THE RELATIONSHIPS BETWEEN LEAF AREA INDEX, PHOTOSYNTHETICALLY ACTIVE RADIATION, CANOPY NITROGEN STATUS, AND STEM GROWTH IN LOBLOLLY PINE STANDS OF DIFFERENT PLANTING DENSITIES

by

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(Under the Direction of Robert O. Teskey and Rodney E. Will)

ABSTRACT

Limitations to stem growth with increases in planting density were examined by ascertaining the relationships between stem growth and projected leaf area index (LAI), annual photosynthetically active radiation (PAR) capture, foliar nitrogen concentration, and canopy nitrogen content. Canopy variables were measured during the fourth growing season in stands of loblolly pine (*Pinus taeda* L.) ranging in planting density from 740 to 4440 trees ha^{-1}. While stem growth rates increased significantly with planting density from 12.0 to 35.2 m^3 ha^{-1} y^{-1}, increases were not proportional, indicating the presence of competition-induced limitations to growth. Stem growth rates were best correlated to annual PAR capture (r^2=0.90). This, in addition to the fact that annual PAR capture per unit LAI increased significantly with planting density, suggests that factors affecting PAR capture were of primary importance in limitations to growth rates with increasing planting density.

INDEX WORDS: *Pinus taeda* L., Loblolly pine, Planting density, Canopy dynamics, Photosynthetically active radiation, Leaf area index, Foliar nitrogen, Intraspecific competition

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ABSTRACT

Limitations to stem growth with increases in planting density were examined by ascertaining the relative contributions of projected leaf area index (LAI), annual photosynthetically active radiation (PAR) capture, foliar nitrogen concentration, and canopy nitrogen content to stand growth. Canopy variables were measured during the fourth growing season in stands of loblolly pine (*Pinus taeda* L.) ranging in planting density from 740 to 4440 trees ha^{-1}. Leaf litter biomass, foliar nitrogen concentration, and intercepted PAR were each sampled at approximately six-week intervals throughout the 2001 growing season. Projected LAI was estimated from litter biomass data, and annual PAR capture was estimated using intercepted PAR measurements and annual incident solar radiation data. At the end of the fourth growing season, mean tree height was 5.1 m, mean diameter at breast height (DBH) was 7.5 cm, and mean standing stemwood volume was 35.5 m^3 ha^{-1}. While stem growth rates increased significantly with planting density from 12.0 to 35.2 m^3 ha^{-1} y^{-1}, increases were not proportional, indicating the presence of competition-induced limitations to growth. Similarly, significant increases in canopy nitrogen content, LAI, and annual PAR capture with planting density were not proportional to density. Nitrogen concentration in current-year foliage decreased significantly with planting density, while there was no influence of density on previous-year foliar nitrogen concentration. Foliar nitrogen concentrations in both age cohorts remained well above what are generally considered to be critical values for loblolly pine (Jokela et al. 1991). Stem growth rates were well correlated with canopy nitrogen content, LAI, and annual PAR capture, with the best predictive relationship occurring between growth and annual PAR capture

(r^2=0.90). Annual PAR capture per unit LAI increased significantly with planting density, indicating variations in canopy structure and foliar display driven by density, or by resultant increases in competition for available light. The increase in the efficiency of PAR capture by LAI at higher planting densities, in addition to the highly significant correlation between growth rate and annual PAR capture suggests that factors affecting PAR capture were of primary importance in limitations to growth rates with increasing planting density.

CHAPTER 1

INTRODUCTION

The forest products industry has historically been a vital component of the southeastern United States' economy. In 1997, forestry along with its related fiber converting activities generated over $120 billion and directly employed 770,000 people (Abt et al. 2002). The South currently produces enough timber to satisfy approximately 60% of the nation's timber demand, and this region alone produces more timber than any other country in the world (Prestemon and Abt 2002). According to the Southern Forest Resource Assessment, the domestic demand for softwood timber is projected to increase by 47 percent between 1996 and 2050 (Prestemon and Abt 2002). The assessment also forecasts a continuing shift in domestic timber production to the South associated with moderate increases in timberland from the conversion of agricultural land in the western and northern regions of the South. However, areas such as the Piedmont of Virginia and Georgia, as well as much of Florida, will see a net decrease in timberland area as a result of increases in residential land use and urbanization (Prestemon and Abt 2002). Consequently, for southeastern states to continue meeting the nation's rising timber demand, it is essential that productivity per hectare be increased on existing timberland. To achieve this end, forest managers typically rely on practices associated with intensive forest management. Similar to methods used in agricultural settings, common strategies employed by intensive management include the use of genetically modified seedling stock, nutrient amendments, the use of herbicides for competition control, and site preparation methods such as bedding, windrowing, or raking. Two of these methods, nutrient amendments and herbicide applications, serve to increase growth by maximizing resources available to targeted trees. For example, nutrient amendments seek to minimize the role of nutrient deficiencies in restrictions to tree growth. Likewise, the use of herbicides benefits targeted trees by reducing interspecific competition for available resources. The manipulation of planting density (altering the dynamics of 'intraspecific' competition) may be another useful strategy to increase growth rates per hectare through the alteration of resource acquisition rates, and effects on photosynthate distribution to different stand components (Waring 1983, Harms et al. 1994, Henskens et al. 2001, Will et al. 2001, Barron-Gafford et al. 2003, Burkes et al. 2003).

