 A	0.674 B
5	0.639 B	0.706 A	0.895 A	0.638 B

Table 5.5. Mean live crown ratios for loblolly pine and red maple grown for five years in monoculture and 50:50 replacement mixtures on the Virginia Piedmont. Means within species and year followed by the same letter are not significantly different at $p < 0.05$.

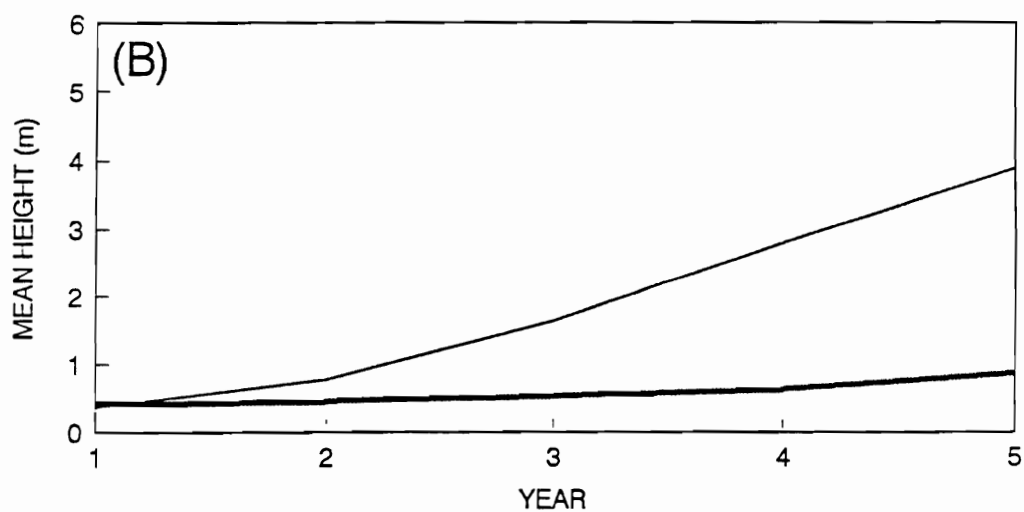
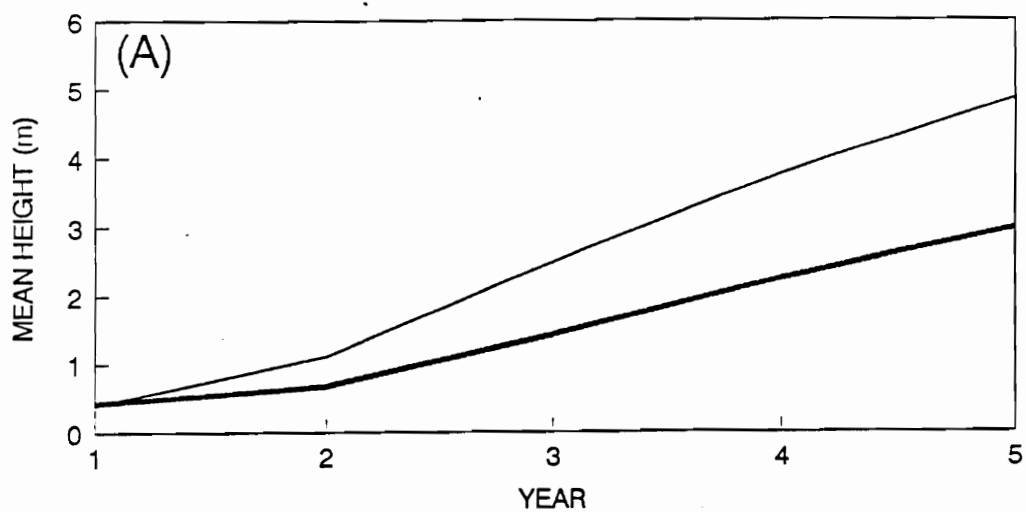
Year	Loblolly Pine		Red Maple	
	Monoculture	Mixed	Monoculture	Mixed
2	0.818 A	0.864 A	0.686 A	0.735 A
3	0.885 A	0.906 A	0.783 A	0.809 A
4	0.777 B	0.874 A	0.792 A	0.776 A
5	0.618 B	0.726 A	0.795 A	0.739 B

Table 5.6. Net photosynthesis ($\mu\text{mol m}^{-2} \text{s}^{-2}$) for upper crowns of planted loblolly pine and red maple grown in weed-free and tall fescue understories on the Virginia Piedmont during the fourth and fifth growing season. Means followed by the same letter are not significantly different ($p < 0.05$) between weed-free and tall fescue stands for a species within the same month and year.

Month, year	Loblolly Pine		Red Maple	
	Weed-free	Tall fescue	Weed-free	Tall fescue
June, 1992	4.6 A	4.8 A	7.1 A	5.2 B
July, 1992	2.6 A	1.6 B	3.5 A	2.0 B
August, 1992	3.2 A	3.4 A	5.3 A	5.9 A
June, 1993	4.7 A	4.7 A	6.4 A	5.2 A
July, 1993	4.1 A	3.9 A	6.4 A	5.0 A
August, 1993	4.1 A	3.7 A	5.5 A	5.7 A

Table 5.7. Midday water potentials (MPa) for planted loblolly pine and red maple grown in weed-free and tall fescue understories on the Virginia Piedmont during the fourth and fifth growing season. Means followed by the same letter are not significantly different ($p < 0.05$) between weed-free and tall fescue stands for a species within the same month and year.

Month, year	Loblolly Pine		Red Maple	
	Weed-free	Tall fescue	Weed-free	Tall fescue
June, 1992	-0.97 A	-1.10 A	-1.21 A	-1.30 A
July, 1992	-1.55 A	-1.55 A	-1.85 A	-1.83 A
August, 1992	-1.02 A	-1.09 A	-1.18 A	-1.12 A
June, 1993	-1.18 A	-1.30 A	-1.61 A	-1.42 A
July, 1993	-1.33 A	-1.35 A	1.63 A	-1.75 A
August, 1993	-1.38 A	-1.34 A	1.34 A	-1.53 A



— LOBLOLLY PINE — RED MAPLE

Figure 5.1. Mean total height for planted loblolly pine and red maple grown under maintained weed-free (A) and planted tall fescue (B) understories for five years on the Virginia Piedmont.

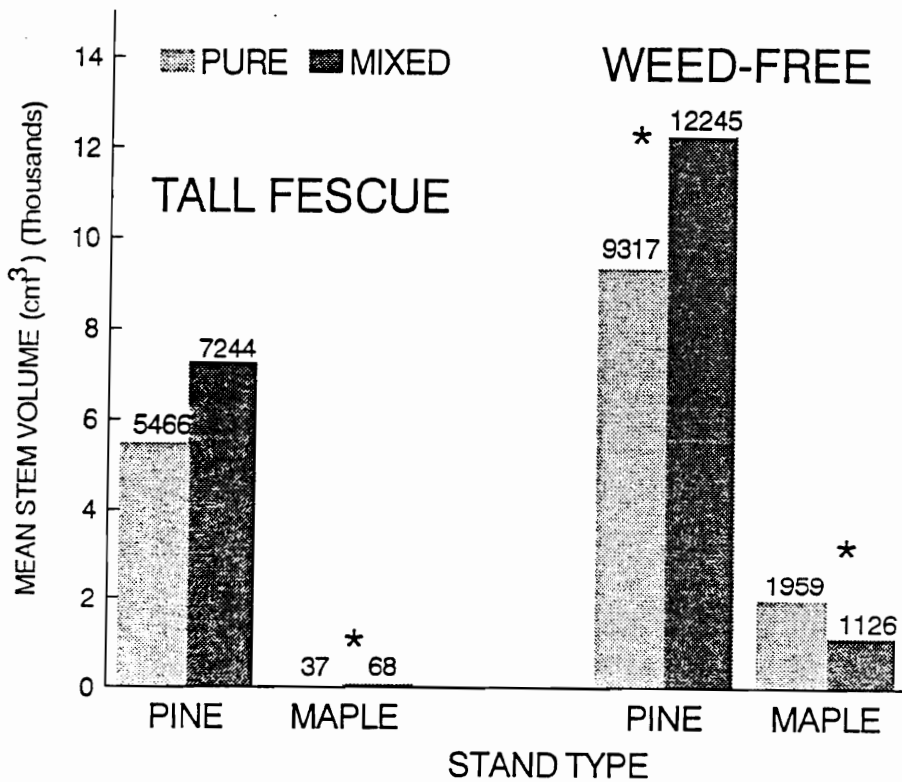


Figure 5.2. Stem volume index after the fifth growing season for planted loblolly pine and red maple grown in monoculture or 50:50 replacement mixtures in tall fescue or maintained weed-free understories on the Virginia Piedmont. Significant ($p < 0.05$) differences between pairs of means within species and herbaceous cover are indicated with an asterisk.

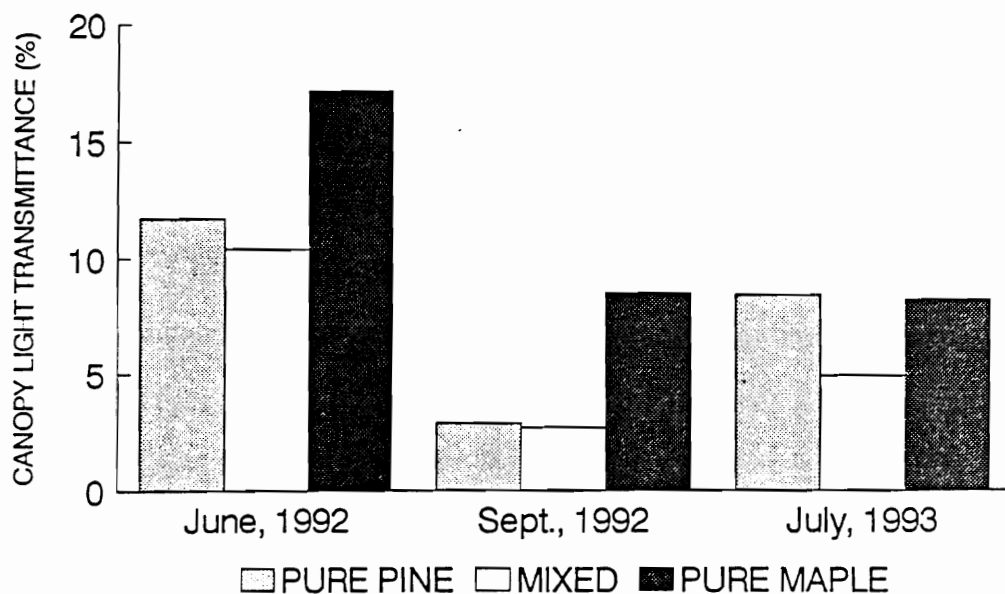


Figure 5.3. Percent canopy light transmittance measured for three dates during the fourth and fifth growing seasons in monoculture and 50:50 replacement mixtures of planted loblolly pine and red maple grown under weed-free conditions on the Virginia Piedmont.

CHAPTER VI

EFFECTS OF PLANTING DENSITY ON COMPETITIVE INTERACTIONS IN MINIATURE STANDS OF LOBLOLLY PINE AND RED MAPLE

INTRODUCTION

Detailed study of competition dynamics in forest stands is often hampered by the relatively long time required for competitive interactions to become resolved. Studies attempting to evaluate changes in the relative competitive abilities of co-occurring tree species in response to changes in environmental conditions, such as increasing atmospheric CO₂ concentration, often become prohibitively expensive due to the tremendous cost associated with fumigation over a several year period. A few studies have attempted to use simulated stands, grown at very high densities, to accelerate the onset of tree to tree competition (Reekie and Bazzaz 1989; Williams et al. 1986; Fredericksen et al. 1993a; Avila 1993).

Comparison between mixed stands grown under high densities with those grown under more typical field conditions may be limited. In companion studies where red maple and loblolly pine were grown under high densities in a greenhouse and more normal densities in the field, competitive outcomes differed drastically (Fredericksen et al. 1993a,b). While other greenhouse conditions may be responsible for this competitive shift, density dependence

of competitive response has been observed in replacement studies and cannot be ruled out (Rejmanek 1989; Firbank and Watkinson 1985; Fredericksen et al 1993a).

The purpose of this study was to determine whether initial planting density of seedling stands under greenhouse conditions affects competitive outcome, relative yield and allometry in miniature stands of loblolly pine and red maple.

METHODS

This study was conducted in a greenhouse on the Virginia Tech campus in Blacksburg, Virginia. Plastic tubs 35.2 x 61.0 cm wide and 43.8 cm deep were filled with a 2:1 mixture of peat moss and vermiculite. Seeds of loblolly pine (mixed Virginia seedlot, Virginia Department of Forestry) and red maple (mixed seedlot, Erie, PA) were cold stratified and planted in monocultures of each species and 50:50 replacement series at a spacing of 1, 2 and 3 inch (2.54, 5.08, and 7.62 cm respectively). Two seeds of loblolly or three seeds of red maple were planted at each location. All but one seedling was removed at each location where more than one seedling germinated. Extra seedlings were grown in vermiculite and used to replace unfilled seed spots that did not germinate. Soil was treated with fungicide (Banrot, Sierra Crop Protection Co.,

Milpitas, CA) at a rate of 2.5 g/m² two weeks after planting to prevent damping off. Stands were maintained under well-watered conditions and fertilized weekly (Peters solution 20-20-20 NPK) to optimize growth. Fertilizer was applied at a rate of 14.6 kg N/ha, 6.3 kg P/ha and 12.1 kg K/ha from 6 to 14 weeks following planting and 29.2 kg N/ha, 12.6 kg P/ha and 24.2 kg K/ha for the remainder of the study. A randomized complete block design was employed with four replications of each stand type and planting density.

All measurements were made on a 6 x 4 row seedling array in the middle of each stand. The widest spacing had one row of seedlings as a buffer from the edge of the tub. Height and diameter 0.5 cm below cotyledons was measured immediately prior to harvest. Leaf, stem and root biomass were determined on a whole stand basis following harvest and drying to constant weight. Stem volume index based on the volume of a cone and height:diameter ratio were calculated based on stem height and diameter measurements. Root-shoot ratio and leaf efficiency (stem weight:leaf weight ratio) were calculated for each species on a whole stand basis. Relative crowding coefficients and relative yield totals (Harper 1977) were calculated for each species for stand biomass by density on a per block basis

Analysis of variance was used for determination of treatment effects with $p < 0.05$ considered significant.

Mean seedling biomass was used as a covariate in analysis of height:diameter ratio, root:shoot ratio and leaf efficiency data (leaf biomass/total biomass). Mean separation was performed using Fisher's protected LSD test.

RESULTS

Red maple dominated in mixed stands regardless of spacing (Figure 6.1). Relative crowding coefficients for loblolly pine and red maple and relative yield totals did not differ significantly among the planting densities. Mean seedling stem volume index was greater for both species as spacing increased (Table 6.1). Loblolly pine stem volume index was greater for seedlings grown in monoculture versus mixture at all planting densities. Red maple stem volume index was not significantly affected by growth in monoculture or mixture at each planting density but the trend was toward greater volume in mixed stands.

Height:diameter ratio became significantly greater in loblolly pine as spacing became narrower suggesting that competitive stress was greater as planting density increased (Table 6.2). Spacing by stand type interaction was not statistically significant ($p < 0.05$). Height-diameter ratios support conclusions drawn from the analysis of variance for relative crowding coefficient data that suggest the competitive outcomes between these species are

not density dependent (Chapter V). However, loblolly pine grown in mixture with red maple at the widest spacing had a significantly greater height:diameter ratio than monocultures, indicating a stronger suppression of pine growth at this density. Height:diameter ratio in red maple did not respond to spacing or stand type.

Leaf efficiency and root:shoot ratio did not vary significantly due to spacing or stand type for either species (data not shown).

DISCUSSION

Dominance of red maple over loblolly pine in mixed stands does not reflect competitive outcomes observed for these species planted in competitive arrays under field conditions (Fredericksen et al. 1993a; chapter V). Fredericksen et al. (1993a) suggested that competitive outcomes between field and greenhouse stands may differ in response to spatial, temporal and environmental factors. Results of this study and the dominance of pine over red maple in another greenhouse study (chapter vii) indicate that initial density did not affect competitive outcomes between these two species. The simultaneous establishment of the two species in both the present study and another greenhouse study (chapter vii) did not appear to influence competitive outcomes under these conditions.

Resource availability appears to be the most important determinant of competitive outcomes in this study. In contrast to field conditions and the greenhouse study outlined in chapter vii, availability of water and nutrients in the present study were maintained at artificially high levels. Red maple appeared to be better able to take advantage of higher levels of available resources. Fredericksen et al. (1993a) suggested that hardwood domination over loblolly pine under similar conditions appeared to be a result of greater below ground resource uptake. They reported hardwood species had higher root surface area but lower leaf area than pines. However, the horizontal expansion of red maple leaves under the conditions of high planting density may have reduced light availability for loblolly pine (Fredericksen et al 1993a). While leaf area was not measured in the present study, the distribution of red maple foliage appeared to reduce incident light on neighboring pines through outward canopy extension. Crown architecture of young loblolly pine is columnar and appeared to exert less influence on neighboring individuals.

Competitive patterns in these stands were reflected by allometric differences in loblolly pine. Higher height:diameter ratios in loblolly pine were consistent with stem volume index measurements. Significant differences between monoculture and mixtures were more

readily detected by stem volume measurements than height:diameter ratios. Based on these results, height:diameter ratio measurements do not represent an improvement over stem volume index as a non-destructive index of competitive stress. Significantly greater height:diameter ratio in monoculture pine observed at the widest spacing may indicate a trend toward greater suppression of loblolly pine by red maple as spacing increases. The absence of a wider planting density in this study prevents determination of this trend. Greater suppression of loblolly pine at wider spacings would run contrary to the observations of (Fredericksen et al. 1993a, b) however this is confounded by growth under greenhouse versus field conditions.

Limitations in the execution of this study must be considered in the interpretation of relative crowding coefficient data. An assumption of replacement series experiments is that stands are carried to constant final yield (de Wit 1960: Roush et al. 1989). This condition might not have been met in the present experiment. Although mortality rates appeared to be highest in the 1-inch spacing, this may have been a result of defoliation by an eriophyid mite rather than a density-dependent response. While the mite was present in all stands containing maple, small seedlings are more likely to succumb to defoliation due to a reduced ability to refoliate.

Although necessary due to the insect infestation, harvesting this study during the first growing season limited its utility in determining competitive outcomes. Termination of this study prior to the onset of constant final yield makes comparisons of relative crowding coefficients between planting densities of limited utility because crowdedness and, therefore, distance from constant final yield is density dependent. High density stands are closer to constant final yield than low density stands. This is especially important in mixed stands of forest tree species since changing environmental conditions under decreasing levels of resource availability would affect growth and survival based on species-specific growth characteristics. Allowing the stands in this study to remain intact over more than one growing season may have also changed competitive outcomes beyond the onset of density dependent mortality. The greater leaf area duration of loblolly pine may permit this species to improve its competitive position relative to red maple while the latter species is dormant (Fredericksen et al. 1993a).

Efforts examining the role of planting density on competitive outcomes and the comparison of these studies to field conditions are faced with a dilemma regarding the maintenance of nutrient and water status. Ideally, water and nutrient regimes would be parallel to field conditions.

Greenhouse grown loblolly pine seedlings best predicted 12 year height growth when soil nitrogen was maintained under field conditions (Li et al. 1991). However, establishment of seedlings at high densities to hasten competitive interactions in a restricted rooting volume would result in a rapid and probably density dependent depletion of soil macronutrients. This interaction could be an artifact of greenhouse culture leading to erroneous conclusions regarding the role of density on competitive outcomes. Manipulating greenhouse soil conditions to first make water the most limiting resource followed by nutrients as stand development progresses would best reflect below ground resource competition under field conditions (Nambiar and Sands 1993).

CONCLUSIONS

Competitive outcomes for red maple and loblolly pine under the greenhouse conditions did not vary in response to initial density. Red maple dominated mixed stands under all planting densities. Results were confounded by the presence of an eriophyid mite infestation on red maple, artificially high resource availability and conclusion of the study prior to constant final yield. Future attempts to measure the role of density on competitive outcomes between these two species should be carried out under field

conditions until constant final yield. Repeated measurements of stand growth would be necessary for the determination of constant final yield and assess the role of time on competitive outcomes.

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Table 6.1. Stem volume index (mm³) for loblolly pine and red maple grown in monoculture and mixed stands under greenhouse conditions.

Spacing (cm)	Loblolly Pine		Red Maple	
	Mixture	Monoculture	Mixture	Monoculture
2.54	57 Bc	278 Ac	481 Ac	160 Ac
5.08	133 Bb	1007 Ab	2073 Ab	750 Ab
7.62	457 Ba	2499 Aa	4771 Aa	2615 Aa

Means followed by a different capital letter within a species indicate significant differences within spacing for monocultures and mixtures for each species. Significant differences in means within a column are indicated by different lower-case letters.

Table 6.2. Height:diameter ratio (mm/mm) for loblolly pine and red maple grown in monoculture and mixed stands under greenhouse conditions.

Spacing (cm)	Loblolly Pine		Red Maple	
	Mixture	Monoculture	Mixture	Monoculture
2.54	116 Aa	108 Aa	53 Aa	52 Aa
5.08	109 Ab	96 Ab	59 Aa	52 Aa
7.62	100 Ac	88 Bc	57 Aa	63 Aa

Means followed by a different letter capital indicate significant differences within spacing for monocultures and mixtures for each species. Significant differences in means within a column are indicated by different lower-case letters.

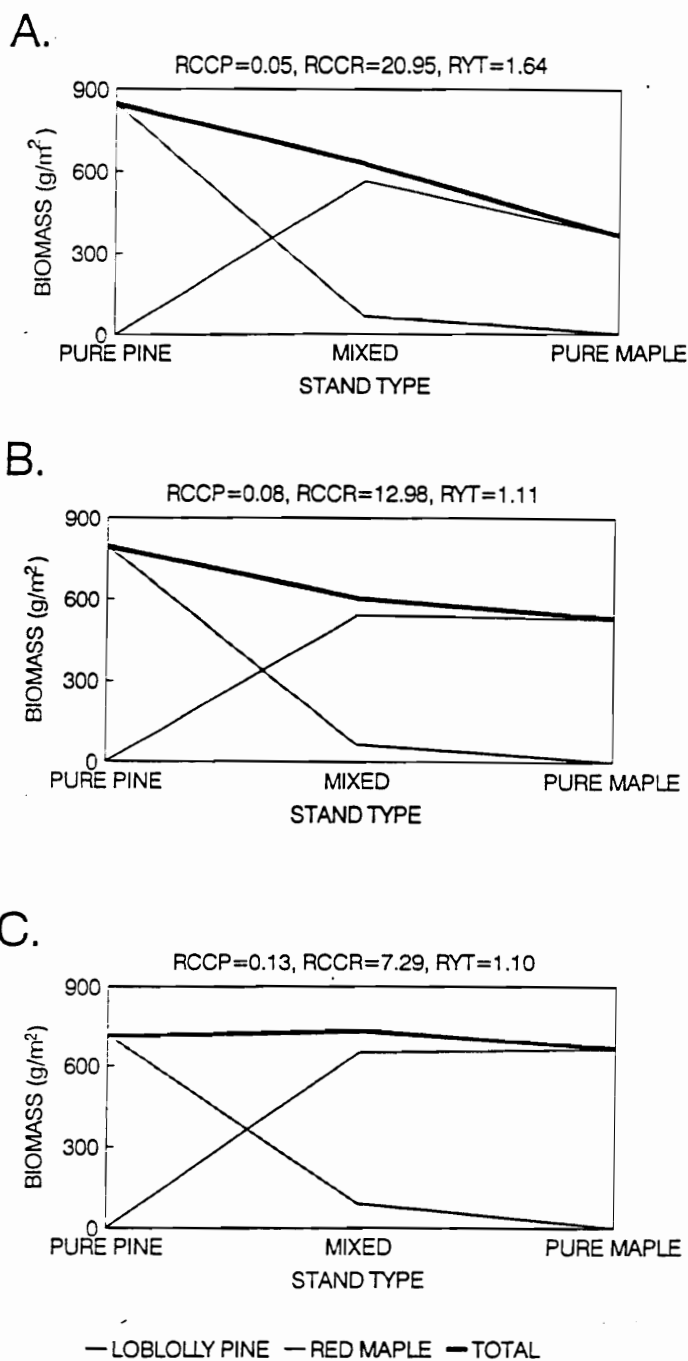


Figure 6.1. Relative yield diagrams with relative crowding coefficients for loblolly pine ($RCCP$) and red maple ($RCCM$) planted at 2.54 cm (A), 5.08 cm (B), and 7.62 cm (C) spacings in pure stands and 50:50 replacement mixtures under greenhouse conditions.

CHAPTER VII

EFFECTS OF CARBON DIOXIDE CONCENTRATION AND WATER AVAILABILITY ON GROWTH AND GAS EXCHANGE IN GREENHOUSE-GROWN MINIATURE STANDS OF LOBLOLLY PINE AND RED MAPLE.

INTRODUCTION

Forest stands developing in the South within the next several decades will grow in an atmosphere with higher CO₂ concentrations as well as rainfall regimes potentially different from today's climate (Clark et al. 1982). Several studies in which tree species of the region have been exposed to CO₂ and water availability regimes attempting to mimic future conditions suggest that species will differ in their response to a changing environment, possibly causing shifts in competitive abilities and, ultimately, changes in stand structure and species composition. (Ceulemans and Mousseau 1994). These changes may require alteration of current silvicultural strategies to maintain the biological and economic integrity of the region's forests.

Loblolly pine and red maple are frequently co-occurring tree species throughout the Piedmont and Coastal Plain physiographic province of the southeastern United States. Competitive interference from hardwood species, including red maple, have been widely reported to reduce growth of loblolly pine (Miller et al. 1991; Glover and

Zutter 1993). In commercial forests where both species occur, expensive vegetation management programs are often instituted to reduce this influence. Determining whether competitive interactions will change between these two species in response to changing CO₂ and water regimes would better allow forest managers to plan vegetation management and silvicultural strategies in southern forests.

Due to the high cost and long duration associated with whole forest stand experiments, miniature scale forest stands are beginning to be used to provide a competition component in CO₂ exposure experiments (Hendrey et al. 1993; Bazzaz and McConnaughay 1992). Miniature stands have shown potential for use in modeling effects of resource availabilities, including CO₂ concentration and water availability, on forest stand dynamics (Williams et al. 1986; Reekie and Bazzaz 1989; Fredericksen et al. 1993; Ceulemans and Mousseau 1994).

The objectives of this study are to determine the effects of atmospheric CO₂ concentration, availability of water and culture in monoculture or mixture on stand development and carbon allocation in miniature stands of loblolly pine and red maple. The effects of availability of these resources on gas exchange dynamics of these stands was also measured. Comparisons were made between growth characteristics of these miniature stands and field grown stands of similar composition.

METHODS

This study was conducted at the Center for Forest Environmental Studies (U. S. D. A. Forest Service) in Dry Branch, Georgia. This study was conducted for two growing cycles over the course of a ten month period.

Plant Culture and Growth Environment

Plastic pots 30 cm in diameter and 37 cm deep were filled with a Cecil series (Clayey, Kaolinitic, Thermic, Typic Hapludults) forest soil from central Georgia. Prior to potting, soil was sifted through a 64 mm (one-quarter inch) hardware cloth screen, and mixed with coarse, washed white sand at a 1:1 ratio to insure adequate drainage.

Loblolly pine seed was obtained from first generation improved trees from the Virginia Piedmont (courtesy Westvaco Corporation, Summerville, SC). Red maple seed was collected from open-pollinated trees in Montgomery County, Virginia. Following stratification, seeds were planted in pots at a 2.54 by 2.54 cm spacing both as pure stands of each species and in 50:50 replacement series mixtures.

Following seedling establishment, pots were placed in Continuous Stirred Tank Reactors (CSTRs) maintained at one of two CO₂ concentrations: One treatment was maintained at

ambient CO₂ concentrations, averaging 401 ppm with a range of 355 to 499 ppm. The elevated CO₂ treatment averaged 798 ppm with a range of 740 to 891 ppm.

CSTRs were enclosed in a greenhouse and exposed to full sunlight. Supplemental lighting was provided by 1000 watt metal halide lights to maintain a 16-hour photoperiod. Seedlings were subjected to two growing cycles to simulate two growing seasons rather than expose seedlings to a single, artificially extended growing season (Samuelson and Seiler 1994). After 9 weeks of growth, supplemental lighting was removed, exposing stands to natural daylengths for eight weeks beginning November 19.

During the first growing cycle, temperature and relative humidity averaged 24°C and 56% respectively. Shortened photoperiod temperature was lowered to approximately 12°C over the course of one week. Temperature and relative humidity averaged 12°C and 62% respectively during the final five weeks of the shortened photoperiod. Seven weeks of cold storage in a cold room at 2°C were used to fulfill chilling requirements. Plastic bags were placed over stands to prevent desiccation during chilling. Following cold storage, 16 hour photoperiods, CO₂ and water treatments were reinstated. Temperature was maintained at 12°C for one week and gradually increased over a week to simulate the beginning of a second growing season. Second growing

season temperature and humidity averaged 25°C and 62% respectively.

All pots were initially well-watered with deionized water for one month. Water stress treatments commenced one month after establishment. Well-watered treatments initially received approximately 2.5 cm of water per week. The amount of water applied to the pots during the eight hour photoperiod was gradually reduced to approximately one cm per week as temperatures decreased. During the second growing cycle, as plants became larger, water was increased to approximately 4 cm per week. Pots in the low water treatment always received half the amount of water given to well-watered pots.

Measurements and Analysis

Unless noted otherwise, all measurements reported in this study were confined to the innermost five by five block of seedlings surrounded on all sides by a buffer consisting of at least two rows of seedlings from the sides of the pots.

Survival, total height and stem diameter 0.5 cm below cotyledons was measured on seedlings at the end of the first growing cycle, immediately prior to cold storage and again during the second growing cycle, immediately prior to harvest. Canopy light transmittance was measured with a

Li-Cor quantum sensor (Li-Cor Inc., Lincoln, NE) by dividing mean light levels at five arbitrarily selected sub-canopy locations in each 25 tree stand by light levels immediately above the stand.

Leaf gas exchange was measured with a Li-Cor 6250 portable photosynthesis system on one seedling per species in each stand. Seedlings used in gas exchange measurements were arbitrarily selected from the second row from the outside edge of the pot. Single seedling photosynthesis measurements were made once during each growing cycle (14 and 46 weeks following planting). The nature of leaf material used for photosynthesis measurements of individual seedlings varied with sampling period due to increasing seedling size over the course of this study. First growing cycle measurements used all foliage for both loblolly pine and red maple. During the second growing cycle, measurements were made on a single, fully expanded leaf near the apex for red maple and two fully expanded fascicles for loblolly pine. Seedlings from the dominant crown position were selected for photosynthesis measurements whenever possible. Seedlings were clipped at groundline and measurement foliage was immediately placed in a 0.25l cuvette while still attached to the stem. Photosynthesis was unaffected by clipping for the duration of the gas exchange measurement. Although not completely eliminated, efforts were made to minimize self-shading of

leaf material in the cuvette. Gas exchange was measured under ambient (360 ppm), then elevated (706 ppm) CO₂ concentrations for each seedling. Elevated CO₂ concentrations were established in the cuvette by injecting a small amount of pure CO₂ gas immediately prior to the elevated CO₂ measurement. Single seedling photosynthesis measurements were calculated on a leaf area and leaf dry weight basis for leaf material in the cuvette during measurement. Leaf area measurements for red maple were made on a one-sided basis with a Li-Cor 3000 area meter (Li-cor Inc., Lincoln, NE). Loblolly pine leaf area was determined on an all-sided basis by measuring fascicle diameter, number, and length of needles in the cuvette (Ginn et al. 1991). Saturating light levels were maintained during measurements with an incandescent light (120V, General Electric PAR white flood light). Average relative humidity and leaf temperature was 29% and 27°C respectively.