There have been many empirical studies describing the effects of density manipulation on stand growth rates (e.g. Worst 1964, Whitsell 1974, Balmer et al. 1975, Shelton 1984, Harms et al. 1994, McCrady and Jokela, 1996, Harms et al. 2000). These studies reported that on a per tree basis, there was an overall negative response of volume growth and tree diameter to density. At the stand level, however, volume growth increased with increasing density primarily due to the greater number of trees per unit land area. As density increased further, stand growth reached a maximum and eventually began to decline, largely due to the effects of low individual tree growth rates and increased tree mortality (Harms and Langdon 1976, Dean and Baldwin 1996). Since stand growth rates were initially greater at higher densities and then later at lower densities, a convergence in total stand volume across densities occurred with age. This convergence is indicative of the maximum growth rate that can be achieved on a given site, with the age of convergence and the maximum growth rate depending primarily on site quality and the intensity of silvicultural inputs to the site (Harms et al. 1994). While similar relationships between density and stand growth rate have been observed for some time (Ware and Stahelin 1950, Worst 1964, Mann and Dell 1971, Shepard 1971, Whitsell 1974, Balmer 1975, Harms and

Langdon 1976), there are still questions regarding the specific nature of the physiological processes involved in restrictions to growth at high densities.

Studies examining the relationship between planting density and growth efficiency (stem growth per unit leaf area or biomass) have found both increases (Burkes et al. 2003) and decreases (Waring 1983, Shelton 1984) in growth efficiency with increasing planting density. Decreases in growth efficiency with density were generally attributed to lower light availability in higher density stands brought about by greater self-shading within canopies (Waring 1983, Shelton 1984). In a study by Shelton (1984), the negative response of growth efficiency to density occurred only in the early stages of stand development, with density effects becoming insignificant as stands aged. There have likewise been several conflicting studies regarding the effects of planting density on biomass partitioning (Pearson et al. 1984, Nilsson and Albrektson 1993, Puri et al. 1993, Burkes et al. 2003). For example, a study in nine-year-old cottonwood stands (*Populus deltoides* Bartr. Ex Marsh) found that the allocation of biomass to stemwood increased relative to fine roots with increasing stand density (Puri et al.1993), whereas in Scots pine (*Pinus* sylvestris L.), Nilsson and Albrektson (1993) found that stemwood allocation decreased with density relative to fine root biomass.

A study of loblolly (*Pinus taeda* L.) and slash (*Pinus elliottii* Engelm.) pine stands in the Coastal Plain of Georgia similarly investigated the role of biomass partitioning in limitations to growth with increasing planting density (Burkes et al. 2003). This study tested the hypothesis that as density increased, an increase in photosynthate allocation to components other than stemwood (mainly foliage and fine roots) would contribute to observed decreases in stem growth (Burkes et al. 2003). However, the opposite effect of density on biomass partitioning was found, with an increase in the partitioning of biomass to stemwood relative to other components in higher density treatments. In the same stands, Barron-Gafford et al. (2003) found that nitrogen acquisition may have contributed to the disproportional response of growth to density at higher densities, as foliar nitrogen concentrations declined below what are generally considered to be critical concentrations (Barron-Gafford et al. 2003). A related study by Will et al. (2001) sought to identify the relative contribution of a host of physiological attributes in limitations to growth rates with increasing density. This study measured net photosynthesis, stem respiration, foliar nitrogen concentration, and intercepted photosynthetically active radiation (PAR) in stands of three different planting densities. The results of this work indicated that restrictions to stand growth rates with density were neither due to decreases in photosynthesis nor to increases in respiration. Instead the authors found that the convergence of growth at the higher densities were primarily dependent on factors associated with canopy size, specifically, leaf area index, intercepted PAR, and canopy nitrogen content (Will et al. 2001).