Whole stand gas exchange was measured 46 weeks following germination using an open photosynthesis system. A plexiglass cuvette, measuring 83 cm high and 11 cm on a side was placed over the innermost five by five array of seedlings. Air with CO₂ concentrations averaging 408 or 806 ppm was pumped into the cuvette above the canopy of the seedling stand at a rate of 10 l min⁻¹. Reference air was drawn just prior to entry into the cuvette. Sample air was

drawn from a single location 5 cm above the soil surface and well below the bottom of the foliage canopy. Reference and sample air was drawn at a flow rate of 1.5 l min^{-1} . Air mixture was provided by a small fan near the top of the cuvette and a high flow rate. Excess air forced out the bottom of the cuvette prevented CO_2 from soil respiration from interfering with measurements. CO_2 concentration and temperature were measured using a Li-cor 6262 $\text{CO}_2/\text{H}_2\text{O}$ analyzer. Photosynthesis data represented a mean of 12 CO_2 concentration measurements, taken at 3 second intervals, beginning immediately after stand photosynthesis reached equilibrium (approximately 5 minutes). Temperature and photosynthetically active radiation averaged 32°C and $730 \mu\text{mol m}^{-2} \text{ s}^{-1}$

Stands were harvested immediately following whole stand gas exchange measurements. Leaves, stems and roots were separated by species within stands, oven dried, and weighed. Whole stand gas exchange measurements were calculated on a total leaf dry weight basis and a total land area basis. All data discussed here were taken 46 weeks following establishment of this study unless noted otherwise.

The study used a split-plot design in which CO_2 concentration was the main plot and the factorial combination of water and stand type were the split-plots. All possible CO_2 , water and stand type combinations were

replicated four times. A fifth block was removed from analysis when differences in light environment within the block were noticed. Analysis of variance was used to determine significance of main effects and interactions. Biomass values for mixed stands were corrected to account for differences in the number of trees initially established per stand relative to monocultures. Data were transformed to minimize unequal variance when appropriate (Gomez and Gomez 1984). Statistical differences of $p < 0.1$ were considered significant throughout the study. Each miniature stand is considered an experimental unit.

Ratio of stem height to diameter was evaluated as an index for above ground competition. Differences in allocation patterns between plant organs in response to CO₂, water and stand type treatments were tested for loblolly pine and red maple separately. A linear regression equation using natural log (ln) transformed leaf dry weight as the dependent variable and ln-transformed root or stem dry weight was fitted for each treatment combination (Causton and Venus 1981). An F-test was used to determine significance of differences between slope (relative organ growth rate) and intercept (initial dry matter investment). This analysis eliminates the confounding influence of treatment-induced plant size on allometric relationships (Eamus and Jarvis 1989).

Photosynthetic acclimation was tested by comparing

photosynthetic rates measured under ambient CO₂ concentrations between individuals or stands grown under ambient versus elevated CO₂ concentrations.

RESULTS

Loblolly pine dominated in all mixed stands regardless of CO₂ or water treatment. Total biomass increased 43% and 34% for loblolly pine and red maple respectively in response to growth under elevated CO₂ (Tables 7.1 and 7.2). Main effect response for water was also significant for both species with greater biomass under well-watered conditions. Total biomass response to growth under monoculture or mixture was species dependent with loblolly pine grown in mixed stands 37% larger than monoculture stands and red maple 72% smaller in mixed stands across water and CO₂ treatments (Table 7.2). No statistically-significant interactions were observed between CO₂ concentration and water or stand type for biomass in either species (Table 7.1).

Analysis of stem volume index measurements suggested that main effects increased in statistical significance between the first and second measurement (Table 7.1). The interaction between CO₂ and water in red maple during the second growing cycle can be summarized as a significant increase in stem volume index due to high CO₂ under high water availability, but not under low water availability.

Main effects responses of leaf, stem and root biomass closely followed total biomass with significant water and stand type main effects in both species (Table 7.3). No significant two- or three-way interactions were observed between CO₂, water or stand type.

Mean stem height main effects for water and stand type were generally significant during both growing seasons (Table 7.4). CO₂ main effects were never statistically significant for this variable. A significant three-way interaction between CO₂, water and stand type was present for stem height in red maple during both growing seasons. Under droughted conditions, monocultures were more responsive to elevated CO₂ compared to mixtures showing a 20% increase versus a 17% decrease in response to growth under elevated CO₂ respectively (Table 7.5). Under well-watered conditions, red maple in monocultures were 10% taller and mixtures were 24% taller under elevated CO₂. Mean height differences between maple and pine in mixed stands decreased significantly between the first and second growing season in all factorial combinations of water and CO₂. Relative heights of the species to one another did not differ significantly between growing seasons when comparing monoculture data except under the low CO₂, low water treatment.

Canopy light transmittance was affected by water status across CO₂ concentrations and stand types (Table

7.6). No other main effects or significant interactions between CO₂, water or stand type were detected.

Height:diameter ratios reflected differences in total biomass and the competitive status of stands for loblolly pine. Height:diameter ratio was higher for loblolly pine under well-watered versus droughted conditions and monoculture versus mixed stands suggesting competition was more intense under these conditions (Table 7.7). Differences in main effects for red maple were not significant although trends observed for water and stand type suggested that these differences may have manifested themselves if the study had been continued for a longer period of time (Tables 7.7 and 7.8).

Red maple allocated a larger proportion of carbon to leaves relative to root biomass when grown under elevated CO₂ (Table 7.9). Monoculture stands of red maple also showed greater leaf versus root allocation relative to red maple grown in mixture (Table 7.10). Higher leaf versus root allocation was also observed in red maple grown under well-watered versus droughted conditions (Table 7.11). Loblolly pine did not show allocation changes between leaves and roots in response to CO₂, water or stand type main effects.

Main effects allocation shifts between leaves and stems were apparent in both species. Monocultures had higher leaf to stem allocation compared to mixed stands

(Table 7.10). Well-watered loblolly pine stands also maintained higher leaf to stem ratio compared to those grown under drought conditions (Table 7.11). In red maple, allocation to leaves was significantly higher under elevated CO₂ (Table 7.9).

Photosynthetic rates expressed on a per unit leaf weight basis were higher when measured under elevated versus ambient CO₂ concentrations for both individual seedlings from monoculture stands and whole monoculture stands of loblolly pine and red maple (Table 7.12, Figure 7.1). Photosynthetic rates of individual seedlings measured under growth environment CO₂ concentrations showed a larger CO₂ response compared to whole stands for monocultures of both species; 296% versus 105% for individuals and stands of loblolly pine respectively and 89% and 77% for individuals and stands of red maple respectively. Downward acclimation of photosynthesis in response to growth under elevated CO₂ was detected in individuals of both species and red maple monoculture stands measured under the lower CO₂ concentration (Figure 7.1). The acclimation response was stronger in red maple relative to loblolly pine. Significant interactions for acclimation between water and stand type were not observed. Acclimation was not detected during photosynthesis measurements of individual seedlings during the first growing cycle for either species (data not shown).

Individual leaf photosynthesis under growing environment CO_2 concentrations was always higher in elevated CO_2 -grown seedlings for both species grown in mixture and monoculture ($P < 0.05$). The only interactions observed in individual seedling photosynthesis measurements was a weaker response for red maple seedlings grown in monoculture stands (Table 7.12, Figure 7.3).

Photosynthetic rates for stands of pure loblolly pine and mixed stands expressed on a per land area basis were greater under the higher level of water availability (Figure 7.4). Water availability did not affect photosynthetic rates of whole stand monocultures of loblolly pine or mixed stands when photosynthesis was expressed on a total leaf weight basis (Figure 7.5). Red maple monoculture whole stand photosynthesis expressed on a total leaf weight basis was higher under dry versus wet conditions. Single seedling conductance was lower in response to elevated CO_2 in red maple grown under high water availability (Figure 7.6). No significant treatment differences were detected in loblolly pine.

DISCUSSION

Growth characteristics of miniature stands reflected field-grown stands in several respects (chapter v). The large size of loblolly pine compared to red maple reflects early

growth patterns for these species grown under field conditions at a wider spacing (Fredericksen et al. 1991, 1993). The impact of growth in monoculture and mixture, where growth with red maple increased loblolly pine size and growth with loblolly pine reduced red maple size relative to monocultures, also followed patterns observed in five-year-old field stands where herbaceous vegetation was controlled (Figure 5.2). However, significant water and stand type main effects in seedling survival in miniature stands did not occur in field grown stands where measures were taken to prevent mortality (Table 7.13).

Droughted stands had higher light transmittance compared to well-watered stands in the present study reflecting field conditions (Figure 5.3). Percent light transmittance was in a similar range in the field and greenhouse studies. The absence of stand type effects do not reflect field conditions where mixed stands tended to have the lowest light transmittance. It is possible that further treatment responses could have developed if the study had been conducted for a longer period of time. The close proximity of the light sensor to the bottom of the canopy in the present study made characterization of canopy light transmittance difficult. As stands grow and lower leaves senesce, more accurate measurements would have been possible.

Loblolly pine seedling biomass response to growth

under elevated CO₂ was similar in magnitude to those reported by other researchers for individually-grown seedlings (Griffin et al. 1993; Sionit et al 1985; Tchapinski et al 1993; Tolley and Strain 1984). Red maple growth response to elevated CO₂ was also similar to those reported in other studies with these species (Bazzaz et al. 1990; Bazzaz and Miao 1993). The apparently delayed response of red maple to elevated CO₂ in the present study was observed by these two studies of 60 and approximately 130 days duration respectively. These results emphasize the importance of study duration on species response to elevated CO₂. In some cases, elevated CO₂ growth enhancement may require 18 months to stabilize (Idso and Kimball 1993).

Although red maple appeared to be suppressed at the conclusion of this experiment, height:diameter ratios did not reflect this condition. Loblolly pine height:diameter ratios responded to water and stand type treatments consistent with expectations regarding competitive stress. Red maple did not show this response despite being under more competitive stress (a higher degree of suppression) compared to loblolly pine. Even though height:diameter ratios reflected competitive status of both species in field stands, differences in allocation patterns between the two species under field versus greenhouse growth conditions appear to preclude the use of this index in

miniature stands.

Stem volume index decreases in red maple from mixed stands between first and second growing season (Table 7.2) may have been caused by experimental error due to extremely small seedling size. Shrinking and swelling of very small seedlings in response to plant water status could result in inaccurate measurements.

Red maple allocation shifts from roots to leaves suggest that this species may be able to respond to growth under elevated CO₂ by maintaining more carbon sources (leaves) while expending less resources toward sinks (roots). An elevated CO₂ growth environment may improve water status to the extent that more water using organs (leaves) can be maintained with less water absorbing biomass (roots). Lower conductance for red maple grown under elevated versus ambient CO₂ may have facilitated higher leaf:root ratios in these individuals. Higher leaf to root biomass under well-watered versus droughted conditions supports this assertion.

, Interplanting with loblolly pine appears to lower leaf:root ratio in red maple suggesting that loblolly pine may compete more aggressively for water forcing red maple to invest proportionally more carbon into roots at the expense of leaf material. Observations of loblolly pine and red maple monoculture stands grown in a greenhouse (chapter VI) verifies that loblolly pine stands deplete

soil water much more rapidly than red maple stands of similar total biomass.

Individual seedling measurements of photosynthesis reflected whole stand responses expressed on a leaf weight basis. However, correlation between individual seedling and whole stand measurements for a given stand varied greatly between species ($r=0.51$ for loblolly pine and 0.01 for red maple monocultures). While photosynthetic response was similar between individuals and stands on a leaf weight basis, interpretation of stand photosynthetic response to CO_2 environment and water availability is affected by expression of data on a leaf weight versus land area basis. Response to growth under elevated CO_2 is stronger on a per land area basis. Photosynthesis expressed on a land area basis appears to be greater because larger leaf canopies are produced under higher levels of CO_2 and water. Expressing photosynthesis on a land area basis more closely approximates net carbon sequestered as tree biomass and provides a stronger mechanistic link between net photosynthesis and biomass compared to measurements expressed on a leaf weight basis. Further studies are needed to determine whether this response changes over time as competition for space, water and nutrients continues to intensify. A similar study with loblolly pine and sweetgum did not show differences between photosynthetic rates expressed on a leaf weight and land area basis suggesting

that other factors may be involved in this response (Chapter IV).

Photosynthetic acclimation in loblolly pine has not been significant in previous experiments (Fetcher et al. 1988). Patterns in individual and stand photosynthesis for loblolly pine in the present study are similar to those of a study of similar design (chapter iv). While acclimation was not significant for individual seedlings in the earlier study, a trend toward acclimation was observed. Source-sink imbalance, manifested as reduced allocation to roots relative to leaves, in red maple grown under elevated CO_2 is characteristic of acclimating seedlings (Stitt 1991; Bowes 1993). Physical restriction of root growth, as evidenced by roots growing to the bottom of pots or curling around outside edges, did not appear to occur in this study and is not considered responsible for acclimation in these seedlings (Arp 1991; Thomas and Strain 1991). Similarly, photosynthetic acclimation in red spruce seedlings could not be attributed to root restriction (Samuelson and Seiler 1994).

Increasing net photosynthetic rates in elevated CO_2 -grown seedlings are often accompanied by lower stomatal conductance (Eamus and Jarvis 1989). While conductance was not measured on a whole stand basis, conductance in individually-measured red maple was significantly lower under elevated versus ambient CO_2 concentrations (Figure

7.6). No other significant differences for individual seedling conductance were observed for either species.

Lower conductance rates in seedlings grown under elevated CO₂ have been attributed to reduction in stomatal density and reduced stomatal opening (Woodward and Bazzaz 1988; Eamus and Jarvis 1989; Ceulemans and Mousseau 1994). Lower conductance and higher net photosynthesis rates in individually-measured red maple seedlings resulted in increased water use efficiency of red maple grown under elevated versus ambient CO₂. The absence of a significant CO₂ x water interaction for any biomass parameter suggests that this adaptation may be of little importance in improving competitive status of red maple in competition with loblolly pine in an elevated CO₂ environment.

The absence of significant interactions between CO₂ and water or stand type treatments at the conclusion of this experiment suggest that competitive interactions in these species will not be influenced by increased atmospheric CO₂ concentrations or changes in moisture regimes.

Discrepancies between the photosynthetic response of individual leaves and whole canopies could result in vastly different estimates of the carbon sink capacity of forests under future atmospheric CO₂ concentrations. Photosynthetic rate differences between individual leaves and whole canopies need to be considered in the development of mechanistic carbon budget models (Amthor 1994).

As with all studies where seedlings are grown in controlled environments, results should be extrapolated to field situations with extreme caution. Loblolly pine and red maple stands may respond to treatments differently depending on seasonal and life stage phenology, planting density, canopy duration density and resource availability. Miniature stands do provide a competition component which tends to dampen plant response to changes in resource availability (Bazzaz and McConnaughay 1992). By mimicking natural systems where plant-plant interactions play an important role in individual plant and ecosystem development, this experimental approach may represent an improvement over the traditional, single seedling approach to global change research.

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Table 7.1. Analysis of variance of mean stem volume index and total biomass for miniature stands of loblolly pine and red maple grown under ambient or elevated CO₂ concentrations (CO₂), well-watered or droughted conditions (water), in monoculture or mixed stands (stand). Mixed stand data for total biomass were corrected to account for differences in the initial number of seedlings established.

Source	df	Stem Volume Index- 1st cycle				Stem Volume Index- 2nd cycle				Total Biomass			
		Loblolly Pine		Red Maple		Loblolly Pine		Red Maple		Loblolly Pine		Red Maple	
		F value	pr > F	F-value	pr > F	F-value	pr > F	F-value	pr > F	F-value	pr > F	F-value	pr > F
Block	3	12.82	0.0001	2.24	0.1208	4.41	0.0182	0.21	0.8853	2.52	0.0902	0.71	0.5581
CO ₂	1	0.22	0.6167	0.01	0.9267	3.15	0.1738	5.68	0.0973	6.80	0.0798	5.33	0.1041
CO ₂ x Block	3	1.18	0.3467	2.15	0.1316	10.63	0.0004	2.12	0.1359	4.97	0.0110	2.15	0.1296
Water	1	20.56	0.0003	3.92	0.0640	154.19	0.0001	16.15	0.0009	65.98	0.0001	26.93	0.0001
CO ₂ x Water	1	0.02	0.8878	1.08	0.3136	0.08	0.7766	3.38	0.0834	0.03	0.8561	0.36	0.5587
Stand	1	0.83	0.3761	17.81	0.0006	52.84	0.0001	130.28	0.0001	38.05	0.0001	158.76	0.0001
CO ₂ x Stand	1	1.25	0.2784	1.04	0.3221	0.00	0.9711	0.38	0.5482	0.03	0.8584	1.48	0.2394
Water x Stand	1	0.06	0.8050	0.15	0.7041	0.85	0.3696	5.41	0.0326	0.44	0.5140	1.03	0.3243
CO ₂ x Water x Stand	1	0.53	0.4786	0.87	0.3645	0.08	0.7750	2.12	0.1635	0.07	0.7971	0.00	0.9937

Table 7.2. CO₂ concentration, water availability, and stand type effects on mean stem volume index and total stand biomass for loblolly pine and red maple grown in miniature stands. Mixed stand data for total biomass were corrected to account for differences in the initial number of seedlings established.

		Mean Stem Volume Index				Total Stand Biomass	
		End First Cycle (mm ³)		End Second Cycle (mm ³)		(g/m ²)	
		Loblolly Pine	Red Maple	Loblolly Pine	Red Maple	Loblolly Pine	Red Maple
CO ₂	Elevated	40.9	28.5	88.3	64.7	1079	408
	Ambient	38.6	29.5	62.7	47.3	756	305
Water	Well-watered	45.8	31.8	97.2	69.7	1129	460
	Droughted	33.9	26.1	54.1	41.3	731	265
Stand Type	Monoculture	39.0	31.8	65.9	70.1	773	559
	Mixture	41.4	23.2	97.7	22.8	1062	154

Table 7.3. Analysis of variance of total leaf, stem and root biomass for miniature stands of loblolly pine and red maple grown under ambient and elevated CO₂ concentrations, well-watered and droughted conditions in monoculture and mixed stands. Mixed stand data for total biomass were corrected to account for differences in the initial number of seedlings established.

Source	df	Leaf Biomass				Stem Biomass				Root Biomass			
		Loblolly Pine		Red Maple		Loblolly Pine		Red Maple		Loblolly Pine		Red Maple	
		F-value	pr > F	F-value	pr > F	F-value	pr > F	F-value	pr > F	F-value	pr > F	F-value	pr > F
Block	3	3.22	0.0472	1.95	0.1572	2.07	0.1404	1.06	0.3897	0.34	0.7977	1.71	0.2007
CO ₂	1	6.72	0.0809	5.79	0.0922	3.01	0.1812	1.85	0.2665	16.25	0.0274	5.96	0.0924
CO ₂ x Block	3	6.54	0.0035	3.88	0.0267	3.29	0.0444	2.87	0.0653	0.58	0.6350	2.46	0.0960
Water	1	79.79	0.0001	60.74	0.0001	39.77	0.0001	35.01	0.0001	10.68	0.0043	26.75	0.0001
CO ₂ x Water	1	0.04	0.8380	0.33	0.5705	0.90	0.3566	0.28	0.6015	0.09	0.7616	0.26	0.6144
Stand	1	49.61	0.0001	425.90	0.0001	12.49	0.0024	145.41	0.0001	9.20	0.0071	215.13	0.0001
CO ₂ x Stand	1	0.01	0.9312	2.37	0.1412	0.11	0.7467	1.21	0.2865	1.03	0.3242	0.89	0.3585
Water x Stand	1	0.55	0.4692	2.19	0.1561	0.33	0.5756	1.45	0.2442	0.47	0.5032	0.03	0.8616
CO ₂ x Water x Stand	1	0.07	0.7909	0.73	0.4051	0.11	0.7452	1.32	0.2665	0.26	0.6157	0.03	0.8756

Table 7.4. Analysis of variance for mean height of loblolly pine and red maple grown in miniature stands for two growing seasons.

Source	df	Loblolly Pine				Red Maple			
		First Season		Second Season		First Season		Second Season	
		F-value	pr > F	F-value	pr > F	F-value	pr > F	F-value	pr > F
Block	3	1.08	0.4744	0.58	0.6687	0.94	0.5204	0.67	0.6252
CO ₂	1	0.04	0.8569	3.21	0.1713	0.01	0.9106	1.72	0.2814
CO ₂ x Block	3	1.02	0.4101	6.02	0.0055	1.87	0.1722	2.45	0.0987
Water	1	14.50	0.0014	136.77	0.0001	0.59	0.4516	17.40	0.0006
CO ₂ x Water	1	1.91	0.1852	1.18	0.2926	7.59	0.0135	5.39	0.0329
Stand	1	1.52	0.2350	7.30	0.0151	9.61	0.0065	68.53	0.0001
CO ₂ x Stand	1	0.04	0.8350	0.33	0.5754	4.04	0.0606	1.57	0.2276
Water x Stand	1	0.00	0.9683	0.17	0.6814	0.00	0.9573	5.92	0.0263
CO ₂ x Water x Stand	1	0.04	0.8441	0.31	0.5872	5.39	0.0330	11.11	0.0039

Table 7.5. Mean height (mm) of loblolly pine and red maple grown in monoculture or mixture under factorial combination of two levels of CO₂ concentration and water availability for two growing cycles. Differences in height between species is expressed as (maple height/pine height)*100.

		Water									
		<u>Droughted</u>				<u>Well-watered</u>					
		<u>Monoculture</u>		<u>Mixture</u>		<u>Stand Type</u>		<u>Monoculture</u>		<u>Mixture</u>	
		<u>Growing Season</u>									
		<u>First</u>	<u>Second</u>	<u>First</u>	<u>Second</u>	<u>First</u>	<u>Second</u>	<u>First</u>	<u>Second</u>	<u>First</u>	<u>Second</u>
CO ₂	Ambient	76	90	74	93	83	115	80	128		
	Loblolly Pine	51	54	47	52	52	72	43	46		
	Red Maple	67	60	63	56	63	63	54	36		
	% Difference										
	p. diff.*	0.04		0.04		0.90		0.01		0.01	
Elevated		73	95	69	105	86	133	82	145		
	Loblolly Pine	48	65	43	43	50	79	51	57		
	Red Maple	66	68	62	41	58	59	62	39		
	% Difference										
	p. diff.*	0.78		0.01		0.75		0.00		0.00	

* Significance of maple/pine mean height differences between first and second growing season within factorial combinations of CO₂, water and stand type were determined with a paired t-test.

Table 7.6. Mean light transmittance and p-values for 46-week-old miniature stands of loblolly pine and red maple grown under two levels of CO₂ concentrations and water availability in monoculture and mixed stands.

		% transmittance	p diff.
CO ₂	Elevated	10.5	0.2124
	Ambient	14.7	
Water	Well-watered	6.8	0.0001
	Droughted	17.9	
Stand Type	Loblolly Pine monoculture	11.6	0.5277
	Mixed	13.7	
	Red Maple monoculture	12.6	

Table 7.7. CO₂ concentration, water availability, and stand type main effects on height:diameter ratio for loblolly pine and red maple grown in miniature stands for two growing seasons.

		Height-Diameter Ratio			
		End First Cycle (mm/mm)		End Second Cycle (mm/mm)	
		Loblolly Pine	Red Maple	Loblolly Pine	Red Maple
CO ₂	Elevated	58.10 A	35.41 A	72.60 A	38.05 A
	Ambient	58.11 A	35.79 A	70.83 A	39.95 A
Water	Well-watered	60.02 A	34.84 A	77.94 A	39.81 A
	Droughted	56.32 A	36.31 A	65.94 B	38.18 A
Stand Type	Monoculture	59.99 A	34.46 A	74.38 A	37.65 A
	Mixture	56.10 B	36.81 A	68.94 B	40.38 A

NOTE: Differences between pairs of means within a species followed by the same letter are not significantly different (p < 0.1).

Table 7.8. Analysis of variance of mean height-diameter ratio for miniature stands of loblolly pine and red maple grown under ambient and elevated CO₂ concentrations, well-watered and droughted conditions in monoculture and mixed stands.

Source	df	End first cycle				End second cycle			
		Loblolly Pine		Red Maple		Loblolly Pine		Red Maple	
		F-value	pr > F	F-value	pr > F	F-value	pr > F	F-value	pr > F
Block	3	5.41	0.0085	5.72	0.0068	1.14	0.3601	1.68	0.2099
CO ₂	1	0.44	0.5546	0.43	0.5587	0.60	0.4940	2.51	0.2112
CO ₂ x Block	3	0.22	0.8784	0.03	0.9935	1.58	0.2299	0.44	0.7286
Water	1	1.88	0.1884	2.83	0.1108	41.24	0.0001	0.80	0.3848
CO ₂ x Water	1	4.30	0.0535	5.57	0.0305	2.33	0.1456	1.99	0.1765
Stand	1	4.39	0.0513	2.46	0.1356	8.70	0.0090	2.36	0.1432
CO ₂ x Stand	1	0.95	0.3441	2.09	0.1669	0.20	0.6572	0.81	0.3816
Water x Stand	1	0.23	0.6362	0.14	0.7117	0.24	0.6310	0.29	0.5975
CO ₂ x Water x Stand	1	1.35	0.2621	1.88	0.1884	1.36	0.2597	7.03	0.0168

Table 7.9. Regression coefficients and coefficients of determination for allometric relations in response to CO₂ treatment. Equations are in the form Y=intercept + slope(X). Levels of significance indicate differences between pairs of coefficients in response to CO₂ concentration.

Species	Relationship (y, x)	CO ₂ concentration	intercept	slope	pdiff.- (intercept)	p diff (slope)	R ²
Loblolly Pine	ln(leaf wt)-ln(root wt)	Elevated	0.73	1.24	0.33	0.42	0.53
		Ambient	0.20	1.58			0.71
Red Maple	ln(leaf wt)-ln(root wt)	Elevated	-0.61	1.09	0.01	0.01	0.95
		Ambient	-0.25	0.83			0.94
Loblolly Pine	ln(leaf wt)-ln(stem wt)	Elevated	0.65	1.30	0.08	0.19	0.91
		Ambient	0.24	1.53			0.91
Red Maple	ln(leaf wt)-ln(stem wt)	Elevated	-0.38	1.61	0.22	0.07	0.91
		Ambient	-0.22	1.32			0.95

Table 7.10. Regression coefficients and coefficients of determination for allometric relations in response to growth in monoculture or mixture. Equations are in the form $Y = \text{intercept} + \text{slope}(X)$. Levels of significance indicate differences between pairs of coefficients in response to water availability.

Species	Relationship (y, x)	Stand type	intercept	slope	pdiff.- (intercept)	p diff (slope)	R ²
Loblolly Pine	ln(leaf wt).-ln(root wt)	Monoculture	0.47	1.36	0.87	0.98	0.62
		Mixture	0.55	1.37			0.63
Red Maple	ln(leaf wt).-ln(root wt)	Monoculture	-0.77	1.18	0.00	0.00	0.87
		Mixture	-0.08	0.54			0.82
Loblolly Pine	ln(leaf wt).-ln(stem wt)	Monoculture	0.16	1.59	0.02	0.05	0.93
		Mixture	0.68	1.27			0.91
Red Maple	ln(leaf wt).-ln(stem wt)	Monoculture	-0.06	1.29	0.99	0.06	0.78
		Mixture	-0.05	0.87			0.81

Table 7.11. Regression coefficients and coefficients of determination for allometric relations in response to water availability. Equations are in the form $Y = \text{intercept} + \text{slope}(X)$. Levels of significance indicate differences between pairs of coefficients in response to water availability.

Species	Relationship (y, x)	Water availability	intercept	slope	pdiff.- (intercept)	p diff (slope)	R ²
Loblolly Pine	$\ln(\text{leaf wt}) - \ln(\text{root wt})$	Well-watered	0.72	1.28	0.86	0.84	0.46
		Droughted	0.63	1.20			0.70
Red Maple	$\ln(\text{leaf wt}) - \ln(\text{root wt})$	Well-watered	-0.50	1.03	0.18	0.09	0.94
		Droughted	-0.31	0.85			0.91
Loblolly Pine	$\ln(\text{leaf wt}) - \ln(\text{stem wt})$	Well-watered	0.70	1.24	0.01	0.01	0.89
		Droughted	-0.09	1.87			0.88
Red Maple	$\ln(\text{leaf wt}) - \ln(\text{stem wt})$	Well-watered	-0.38	1.54	0.53	0.88	0.92
		Droughted	-0.29	1.51			0.89

Table 7.12. Analysis of variance for photosynthesis of individual seedlings and whole miniature stands of loblolly pine and red maple measured under growth environment CO₂ concentrations under well-watered and droughted conditions. Individual seedlings were measured in monocultures and mixed stands and whole stand measurements were made for monocultures only.

Source	df	INDIVIDUALLY-MEASURED SEEDLING PHOTOSYNTHESIS						WHOLE STAND PHOTOSYNTHESIS											
		LEAF WEIGHT BASIS						LEAF WEIGHT BASIS						LAND AREA BASIS					
		Loblolly Pine			Red Maple			Loblolly Pine			Red Maple			Loblolly Pine			Red Maple		
		F-value	pr > F		F-value	pr > F		F-value	pr > F		F-value	pr > F		F-value	pr > F		F-value	pr > F	
Block	3	1.81	0.1892		1.32	0.3051		7.45	0.0190		2.55	0.1515		4.94	0.0463		1.20	0.3873	
CO ₂	1	112.32	0.0018		40.55	0.0078		15.32	0.0296		5.03	0.1107		31.06	0.0114		33.98	0.0101	
CO ₂ x Block	3	0.38	0.7718		1.15	0.3597		2.46	0.1604		2.61	0.1467		3.38	0.0954		0.60	0.6395	
Water	1	0.08	0.7800		8.51	0.0106		0.02	0.9057		8.85	0.248		29.37	0.0016		0.45	0.5270	
CO ₂ x Water	1	0.71	0.4136		0.07	0.7902		0.11	0.7526		7.42	0.0345		0.13	0.7336		5.50	0.0575	
Stand	1	0.12	0.7304		7.13	0.0175													
CO ₂ x Stand	1	0.09	0.7657		14.81	0.0016													
Water x Stand	1	0.04	0.8416		1.37	0.2600													
CO ₂ x Water x Stand	1	0.04	0.8431		0.08	0.7747													

Table 7.13. Mean survival of loblolly pine and red maple seedlings grown n miniature stands after 46 weeks.

Treatment	Level	Loblolly Pine		Red Maple	
		% Survival	p diff.	% Survival	p diff.
CO ₂	Elevated	95	0.5033	83	0.5629
	Ambient	95		79	
Water	Well-watered	97	0.0220	89	0.0034
	Droughted	93		73	
Stand Type	Monoculture	97	0.0887	87	0.0381
	Mixture	94		75	

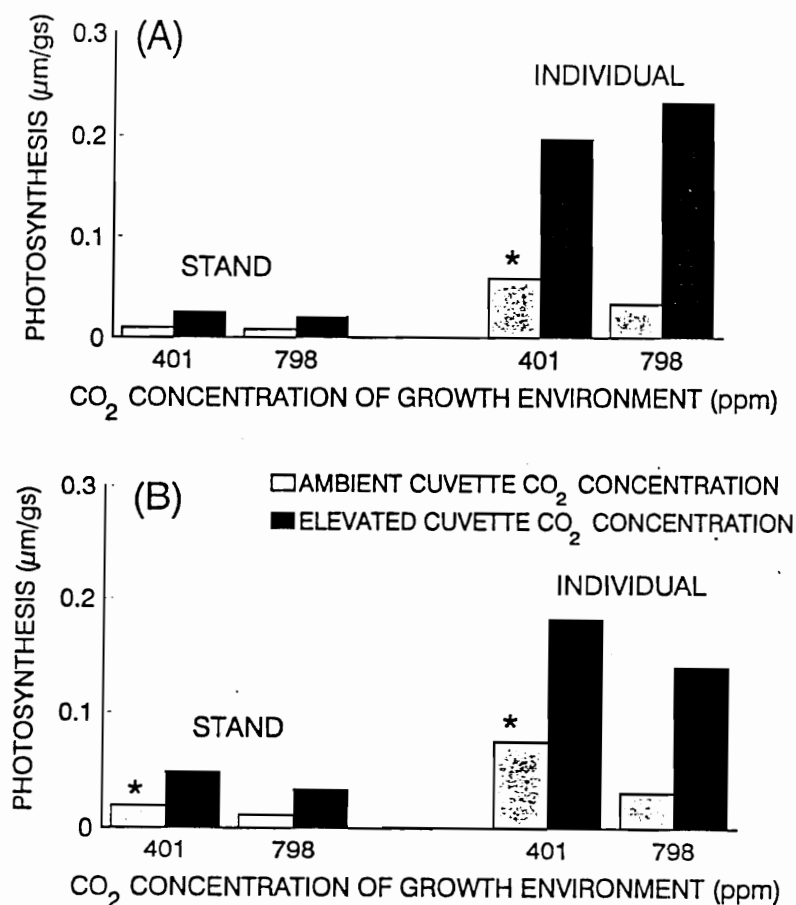


Figure 7.1. Photosynthesis rates in whole miniature stands and individual seedlings from these stands for loblolly pine (A) and red maple (B) grown under ambient (401) and elevated (798) ppm CO₂ concentrations. Ambient cuvette CO₂ concentrations were 360 ppm for individual seedlings and 401 ppm for stands. Elevated cuvette CO₂ concentrations were 706 for individual seedlings and 798 ppm for stands. Significant differences in photosynthetic rates between growth environments within measurement CO₂ concentrations within stand and individual measures for a species are marked with an asterisk.

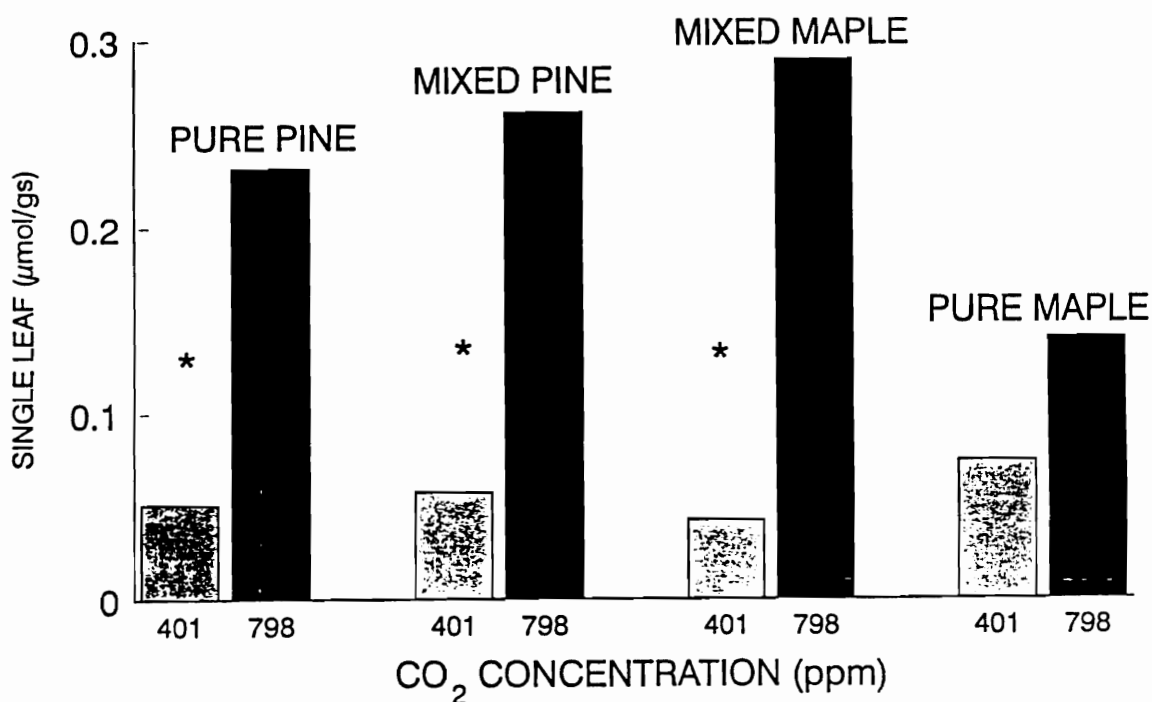


Figure 7.2. Photosynthesis rates for single seedlings from miniature stands of loblolly pine and red maple monocultures and 50:50 replacement mixtures (mixed) for ambient and elevated CO₂ concentrations. Photosynthesis rates were measured under growth environment CO₂ concentrations. Significant differences within a species and stand type are marked with an asterisk ($p < 0.05$).

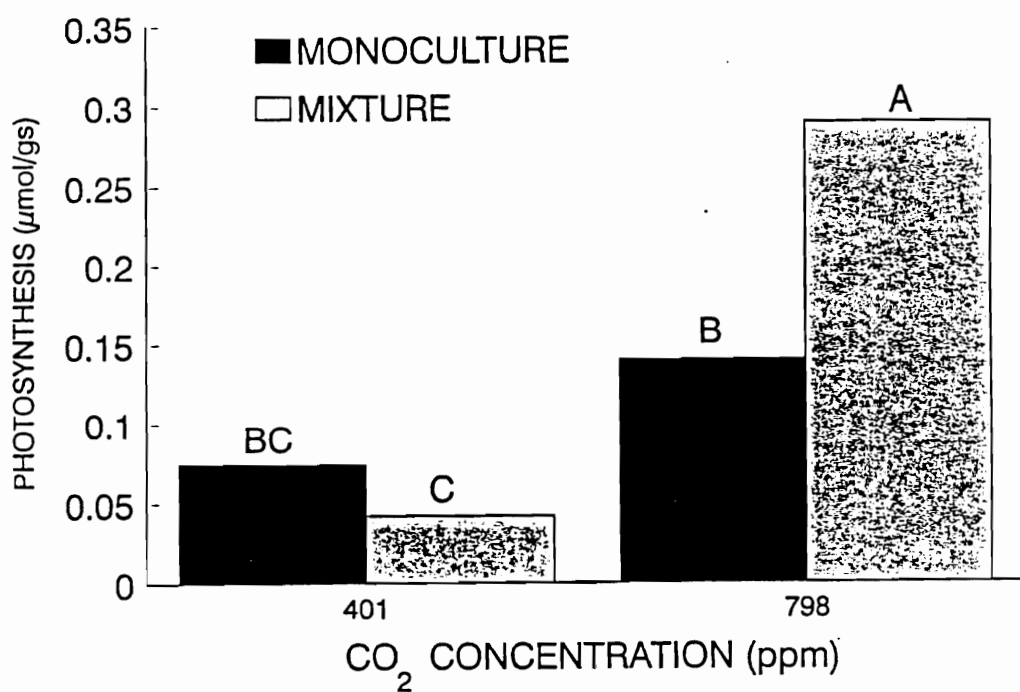


Figure 7.3. Photosynthesis rates from single red maple seedlings from monocultures and 50:50 replacement mixtures grown and measured under ambient and elevated CO₂ concentrations. Means labelled with the same letter are not significantly different at the $p < 0.05$ level.

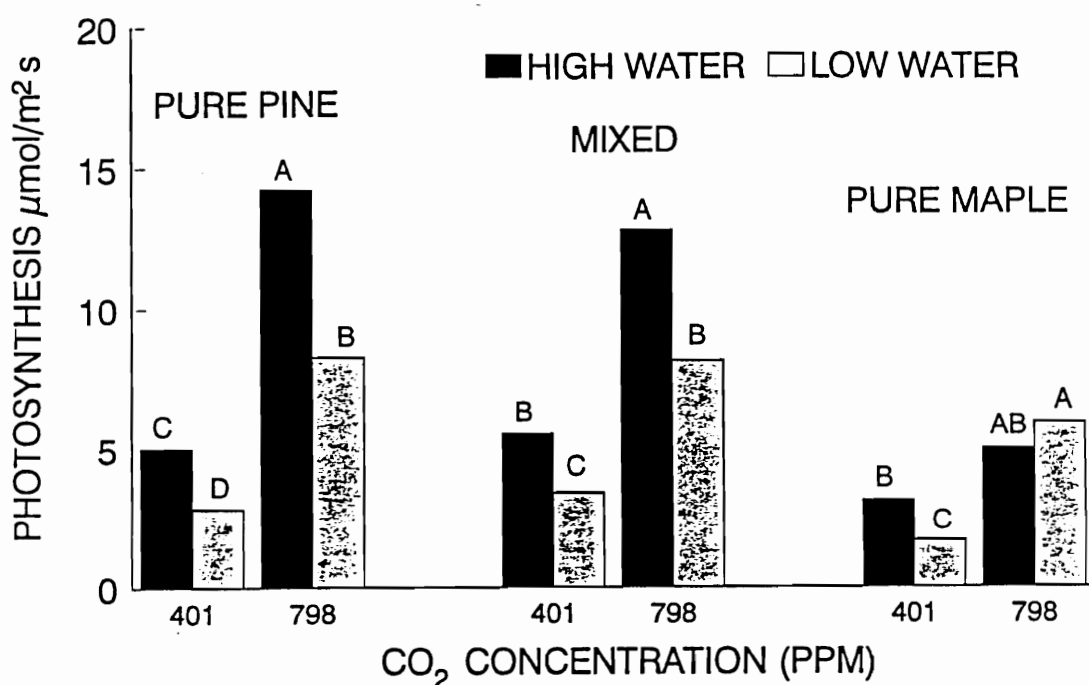


Figure 7.4. Stand photosynthesis expressed on a per unit land area for miniature stands of loblolly pine and red maple monocultures and 50:50 replacement mixtures (mixed) for factorial combinations of CO₂ concentration and water availability. Photosynthesis rates were measured under growth environment CO₂ concentrations. Factorial combinations of CO₂ concentration and water availability within a stand type labelled with the same letter are not significantly different at the $p < 0.05$ level.

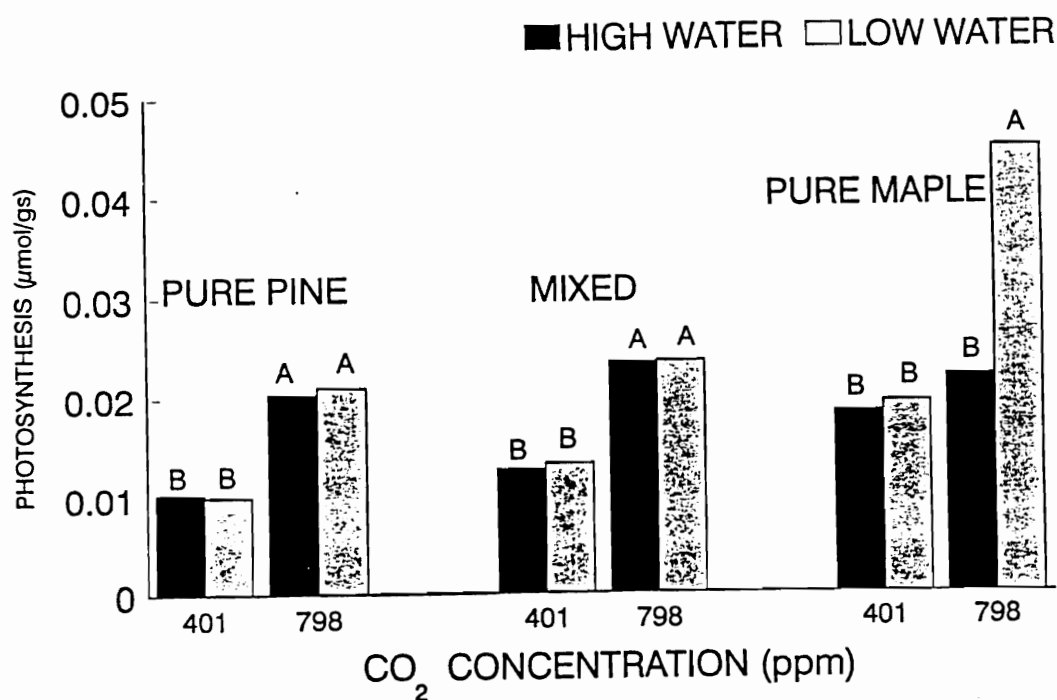


Figure 7.5. Stand photosynthesis per unit leaf weight for miniature stands of loblolly pine and red maple monocultures and 50:50 replacement mixtures (mixed) for factorial combinations of CO₂ concentration and water availability. Photosynthesis rates were measured under growth environment CO₂ concentrations. Factorial combinations of CO₂ concentration and water availability within a stand type labelled with the same letter are not significantly different at the $p < 0.05$ level.

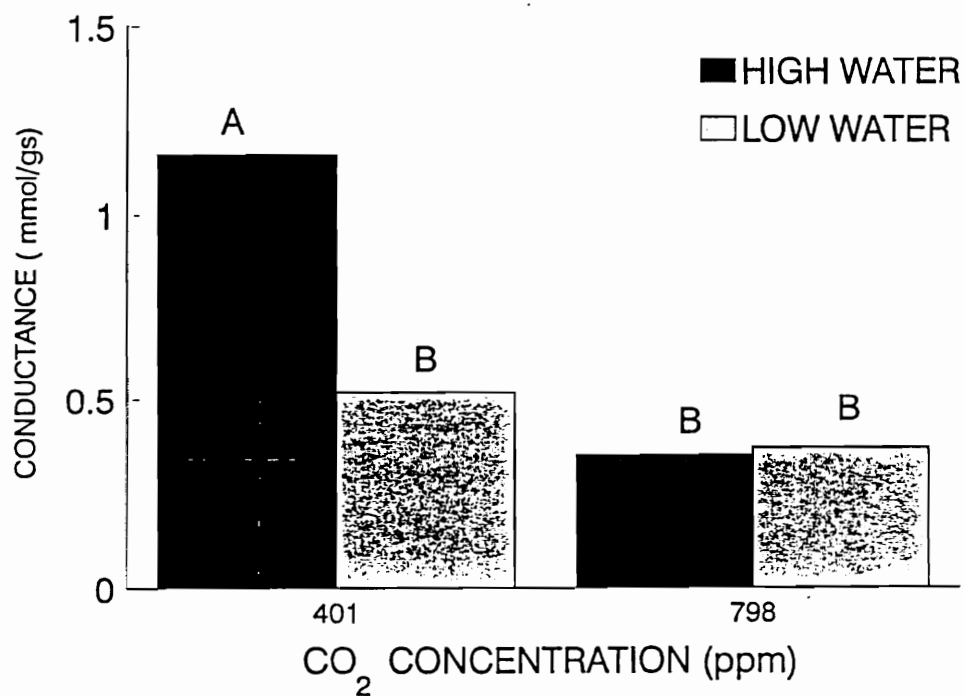


Figure 7.6. Stomatal conductance for single red maple seedlings grown under droughted and well-water conditions and measured and grown under ambient and elevated CO₂ concentrations. Means labelled with the same letter are not significantly different at the $p < 0.05$ level.

CHAPTER VIII

EFFECTS OF ROOTING VOLUME AND AMBIENT CO₂ CONCENTRATION ON GROWTH AND ALLOMETRY OF INDIVIDUALLY-GROWN LOBLOLLY PINE AND RED MAPLE SEEDLINGS.

INTRODUCTION

Researchers have typically used seedlings grown as individuals to predict community response to increasing atmospheric CO₂ concentrations. However, predictions of species performance under elevated CO₂ can vary considerably between estimates based on individually-grown seedlings and those grown under competitive conditions (Williams et al. 1988; Reekie and Bazzaz 1989; Bazzaz and McConnaughay 1992). These authors found individually-grown seedlings to be more responsive to elevated CO₂ growth enhancements compared to those grown in competition with others.

Allocation response to growth under elevated CO₂ have been reported to be dependent on available rooting volume (Arp 1991; Idso and Kimball 1994). Total biomass in cotton plants was responsive to growth under elevated CO₂ in the larger of two pot sizes only (Thomas and Strain 1991). Plants in the smaller pots reduced photosynthetic capacity due to insufficient rooting volume earlier than those in large pots. Arp (1991) summarizing several studies with herbaceous plants and cereal crops reported seedling root shoot ratio responded to growth under elevated CO₂ more

strongly when pot size was large. However, tree species may respond differently. Red spruce seedlings allocated more growth toward leaves in the larger of two pot sizes independent of CO₂ treatment (Samuelson 1992).

The objectives of this experiment were to evaluate the effects of container size on CO₂ response in loblolly pine and red maple. Comparisons in organ allocations between these seedlings and others grown in competition with one another are also made.

METHODS

This study was conducted at the Center for Forest Environmental Studies (U. S. D. A. Forest Service) in Dry Branch, Georgia. This study was conducted for two growing cycles over the course of a ten month period.

Plant Culture and Growth Environment

Nursery containers 175 and 1000 cm³ (Ray Leach Nursery, Canby, OR) were filled with a Cecil series (Clayey, Kaolinitic, Thermic, Typic Hapludults) forest soil from central Georgia. Prior to potting, soil was sifted through a 64 mm (one-quarter inch) hardware cloth screen and mixed with coarse, washed white sand at a ratio of 5 parts sand to 1 part soil by volume to insure adequate drainage.

Loblolly pine seed was obtained from first generation improved trees from the Virginia Piedmont (courtesy Westvaco Corporation, Summerville, SC). Red maple seed was collected from open-pollinated trees in Montgomery county, Virginia. Following stratification, several seeds of loblolly pine or red maple were planted in each container. Following establishment, all but the largest seedling was removed from each container. Seedlings were maintained under CO₂, temperature and photoperiod conditions described in chapter VII. Pots were maintained under well-watered conditions.

Data analysis

Seedlings were harvested 46 weeks after planting and separated into leaves, stems and roots. Stem volume index was determined based on stem height and diameter 0.5 cm below cotyledons. Dry weights of individual seedlings were determined following drying to a constant weight. Container size and CO₂ response within a species were analyzed with analysis of variance using a split-plot design with CO₂ concentration as the main plot and pot size as the split-plot. Each experimental unit consisted of the mean of six to eight seedlings.

Differences in allocation patterns between plant organs in response to CO₂ and container size were tested for

loblolly pine and red maple separately. A linear regression equation using natural log (ln) transformed leaf dry weight as the dependent variable and ln-transformed root or stem dry weight was fitted for each treatment combination (Causton and Venus 1981). An F-test was used to determine significance of differences between slope (relative organ growth rate) and intercept (initial dry matter investment). This analysis eliminates the confounding influence of treatment-induced plant size on allometric relationships (Eamus and Jarvis 1989).

RESULTS

All biomass variables and stem volume index were significantly larger in the larger container size (Table 8.1). Total and organ biomass increased under elevated CO₂ in loblolly pine with 27 and 33% total biomass increases due to growth in elevated CO₂ for 1000 and 175 cm³ containers respectively. Red maple total and organ biomass response to elevated CO₂ was not significant at $p < 0.1$ with the exception of leaf biomass. No significant interactions between CO₂ concentration and container size were detected for any biomass variable or stem volume index. Statistical significance of CO₂ response for biomass variables and stem volume index tended to be higher for the smaller container size. Total stem height did not change significantly in

response to CO₂ concentration. Relative height of red maple to loblolly pine did not change in response to CO₂ treatments, averaging 61% in small containers and 65% in large containers.

Container size had a significant effect on allocation patterns between leaves and stems in loblolly pine (Table 8.2); Seedlings grown in the 175 cm³ containers allocated a greater proportion of carbon to leaves at the expense of root relative to seedlings grown in the larger container size. No other seedling size-independent allocation differences were detected for either species in response to container size (Table 8.2).

DISCUSSION

Loblolly pine grown in small containers had greater allocation in response to elevated CO₂. No other significant allocation responses to CO₂ environment were detected. The statistically-weak response of red maple to elevated CO₂ is not consistent with previous results for seedlings of similar age (Bazzaz and Miao 1993; chapter vii). These results are especially unexpected regarding comparison with seedlings grown in competitive arrays (chapter vii). The weak response of seedlings to CO₂ in the present study appears to be due to the high variability in red maple seedling size. Mean biomass response to growth

under elevated CO₂ is within the range reported in the previously-cited study. Competitive interactions usually dampens seedling growth response to elevated CO₂ (Bazzaz and McConnaughay 1992). While nutrient deficits are unlikely to have occurred during the course of this study, periodic water deficits may have suppressed growth across CO₂ treatments. The absence of a significant interaction between container size and CO₂ concentration on organ and total biomass concur with previous work with red spruce (Samuelson 1992).

Relative mean height of red maple to loblolly pine was similar to those of seedlings of the same age grown in miniature monoculture stands (chapter vii). In contrast, red maple seedlings grown in mixture were much smaller relative to loblolly pine from mixtures suggesting that competitive interactions affect response to elevated CO₂.

Increased allocation to leaves at the expense of roots in loblolly pine suggests that this species may be capable of more efficient internal water use under elevated CO₂ (Tyree and Alexander 1993). However, root:shoot ratio response of this species to elevated CO₂ has been extremely variable (Rogers et al. 1983; Tolley and Strain 1984; Sionit et al. 1988). The inconsistency of response of this allometric parameter may also be influenced by other factors including plant age, duration of study or other environmental conditions (Enoch and Zieslin 1988).

Smaller containers, where resources are more likely to become limiting, showed a more nearly significant response to elevated CO₂. Differences in significance between large and small pots may have been influenced by variable growth characteristics of individual seedlings independent of CO₂ concentration. These differences would be more pronounced in the larger pot size where the potentially greater growth variation can occur compared to smaller pot sizes.

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Table 8.1. Biomass, stem volume index and total height for loblolly pine and red maple seedlings grown for two growing cycles under ambient or elevated CO₂ concentrations in two container sizes.

		Loblolly Pine				Red Maple			
	Pot Size (cm ³)	Ambient	Elevated	p diff	Ambient	Elevated	p diff		
Total Biomass (g)	1000	1.47	1.87	0.07	0.85	1.08	0.15		
	175	0.56	0.75	0.01	0.43	0.53	0.13		
Leaf Weight (g)	1000	0.94	1.22	0.06	0.20	0.28	0.09		
	175	0.32	0.44	0.03	0.06	0.09	0.09		
Stem Weight (g)	1000	0.22	0.27	0.21	0.15	0.19	0.11		
	175	0.10	0.11	0.03	0.09	0.11	0.05		
Root Weight (g)	1000	0.32	0.39	0.08	0.49	0.61	0.21		
	175	0.14	0.19	0.00	0.28	0.33	0.16		
Stem Volume Index (mm ³)	1000	140.9	198.0	0.05	157.28	182.90	0.51		
	175	51.70	64.02	0.05	61.52	74.40	0.12		
Total Height (mm)	1000	126.3	139.5	0.25	77.7	85.2	0.44		
	175	81.7	86.4	0.15	52.8	56.5	0.24		

Table 8.2. Regression coefficients and coefficients of determination for allometric relations in individually-grown loblolly pine and red maple in response to container size. Equations are in the form $Y = \text{intercept} + \text{slope}(X)$. Levels of significance indicate differences between pairs of coefficients in response to container size.

Species	Relationship (y, x)	Pot size (cm ³)	intercept	slope	pdiff.- (intercept)	p diff (slope)	R ²
Loblolly Pine	ln(leaf wt) - ln(root wt)	1000	0.28	2.00	0.00	0.01	0.58
		175	0.00	3.11			0.61
Red Maple	ln(leaf wt) - ln(root wt)	1000	0.04	1.09	0.01	0.14	0.60
		175	-0.01	0.83			0.56
Loblolly Pine	ln(leaf wt) - ln(stem wt)	1000	0.32	1.32	0.01	0.73	0.43
		175	0.10	1.41			0.50
Red Maple	ln(leaf wt) - ln(stem wt)	1000	0.03	0.43	0.06	0.42	0.53
		175	-0.03	0.36			0.48

Table 8.3. Regression coefficients and coefficients of determination for allometric relations in individually-grown loblolly pine and red maple in response to ambient CO₂ concentration and rooting volume. Equations are in the form Y=intercept + slope(X). Levels of significance indicate differences between pairs of coefficients in response to CO₂ concentration.

Species	Relationship (y, x)	CO ₂ concentration	Pot size (cm ³)	intercept	slope	pdiff - (intercept)	p diff (slope)	R ²
Loblolly Pine	ln(leaf wt).-ln(root wt)	Elevated	1000	0.30	1.45	0.49	0.23	0.42
		Ambient	1000	0.39	0.95			0.30
	ln(leaf wt).-ln(root wt)	Elevated	175	0.08	1.65	0.33	0.08	0.57
		Ambient	175	0.15	0.96			0.34
Red Maple	ln(leaf wt).-ln(root wt)	Elevated	1000	0.04	0.44	0.89	0.39	0.49
		Ambient	1000	0.05	0.35			0.56
	ln(leaf wt).-ln(root wt)	Elevated	175	-0.03	0.39	0.30	0.15	0.51
		Ambient	175	0.00	0.22			0.31
Loblolly Pine	ln(leaf wt).-ln(stem wt)	Elevated	1000	0.37	1.73	0.19	0.41	0.59
		Ambient	1000	0.23	2.13			0.48
	ln(leaf wt).-ln(stem wt)	Elevated	175	0.04	3.00	0.63	0.74	0.59
		Ambient	175	0.01	2.79			0.63
Red Maple	ln(leaf wt).-ln(stem wt)	Elevated	1000	0.05	1.14	0.74	0.32	0.53
		Ambient	1000	0.06	0.90			0.66
	ln(leaf wt).-ln(stem wt)	Elevated	175	-0.01	0.85	0.53	0.38	0.58
		Ambient	175	0.01	0.60			0.33

CHAPTER IX

EFFECTS OF SHADING ON GROWTH AND PHOTOSYNTHETIC RESPONSE OF FOUR PIEDMONT TREE SPECIES

INTRODUCTION

Shade tolerance is a widely used but mechanistically poorly understood concept used by silviculturalists to categorize the ability of a tree species to persist in a mature forest understory. Shade tolerance classifications have been published in numerous forestry textbooks but their development and interpretation is purely anecdotal. Unevenaged silvicultural strategies, which inherently favor shade tolerant species, are increasingly mandated for public land in the southeast. Foresters might be better able to maintain a component of intolerant species under these management regimes, given a better understanding of the mechanisms underlying shade tolerance. Identifying physiological characteristics associated with shade tolerance could eventually aid in the selection of appropriate genotypes for establishment under low light availability associated with the regeneration niche in unevenaged stands.

Researchers have identified above and below-ground components to shade tolerance. Several photosynthetic characteristics have been associated with shade tolerant plants including more leaf area, higher photosynthetic

efficiency and lower respiration per unit leaf area under low light conditions (Loach 1967; Teskey and Shrestha 1985; Walters and Field 1987). Additionally, below-ground processes play a role in determining species shade tolerance including drought and disease resistance (Kozlowski et al 1991). While it is recognized that ability to retain adequate photosynthetic rates is necessary for persistence in the understory, the direct role of light availability on the maintenance of this process over the course of years is not known.

The objectives of this study are to describe photosynthetic processes as well as growth and allocation characteristics directly affected by light availability in four co-occurring Piedmont tree species of different shade tolerance. Species used in this study were loblolly pine (Pinus taeda) and yellow-poplar (Liriodendron tulipifera), both shade intolerant, Eastern white pine (Pinus strobus), intermediate tolerance, and red maple (Acer rubrum), tolerant (Spurr and Barnes 1980). These species were selected to represent a range of shade tolerance of dominant tree species on the Virginia Piedmont. Changes in photosynthetic characteristics occurring between the first and second growing season in response to growth environment light availability are also discussed.

METHODS

This study was conducted in an open field at the Reynolds Homestead Forest Resources Research Center in Critz, Virginia. Shade frames 2.1 by 2.1 meters wide 1.2 meters high were constructed from two by two inch lumber anchored to the ground with metal posts. Light intensity treatments were provided with black polypropylene shade fabric, marketed as 80 and 63%, draped over frames as well as an unshaded control. Light extinction as measured with a Li-cor quantum sensor (Li-cor, Inc., Lincoln, NE) on a clear day was found to be 89 and 79% for the two shade treatments respectively. A 30 cm gap was left between the bottom of shade fabric and ground level to prevent heat buildup (Loach 1967). Adjacent shade treatments were 2.4 meters apart to prevent overlap of shade treatments. Shade treatments were replicated four times and arranged in a complete randomized design.

Seedlings of loblolly pine, red maple, yellow-poplar (all 1-0) and white pine (2-0) were obtained from the Virginia Department of Forestry and planted in early May in five gallon (31.75 cm wide and 27.9 cm high) plastic pots containing a 1:1 mixture of A and B horizon of native soil (Wickham Series, Fine-loamy, mixed, thermic Typic Hapludults and sand. Pots were buried such that the soil surface inside pots was at ground level. Each pot was at

least 46 cm from the edge of the shade frame. Buried pots were arranged under each shade frame in a four by four plot with four individuals of each species randomly located within each plot. Water was provided as ambient rainfall; however, irrigation was provided when necessary to prevent seedling mortality. Shade frames were removed between mid-December and late March between the first and second growing season. Seedling stem height and diameter were measured at the onset of the study.

Differences in allocation patterns between plant organs in response to growth environment light level were tested separately for each species. A linear regression equation using natural log (ln) transformed leaf dry weight as the dependent variable and ln-transformed root, stem and root + stem dry weight was fitted for open grown and the 63% shade treatment for each species (Causton and Venus 1981). An F-test was used to determine significance of differences between slope (relative organ growth rate) and intercept (initial dry matter investment). This analysis eliminates the confounding influence of treatment-induced plant size on allometric relationships (Eamus and Jarvis 1989).

Photosynthetic light response curves were constructed for four seedlings of each species during the first (early September) and second (late August) growing seasons. Leaf material consisting of one fully-expanded fascicle or leaf

near the seedling apex was placed in the cuvette of a Li-Cor 6250 portable photosynthesis system. Shade levels were established with shade fabric (Table 9.1) under a uniform light source (12V, 75W General Electric EYF incandescent light). Cuvette temperature and relative humidity was $31^{\circ}\text{C} \pm 1$ and $49\% \pm 7$ for the 1993 growing season and $31^{\circ}\text{C} \pm 1$ and $60\% \pm 6$ for the 1994 measurements respectively.

Light saturated net photosynthesis rates (P_{max}), dark respiration (R_d) and light compensation point (LCP) were calculated using the equation in Statistical Analysis System Non-linear regression procedure (SAS Institute, Cary, NC).

$$P_s = P_{\text{max}} [1 - (1 - R_d/P_{\text{max}})^{(1 - (PPFD/LCP))}]$$

where P_s equals net photosynthesis, PPFD equals photosynthetic photon flux density and R_d equals dark respiration (Hanson et al. 1988). Quantum efficiency (E) was calculated from the initial slope of each curve using the first derivative of the above function with respect to PPFD equals LCP (Nowak 1991).

$$E = (P_{\text{max}}/LCP) (1 - ((R_d/P_{\text{max}})) (\log(1 - R_d/P_{\text{max}}))$$

LCP, R_d , P_{max} , and E were determined for each seedling measured and significance of growth environment was

determined for each variable using analysis of variance. Duncan's new multiple range test was used for mean separation within a species.

Analysis of biomass and stem dimensions was performed using analysis of variance. Data were transformed to alleviate unequal variance when necessary (Gomez and Gomez 1984). Stem volume index at establishment was used as a covariate for analysis of biomass data. Height and diameter at establishment were used as covariates for analysis of final height and diameter data respectively.

RESULTS

All species responded to shade treatments with decreased biomass compared to open grown (Table 9.2). Loblolly pine was the most sensitive species to shade with total seedling biomass averaging 9% open-grown values for the 80% shade cloth. Red maple and yellow-poplar had the smallest growth reduction due to shade (52 and 53% respectively for 80% shade) with white pine showing intermediate biomass reduction (49%).

Stem height (Table 9.3) was significantly increased under the 80% shade treatment compared to open-grown for yellow-poplar but significantly reduced in loblolly pine in both shade treatments. White pine and red maple showed non-significant height differences. Stem diameter was

significantly reduced by shade for all species. Stem volume index changes in response to shade became more pronounced over time in loblolly pine with seedlings in the 80% shade treatment 24 and 8% the size of open-grown seedlings during the first and second growing seasons respectively. Stem volume index response to shade did not change for other species between the first and second growing season except differences between white pine grown under the two shade treatments became non-significant (Table 9.4).

Specific leaf area increased as light availability was reduced (Table 9.5). Differences between shade treatments became more pronounced during the second growing season in all species.

Allocation shifts between leaves and roots in response to shade treatment occurred in red maple where shade-grown trees allocated a higher proportion of growth to leaves per unit root dry weight compared to open-grown (Table 9.6). No other species displayed this trend. Shade-induced differences in leaf weight:stem weight ratio occurred in both pine species, but neither hardwood species, with pines having higher allocation to leaf weight when grown under shade. Loblolly pine was the only species to have significantly higher allocation to leaves relative to stem + root biomass combined under shaded conditions.

Quantum efficiency (E) was higher for hardwoods

compared to pines under all light levels (Table 9.7). Response to shade differed between species between the first and second growing seasons: E was higher for open-grown yellow-poplar compared to shade-grown trees during the second, but not the first, growing season. White pine and red maple showed significant shade response during the first, but not during the second growing season. Dark respiration per unit leaf area was greater for open grown seedlings during both growing seasons in all species measured except white pine. During the first growing season, $P_{\max}$ was higher for open-grown seedlings of yellow-poplar and red maple, but this response was not observed during the second growing season. Light Compensation Point (LCP) was lower with increasing shade for all species except yellow-poplar during the second growing season. LCP was higher during the second growing season under all shade levels for every species except red maple. The chlorophyll fluorescence parameter F_v/F_m decreased with increasing shade treatment in all cases averaging 0.65 in open grown seedlings across species and years versus 0.72 and 0.76 for the 65 and 80% shade levels respectively. These differences were significantly different for white pine during the first growing season and red maple during both growing seasons.

DISCUSSION

Relative biomass reduction due to growth under shade generally reflects recognized species differences in shade tolerance with loblolly pine, the most intolerant species, showing the greatest growth reduction. Yellow-poplar, though considered shade intolerant, did not show as great a growth reduction as might be expected. Rapidly growing seedlings of this species growing under forest understories are not uncommon, however they have been observed to succumb rapidly if not released (personal observation). Increased height growth under shaded conditions in this species may reflect the need for seedlings to remain in a dominant position. Strong stem growth may be an important adaptation allowing this species to outcompete rapidly growing species associated with high quality sites that yellow-poplar eventually dominates (Beck 1990). Better than expected growth under low light but adequate water may suggest that drought stress may be a more important factor precipitating the mortality of this species in the understory.

As expected, stem volume index closely reflected stem biomass response to shade levels (Table 9.4). However, stem weight was the biomass variable least sensitive to shade. This is not surprising since roots and leaves are strong carbon sinks making stem growth a low priority for

carbon allocation. Slow responsiveness of stem growth makes non-destructive measurements of seedling growth less meaningful and may lead to erroneous conclusions regarding the effects of shade on seedling growth. Stem diameter appears to be the non-destructive measurement most closely correlated with total biomass differences associated with light environment (Morris et al. 1990; Elliott and White 1993).

Root biomass has been widely reported to be more sensitive to light environment than leaf or stem biomass (Neufeld 1983; Gottschalk 1987). The inability of root growth to keep up with aboveground growth is considered to be the eventual cause of seedling death in forest understories (Spurr and Barnes 1980). These data do not indicate reduced allocation to roots under shade suggesting that this may be a size-dependent response.

Increased $P_{\max}$ observed under the 63% shade treatment compared to open-grown individuals in loblolly pine, white pine and red maple are inconsistent with the findings of previous researchers (Loach 1967; Teskey and Shrestha 1985; Holmes and Cowling 1991; Ellsworth and Reich 1992) who reported a decrease in $P_{\max}$ in seedlings grown in a shaded environment. However $P_{\max}$ did not differ significantly between shaded and open-grown Rhus lucida, a heliophilus southern African shrub species (Midgley et al 1992). Although leaf nitrogen content has been correlated with

$P_{\max}$ /area in temperate tree species (Reich et al. 1990; Ellsworth and Reich 1992), it is unlikely that nitrogen deficiencies played a role in reduced photosynthetic capacity of open-grown seedlings.

Lower respiration rates per unit leaf area in shaded versus open-grown plants are consistent with previous studies (Loach 1967; Midgley et al. 1992). Red maple, the most tolerant species in this study, had the highest respiration rates under shaded conditions, contrary to the suggestion that shade tolerant species have lower respiration rates when grown under shaded conditions (Loach 1967). Photosynthetic parameters found in the present study exhibited characteristics similar to species Loach described as tolerant. The observation of generally lower light compensation point with growth under shade is consistent with earlier work (Loach 1967; Midgley et al 1992; Holmes and Cowling 1991).

Decreased F_v/F_m ratio with higher light availability has been correlated with light-induced photoinhibitory damage in plants subjected to one or several environmental stresses (Bolhar-Nordenkamp et al. 1989). However, interpretation of this parameter must be made with care since decreased F_v/F_m ratio, when caused by a decrease in F_v , as it was throughout this study (data not shown) indicates a reduction in non-photochemical quenching. Non-photochemical quenching can occur as a result of non-

radiative photon de-excitation, primarily attributed to heat loss and transfer of energy to photosystem I (Bolhar-Nordenkamp et al. 1989).

Reduced growth under shaded conditions without competition for water are not consistent with increased quantum efficiency and maximum photosynthetic rate under the 63% shade treatment. Dark respiration was usually reduced by growth under shaded conditions but this response occurred in both shade tolerant and intolerant species suggesting that this characteristic may not be associated with species difference in shade tolerance. Other important characteristics describing response to shade may be long-term carbon uptake and allocation (Givnish 1988).

Quantum efficiency and maximum photosynthetic rate decreased in all species except red maple between the first and second growing season suggesting reduced photosynthetic activity per unit leaf area. It seems unlikely that this is due to greater exploitation of water or nutrients by the pines or yellow-poplar since much of the rooting material was not exploited. Reduced photosynthetic capacity per unit leaf area in these intolerant and intermediate tolerant species may contribute to their eventual failure in the understory. Photosynthetic parameters did not change over time in response to shade treatments suggesting that photosynthetic acclimation to light level may not be a factor associated with shade tolerance or its change over

time. This cannot be determined conclusively on the basis of these data since the duration of this study may have been insufficient for these changes to take place.

For all species, specific leaf area was sensitive to shade treatment, becoming increasingly so during the second growing season. Increasing SLA may allow seedlings to harvest light more effectively under low light conditions, but also makes these seedlings more vulnerable to water stress (Jones and McLeod 1990; Loach 1970). While changes in SLA may help explain how a seedling adapts to growth under low light, the results of this study suggest that plasticity of this morphological characteristic does little to explain shade tolerance differences between species: Loblolly pine and yellow-poplar, the two most shade intolerant species in this study, showed the greatest SLA plasticity, suggesting that SLA is a symptom of growth under shade rather than an adaptation to a low light environment.

Increased leaf weight ratio observed in loblolly pine grown under shade is consistent with other shade intolerant tree species (McClendon and McMillen 1982; Holmes and Cowling 1993). However, these studies and the present one did not account for differences in water status between seedlings shaded with nursery shade cloth and those grown in forest understories in competition for water with overstory trees. Soil water contents were likely to remain

higher under shade cloth compared to open-grown seedlings due to reduced soil evaporation and lower total transpiration from smaller seedlings. Differences in plant water status between shade cloth and understory grown individuals could potentially confound allometric relationships between roots and shoots. It is plausible that increased drought stress in forest understory seedlings could result in increased root:shoot ratio that would confound reported increases in leaf weight ratio. Another problem associated with this study and others using artificial shade treatments is the imperfect simulation of canopy light extinction with nursery shade cloth. Sunflecks and red/far-red ratios associated with forest canopies are not provided by this material (Holmes and Cowling 1991).

Experimental conditions in this study were intended to isolate the influence of light on growth and photosynthesis. Further research of shade tolerance characteristics of tree species would benefit by introducing competition for water and nutrients from overstory species associated mature forests. The importance of competition has been demonstrated in early studies of shade tolerance (Spurr and Barnes 1980). Whole plant carbon balance must also be considered to better understand the mechanisms underlying tolerance (McClendon and McMillen 1982; Givnish 1988; Walters et al. 1993).

CONCLUSIONS

Seedlings grown under shade exhibited reduced dark respiration and light compensation point and increased specific leaf area. Shading-induced differences in photosynthetic characteristics did not become more or less pronounced between the first and second growing season suggesting that an acclimation mechanism may not alter shade tolerance over time. However, reduced photosynthetic capacity over time in all species, except the shade tolerant red maple may contribute to eventual failure under low light levels.

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Table 9.1. Average cuvette light levels ($\mu\text{mol m}^{-2} \text{s}^{-1}$) for construction of photosynthetic light response curves using four Piedmont tree species (n=10).

First Growing Season		Second Growing Season	
Mean	S. D.	Mean	S. D.
1210	20	1143	25
364	14	348	19
122	30	106	13
45	14	32	10
19	8	13	5
0	0	0	0

Table 9.2. Biomass of seedlings of four tree species grown under three levels of light availability for two growing seasons on the Virginia Piedmont.

	Shade Fabric (%)	Loblolly Pine		White Pine		Red Maple		Yellow Poplar	
		Mean	% open-grown	Mean	% open-grown	Mean	% open-grown	Mean	% Open grown
Total Biomass (g)	0	133.9 A		48.7 A		85.0 A		101.7 A	
	63	38.5 B	29	22.7 B	47	50.5 B	59	50.3 B	49
	80	11.6 C	9	24.0 B	49	43.8 B	52	54.4 B	53
Leaf Biomass (g)	0	58.2 A		17.8 A		19.6 A		24.6 A	
	63	17.7 B	30	9.1 B	51	12.2 B	62	14.9 A	61
	80	5.2 C	9	9.8 B	55	11.9 B	61	16.7 A	68
Stem Biomass (g)	0	50.5 A		14.3 A		24.3 A		35.8 A	
	63	12.8 B	25	6.5 B	45	17.1 A	70	18.8 A	53
	80	4.0 C	8	7.3 B	51	16.0 A	66	23.9 A	67
Root Biomass (g)	0	25.2 A		16.8 A		41.0 A		41.2 A	
	63	8.2 B	32	7.1 B	42	21.2 B	52	16.6 B	40
	80	2.4 C	10	6.8 B	40	15.9 C	39	13.9 B	34

NOTE: Means within a species followed by the same letter are not significantly different at $p < 0.05$.

Table 9.3. Height, diameter and height:diameter ratio of seedlings of four tree species grown under three levels of light availability for two growing seasons on the Virginia Piedmont.

	Shade Cloth (%)	Loblolly Pine			White Pine			Red Maple			Yellow Poplar		
		Mean	% Open-grown		Mean	% Open-grown		Mean	% Open-grown		Mean	% Open-grown	
Total Stem Height (cm)	0	97.7 A			47.5 A			88.5 A			78.7 B		
	63	66.3 B	68		43.3 A	91		91.7 A	104		87.8 AB	112	
	80	48.6 C	50		49.0 A	103		100.4 A	113		105.3 A	134	
Stem Diameter (mm)	0	16.4 A			10.5 A			13.8 A			16.8 A		
	63	10.9 B	66		7.6 B	72		11.7 B	85		13.2 B	78	
	80	6.4 C	39		7.9 B	75		10.8 B	78		13.7 B	82	
Height:Diameter Ratio	0	6.1 A			4.6 B			6.5 B			4.8 C		
	63	6.3 A	103		5.7 A	119		8.0 A	123		6.6 B	138	
	80	7.4 A	121		6.2 A	135		9.4 A	145		7.8 A	162	

NOTE: Means within a species followed by the same letter are not significantly different at $p < 0.05$.

Table 9.4. Stem Volume Index for seedlings of four tree species grown under three levels of light availability for two growing seasons on the Virginia Piedmont.

		1st Growing Season		2nd Growing Season	
	Shade Cloth (%)	Mean	% open-grown	Mean	% open-grown
Loblolly Pine	0	54.1 A		78.3 A	
	63	33.1 B	61	21.5 B	27
	80	13.0 C	24	6.5 C	8
White Pine	0	43.1 A		14.8 A	
	63	18.4 C	43	7.0 B	47
	80	32.3 B	75	8.6 B	59
Red Maple	0	116.3 A		53.9 A	
	63	105.6 A	91	36.7 A	68
	80	63.3 A	54	32.9 A	61
Yellow-Poplar	0	167.3 A		72.0 A	
	63	83.7 A	50	43.4 A	60
	80	130.9 A	78	57.3 A	79

NOTE. Means within a species for the same growing season followed by the same letter are not significantly different at p < 0.05.

Table 9.5. Specific Leaf Area (cm^2/g) for seedlings of four tree species grown under three levels of light availability for two growing seasons on the Virginia Piedmont.

	Shade Cloth (%)	1st Growing Season		2nd Growing Season	
		Mean	% open-grown	Mean	% open-grown
Loblolly Pine	0	238 B		142 B	
	63	324 A	136	331 A	233
	80	371 A	156	374 A	263
White Pine	0	274 B		233 B	
	63	282 B	103	301 A	129
	80	327 A	119	328 A	141
Red Maple	0	148 B		109 B	
	63	172 AB	116	179 A	164
	80	213 A	144	188 A	172
Yellow-Poplar	0	183 B		165 C	
	63	301 A	164	272 B	165
	80	376 A	205	397 A	241

NOTE: Means within a species for the same growing season followed by the same letter are not significantly different at $p < 0.05$.

Table 9.6. Regression coefficients and coefficients of determination for allometric relations in response to light availability for two-year-old sapling of four Piedmont tree species. Equations are in the form $Y = \text{intercept} + \text{slope}(X)$. Levels of significance indicate differences between pairs of coefficients in response to light availability.

Species	Relationship (y, x)	Shade cloth (%)	intercept	slope	pdiff.-(intercept)	p diff (slope)	R ²
Loblolly Pine	$\ln(\text{leaf wt}) - \ln(\text{root wt})$	0	0.73	1.02	0.62	0.63	0.82
		63	0.41	1.13			0.78
White Pine	$\ln(\text{leaf wt}) - \ln(\text{root wt})$	0	0.47	0.85	0.75	0.64	0.68
		63	0.27	0.96			0.66
Red Maple	$\ln(\text{leaf wt}) - \ln(\text{root wt})$	0	-1.23	1.13	0.00	0.00	0.90
		63	-1.57	1.32			0.62
Yellow-Poplar	$\ln(\text{leaf wt}) - \ln(\text{root wt})$	0	-1.41	1.20	0.17	0.34	0.61
		63	0.43	0.79			0.33
Loblolly Pine	$\ln(\text{leaf wt}) - \ln(\text{stem wt})$	0	0.88	0.81	0.00	0.00	0.92
		63	-0.68	1.36			0.95
White Pine	$\ln(\text{leaf wt}) - \ln(\text{stem wt})$	0	0.67	0.83	0.06	0.04	0.80
		63	-0.19	1.23			0.83
Red Maple	$\ln(\text{leaf wt}) - \ln(\text{stem wt})$	0	0.21	0.87	0.11	0.21	0.92
		63	-0.42	1.04			0.88
Yellow-Poplar	$\ln(\text{leaf wt}) - \ln(\text{stem wt})$	0	-0.24	0.97	0.66	0.80	0.92
		63	-0.02	0.92			0.75
Loblolly Pine	$\ln(\text{leaf wt}) - \ln(\text{stem} + \text{root wt})$	0	0.23	0.89	0.01	0.00	0.92
		63	-0.92	1.24			0.94
White Pine	$\ln(\text{leaf wt}) - \ln(\text{stem} + \text{root wt})$	0	0.02	0.83	0.34	0.25	0.76
		63	-0.57	1.07			0.78
Red Maple	$\ln(\text{leaf wt}) - \ln(\text{stem} + \text{root wt})$	0	-1.37	1.04	0.29	0.22	0.95
		63	-2.06	1.25			0.82
Yellow-Poplar	$\ln(\text{leaf wt}) - \ln(\text{stem} + \text{root wt})$	0	-1.74	1.12	0.41	0.69	0.82
		63	-0.93	1.02			0.65

Table 9.7. Photosynthesis characteristics of four tree species grown under three levels of light availability for two growing seasons on the Virginia Piedmont. Measurements were made during September of the first growing season and August of the second growing season.

	Shade Cloth %	Growing Season					
		Loblolly Pine		White Pine		Red Maple	
		First	Second	First	Second	First	Second
Quantum Efficiency	0	0.0145 A	-	0.0131 B	0.0111 A	0.0648 A	0.0453 A
	63	0.0136 A	0.0120 A	0.0197 A	0.0101 A	0.0436 B	0.0470 A
	80	0.0167 A	0.0111 A	0.0166 A	0.0115 A	0.0438 B	0.0536 A
Dark Respiration ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	0	-0.559 A	-	-0.443 A	-0.820 A	-1.955 A	-1.782 A
	63	-0.507 A	-0.936 A	-0.467 A	-0.480 B	-1.185 B	-1.349 B
	80	-0.367 B	-0.414 B	-0.349 A	-0.499 B	-1.018 C	-1.136 C
Maximum	0	3.973 B	-	3.089 B	2.004 B	10.380 A	5.596 B
Photosynthesis ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	63	5.007 A	2.051 A	3.541 A	2.678 A	6.585 B	6.667 A
	80	2.956 C	2.498 A	2.766 B	2.067 B	6.515 B	5.593 B
Light Compensation	0	42.3 A	-	38.0 A	118.6 A	32.8 A	48.3 A
Point ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	63	43.7 A	106.5 A	24.8 B	68.5 AB	36.5 A	32.6 B
	80	27.1 B	42.7 B	26.7 B	55.1 B	25.5 B	30.5 B
Fv/Fm	0	0.789 A	0.615 A	0.790 B	0.496 A	0.711 B	0.629 B
	63	0.821 A	0.731 A	0.854 A	0.738 A	0.785 A	0.705 AB
	80	0.833 A	0.729 A	0.858 A	0.754 A	0.789 A	0.738 A

NOTE: Means within a species during the same year followed by the same letter are not significantly different at $p < 0.05$.

CHAPTER X

SYNTHESIS

Although not always stated explicitly, forestry research conducted in a greenhouse must always carry a disclaimer that results may not necessarily reflect outcomes in the field. Greenhouse studies have traditionally been used to study within-plant mechanisms and processes. Differences in availability of light, nutrients, water and space as well as duration of study, competitive interactions and plant phenology are some of the factors confounding comparisons between greenhouse and field conditions. While mimicking of field conditions in the greenhouse is not possible at this time, efforts to couple greenhouse conditions with those under a specific field setting can allow researchers to extrapolate results from greenhouse to field with less uncertainty.

Among the objectives of this series of studies are the qualitative comparison of growth, competitive interactions, allometry and photosynthesis in experimental stands of similar composition under greenhouse and field conditions. Specific questions to be addressed when comparing field and greenhouse studies are as follow: 1. Do studies respond similarly to treatments held in common? 2. How should paired field-greenhouse studies be designed to best facilitate comparison? 3. What response variables should be

measured and compared and do these change over time? 4.

Can final competitive outcomes be predicted using miniature stands or should the scope of applicability be limited to understanding competitive processes?

COMPARING RESULTS BETWEEN GREENHOUSE AND FIELD STANDS.

The greenhouse experiment described in chapter vii showed several similarities to the field study (chapter v) with respect to competitive status and response to treatments held in common. In both studies, relative competitive status of species was similar with loblolly pine dominating all mixed stands, suggesting that environmental conditions with respect to relative species growth were adequately simulated. Growth in monoculture and mixture under greenhouse conditions produced the same relative effect on species in the field-grown study under weed-free conditions, suggesting that stand composition effects were independent of scale.

Changes in competitive abilities based on relative heights of red maple and loblolly pine changed over time in the field study with ratio of pine to maple mean height first increasing and then decreasing near the conclusion of the study. In most factorial combinations of CO₂ and water in the greenhouse study, pine/maple height increased between the first and second growing cycle. This response

was especially strong in mixed stands. Duration of the greenhouse study was not sufficient to determine whether this trend would continue or red maple growth would accelerate relative to loblolly pine as was the case with the field-grown stands. Increased height growth of pine relative to maple occurred during the second growing season despite the absence of winter photosynthesis in these stands.

In the field study, height growth for either species was not significantly influenced by growth in monoculture or mixture. In the greenhouse, height differences were very strongly influenced by stand type, especially in red maple where seedlings from mixtures were not as tall as monocultures. For red maple, apparent resource availability manifested itself differently between greenhouse and field with regard to competitive status. Red maple height was more strongly suppressed by loblolly pine in well-watered stands in the greenhouse while maple in the field was smaller relative to pine in tall fescue plots where water is thought to be more limiting relative to weed-free conditions. Red maple height growth was also positively correlated with site quality under both weed-free and tall fescue conditions. Suppression of red maple in well-watered greenhouse stands may have been hastened by negative interference from loblolly pine earlier in the relative ages of these stands compared to the field study

where red maple was not influenced by loblolly pine for a longer time due to wider initial spacing.

Height:diameter ratio, the only allometric variable measured in both the greenhouse and field showed varying responses to stand type and drought treatment.

Height:diameter ratio was not significantly different between loblolly pine grown in weed-free versus tall fescue in the field but significant differences were found between well-watered and droughted conditions during the second growing cycle in the greenhouse. However, loblolly pine monocultures had significantly higher height:diameter ratio versus mixed stands in both studies. Red maple had significant height:diameter responses for monoculture versus mixtures and weed-free versus tall fescue in the field but no significant main effects were present in the greenhouse.

Photosynthetic response of field grown stands was similar to greenhouse stands in that photosynthetic rates expressed on a leaf weight basis were not significantly different between water treatments in the greenhouse or herbaceous cover in the field. Growth in monoculture or mixture also did not affect photosynthetic response in either study. The linkage of greenhouse and field studies where ambient CO₂ concentration is a variable in both studies will prove especially interesting regarding the mechanisms underlying photosynthetic acclimation.

Acclimation has often been attributed to resource limitations and pot binding, neither of which appeared to accompany acclimation in the greenhouse studies (chapters iv and vii). Resource limitations have been used to explain the occurrence of acclimation in greenhouse, but not field studies (Bowes 1991; Long and Drake 1991).

The greenhouse and field studies differ in many ways with regard to total resource availability, density, presence of pathogens, extent and duration of drought, phenology and stand ontogeny. Differences in competitive outcome between greenhouse studies described in chapters VI and vii suggest that water and nutrient availability, but not density may play overriding roles in determining competitive outcomes at small spacings.

However, stand density, when comparing between the scales used in the greenhouse with the field and the timing of the onset of competition had a striking influence on tree form and allocation in the field. In the greenhouse, successful competitors in mixed stands were able to capture aboveground space from associated species through horizontal extension of foliage and belowground with horizontal extension of roots. Under high resource availability (chapter vi), red maple was most successful accomplishing the former through the production of large leaves. Under lower resource availabilities (chapter vii), loblolly pine produced large secondary needles which

overtopped red maples. In the field, where the spatial scale was much larger, branches were a more important determinant of competitive outcomes. Loblolly pine occupies horizontal space more quickly than red maple through horizontal extension of branches. Belowground, red maple grown under high resource availability had large, fan-like fibrous root systems far more extensive than those grown in the native soil. Higher soil strength in the native soil appeared to reduce the rate and extent of soil exploration. Inherent morphological differences between saplings and seedlings in miniature stands can make comparison between architectural characteristics difficult between greenhouse and field studies.

Regardless of final competitive outcomes, growing seedlings in competitive regimes appears to provide an improvement over single seedling studies. Under field conditions, plants typically experience a free growth period where plants occupy previously empty growing space (Oliver and Larson 1990). At this stage, growth is limited by environmental conditions and inherent growth characteristics. Typically, this period is short and an individual and its neighbors soon grow to the extent that they begin competing with one another for resources. In typical greenhouse experiments, plants are maintained under free growth conditions throughout the duration of the study. Plants grown in competitive regimes undergo free

growth followed by growth in competition with neighbors, conditions associated with early stand conditions.

Growth in monoculture and mixture in the greenhouse also provides a more realistic pattern of resource availabilities compared to individual seedlings since species differ in resource needs and depletion patterns (Tilman 1988). Species-specific resource uptake patterns likely resulted in differences in growth observed within a species between monocultures and mixtures. Competition and the maintenance of low resource availability in the greenhouse also produces lower-than optimum growth rates associated with seedlings in young forest stands under all but the most intensive management regimes.

Intense competition for light may slow the rate of nutrient depletion in miniature stands relative to individual seedlings. Several greenhouse studies with individually-grown tree seedlings have reported growth and photosynthetic characteristics to be dependent on adequate nutrient availability (Griffin et al. 1993; Tissue et al. 1993; El Kohen and Mousseau 1994). Further research is needed to determine the rate of nutrient depletion and its role on the responsiveness of tree species to increasing atmospheric CO₂ concentration under field conditions.

Based on observations of this study, red maple will become dominant if resource availabilities are sufficiently high to produce leaves large enough to extend over pine

apices. Loblolly pine does not effectively compete for aboveground space until secondary needles are produced. In water limited situations, Loblolly pine appears to compete most effectively by depleting available water more rapidly than red maple. Fredericksen (1991) suggested that competitive outcomes may depend on intensity of interference at critical stages of development. In miniature stands, this critical period is likely to occur sooner in the life of the seedling compared to field stands. Determining the extent to which species response to competition is age-dependent would be a valuable next step in miniature stand research.

DESIGN OF PAIRED GREENHOUSE-FIELD STUDIES.

The results of this series of studies suggests a number of potential improvements for future paired studies. Further work with these species would benefit from a more definitive determination regarding the role of initial spacing on individual and stand processes. Repeating the experiment where initial spacing was varied (chapter vi) under environmental conditions better approximating field conditions would better address this question. A mixed species spacing study under field conditions could further improve understanding of the mechanisms differentiating field and greenhouse responses.

The use of native soil appears to be crucial in efforts to establish competitive relationships observed in the field. These soils provided an edaphic environment similar to field conditions with respect to nutritive properties in that they did not receive regular input of macronutrients typical of greenhouse studies. The role of soil physical properties on competitive interactions should be considered when establishing greenhouse competition studies between conifers and hardwoods. Hardwood root systems appear to be better adapted for the exploitation of well-developed soils while pines are more tolerant of former agricultural soils where soil structure has been degraded (Oliver and Larson 1990). Greenhouse studies using native soils with poor structure appear to provide a good simulation of forest soil conditions over much of the Piedmont.

Even though these studies may not be carried out to the final resolution of competitive outcomes, species in field and greenhouse studies should have similar competitive status under the specified treatments. This would allow simulation of resource depletion patterns similar to field conditions. Relative size differences associated with inherent interspecific growth rate differences can be regulated by manipulating growing conditions to maintain competitive status between species at a desired level. This would require altering

environmental variables such as light, temperature, water or nutrients to accelerate or retard growth of one species relative to the other if competitive status does not reflect field conditions.

Not all species may be compatible for use in paired studies. Species with widely varying regeneration niches, establishment periods or high mortality rates may be difficult to establish and show misleading responses. Pairing greenhouse and field studies appear to be best suited for species of similar growth form and site requirements. Conifer species appear to be especially well-suited since columnar architecture of seedlings in miniature stands approximates that of young field-grown seedlings. If species are genetically diverse, efforts should be made to use offspring from individuals from the same ecotype and provenance. Ideally, initial spacing in the greenhouse component should be sufficiently large to allow each species a free growth period of a duration that is as typical of field conditions as possible.

Species life form should also be considered when establishing competition experiments. Many hardwood species, including red maple and sweetgum regenerate largely through stump sprouts. Little is understood about age and size characteristics of stump sprouts making simulation of this life form difficult. Seedling sprouts of hardwood species seem to provide the most feasible

alternative to stump sprouts in competition studies (Perry et al. 1993).

In the present studies, establishment of similar water stress treatments under field and greenhouse conditions proved to be difficult. The tall-fescue treatment did not provide an effective surrogate for water stress treatments. Lower water availability on tall-fescue plots is confounded by several factors including nutrient dynamics and soil temperature (Nambiar and Sands 1993) and possibly allelopathy (Fredericksen 1991). Increased size of red maple seedlings in mixed stands in tall fescue indicated that the presence of pine benefitted red maple by shading herbaceous vegetation (Fredericksen et al. 1993). It is not likely that interplanting with loblolly pine would have benefitted red maple if a water stress treatment had been imposed directly.

While the tall-fescue treatment did not substitute perfectly as a water stress treatment, water availability did appear to play a role in growth reduction in this treatment. Midday xylem water potentials during the third growing season were significantly greater in tall fescue (Fredericksen et al. 1993). This response was not detected during the fourth or fifth growing season (chapter v). The potential existed for growth in very young red maple seedlings to be reduced by reduction or changes in light quality from overtopping tall fescue (Horsley 1993).

However, neither height nor stem volume index was reduced by simulated shading in red maple (chapter xi). Reduced total biomass of red maple under drought (chapter vii), shade (chapter xi), and tall fescue (chapter v) was rarely accompanied by reduced photosynthetic rates suggesting that whole plant respiration increases under stressful conditions may account for size differences.

Matching water stress and nutrient treatments between field and greenhouse would ideally be accomplished through measurement of xylem water potential and foliar nutrient content (Mitchell et al. 1993; Morris et al. 1993). Providing water and nutrient concentrations at similar levels between field and greenhouse should prevent development of nutrient deficiencies and permit survival to be maintained at similar levels under both settings.

Other factors may play a role in stand development in the field that are difficult to account for in the greenhouse. Pathogen outbreaks, snow and ice damage can influence competitive dynamics. On the Virginia Piedmont, loblolly pine is vulnerable to bending and breakage from winter storms to a greater extent than red maple, potentially improving the competitive status of the hardwood species as stands age. Storm damage may be simulated in the greenhouse by top clipping.

RESPONSE VARIABLES

Stem volume index is a commonly used response variable in forest competition studies. This variable is attractive to researchers because it is easy to measure, non-destructive and is highly correlated with stem biomass (chapter xi). As trees mature, this variable most closely approximates a harvest index. Problems arise when measuring small seedlings. Hardwoods, especially red maple, in miniature stands and individually-grown seedlings show highly variable stem morphology making accurate determinations of stem volume index difficult. Very small seedlings also appear to be prone to shrinking and swelling as water status changes confounding comparisons between water stress treatments and repeated measurements. Stem volume index may be a poor indicator of carbon assimilation under low resource availability since allocation to leaves and roots is preferential. In contrast to field stands, treatment-dependent changes in height:diameter ratio do not appear to be occurring under greenhouse conditions. These shifts may be dependent on radial growth increases over a longer period of time. Relative height may be the most valuable indicator of competitive status because of its descriptiveness of canopy dominance.

At least two approaches may help overcome difficulties associated with non-destructive measurement of stand growth: 1. Conduct studies for a sufficient period of time to allow stem biomass to better reflect total seedling

biomass. 2. Construct allometric yield equations based on measurements of biomass from destructively harvested single seedling measurements made at various stages of the study. Based on these estimates, whole stand photosynthetic rates could be made on a repeated basis.

DURATION OF EXPERIMENTS

The most definitive systematic competition studies have used annual plants where interference interactions can be measured from germination through senescence or until constant final yield is attained (de Wit 1960; Roush et al. 1990). This is generally not feasible with forest stands due to long lifespans of forest species. Additionally, the concept of constant final yield is not meaningful when more than one species of a perennial is present since the life of a stand is sufficiently long for resource turnover to occur between individuals and species. Longevity of forest stands and the slowness of competitive outcomes to develop forces researchers to concentrate on plant and stand processes associated with the earliest stages of competition. Since the conclusion of competitive interactions cannot be determined with certainty unless one species eliminates the other, researchers must judge when critical stand processes are complete.

In the greenhouse study (chapter VIII, size

differences between species in response to treatments between the first and second growing cycle suggest that stand structure was still changing and competitive outcomes may not have been completely determined. Red maple seedlings are shade tolerant and have been observed to persist in the understory and respond rapidly to release (Walters and Yawney 1990) or maintain height growth despite increasing suppression by loblolly pine (chapter vii). To fully determine the effects of CO₂ on competitive interactions with and without the influence of water, this study would need to be conducted over a longer period of time to determine whether competitive hierarchies between loblolly pine and red maple change in response to resource availability. Since red maple appears to persist indefinitely in loblolly pine-dominated stands under some natural conditions, one of the following scenarios would have to be satisfied in order for the miniature stands to be a more effective predictor of future CO₂ environments:

1. Red maple continues to survive under low CO₂, but not high CO₂.
2. Red maple persists long enough to dominate or become co-dominant with loblolly pine under either or both CO₂ concentrations.
3. Loblolly pine senesces in either or both of the treatments due to causes that are attributable to other than experimental conditions.

The conclusiveness of miniature stand studies would increase through the use of less persistent species.

The applicability of miniature stands appears to be greatest in exploring mechanisms associated with eventual competitive outcomes in response to varying resource availabilities rather than in determining actual outcomes. Given the aforementioned constraints, competitive interactions between loblolly pine and sweetgum and loblolly pine and red maple will not change in a future high CO₂ environment. Species response to atmospheric CO₂ does not appear to be mediated through availability water for loblolly pine and red maple or water and nutrients for loblolly pine and sweetgum.

The results of these studies suggest that addition of a competition component can change inferences regarding competitive outcomes in greenhouse studies. Questions remain regarding the comparability of greenhouse and field competition studies. With further improvements, including suggestions discussed here, greenhouse and field studies may be linked with greater success.

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VITA

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A handwritten signature in cursive script, reading "John W. Groninger". The signature is written in dark ink and features a prominent, sweeping flourish at the end.