The overall objective of the current study was to further examine the relationship between three key physiological attributes, leaf area index, annual PAR capture, and foliar nitrogen status, thought to control tree and stand growth by ascertaining the relative importance of these factors across a wide range of stand densities. By using stands of vastly differing planting densities (740 to 4440 trees ha^{-1}), the effects of and potential interactions between leaf area index, PAR capture, and foliar nitrogen status can be separated. The hypotheses of the study were: (1) individual tree diameters would respond negatively to increases in planting density because of a greater level of intraspecific competition for site resources in these stands; (2) there would be concurrent increases in stand-level stem volume and stem growth rates with planting density because of a greater capacity for stands with more trees per hectare to exploit available site resources; and (3) foliar nitrogen content, leaf area, and annual PAR capture would each be positively influenced by planting density, also because of an increased capacity to acquire and utilize site resources. These general hypotheses were used to formulate the specific objectives of this study, which were to determine: (1) the effects of planting density on leaf area index (2) the effects of planting density on seasonal changes in foliar nitrogen concentration throughout the canopy, (3) the effects of planting density on canopy nitrogen content (4) the effects of planting density on seasonal as well as annual PAR capture, and (5) the relationship between stand level growth and each of the measured canopy variables as density increased.

CHAPTER 2

LITERATURE REVIEW

Competition, growing space, and planting density

There are nine fundamental interactions between individuals in any ecological community (Haskel 1949, Burkholder 1952, Dyer 1996). These interactions are neutralism, direct-interference competition, resource-use competition, amensalism, commensalism, parasitism, predation, proto-cooperation, and mutualism (Haskel 1949, Burkholder 1952). In plant communities, resource-use competition between individuals is the dominant relationship (Tansley 1920). That is, competition for available resources is the primary factor affecting the development and functioning of individuals in plant communities. The abstract notion of 'growing space' is often used to conceptualize the finite nature of resource availability in a system, specifically in the context of competition between individuals. Although growing space has been traditionally defined in silvics as encompassing only the physical volume taken up by trees in a community (Smith 1997), Oliver and Larson (1990) describe an expanded concept of growing space that integrates the supply of available resources on a site (physical space, nutrients, water, light, etc.) and the demand for these resources by individuals on that site. Using this modified definition, the quantity of available growing space associated with a site increases or decreases with resource availability, and inversely with plant demand for resources. For a given amount of resource, the level of competition for growing space between individuals in a forest stand is a direct function of stand density and tree size in relation to resource availability (Zedaker 1982). A description of competition by Clements et al. (1929) is an especially apt summarization: “Competition arises from the reaction of one plant upon the physical factors about it and the effect of these modified factors upon its competitors. In the exact sense, two plants, no matter how close, do not compete with each other as long as the water content, the nutrient material, the light, and heat are in excess of the needs of both. When the immediate supply of a single necessary factor falls below the combined demands of the plant, competition begins.”

Plants react to increases in density and related increases in competition for growing space through plasticity and mortality (Harper 1977). Plasticity is the capacity of a plant to modify various aspects of its developmental pattern or phenology (e.g. size, growth rate, composition of components) based on varying environmental conditions. In general, when there is a high level of competition for growing space (e.g. high planting density), individual plants grow more slowly and are therefore smaller than plants growing with less competition. When a plant can no longer compensate for density-induced stress through plasticity, mortality occurs (Hutchings and Budd 1981).

Resource availability, growth, and planting density

Limitations in the availability of light, nutrients, and water are often cited as the primary drivers of competition in forest stands. Gradients in light availability have been shown to significantly alter growth rates, morphology, and seedling establishment in forest communities (Lieffers et al. 1993, Elliott and Vose 1995, Kikuzawa and Umeki 1996, Messier et al. 1999, McGuire et al. 2001). For example, a study in longleaf pine stands (*Pinus palustris* Mill.) found that gaps created by tree removal resulted in greater growth for both longleaf pine seedlings and other understory vegetation (McGuire et al. 2001). Out of all variables measured (light availability, nitrogen availability, and gravimetric soil moisture content), the authors found that increases in available light accounted for the most variation in understory and pine seedling biomass (McGuire et al. 2001).

Several studies have reported decreased rates of nutrient acquisition and tree growth in response to high levels of interspecific competition between trees and herbaceous vegetation (e.g. Elliot and White 1987, Morris et al. 1993). Likewise, several studies have shown that water limitations can adversely affect the growth of competing individuals, particularly in dry regions (McMurtrie et al. 1990, Nambiar and Sands 1993, Jose 2003). For pine stands in the southeastern United States, limitations in nutrient availability seem to play a larger role than do limitations in water availability. For example, there have been many studies illustrating large increases in stand growth with nutrient amendments (e.g. Albaugh et al. 1998, Samuelson et al. 2000), while similar studies with irrigation suggest only marginal improvements in growth (Albaugh et al. 1998, Samuelson et al. 2001). It is possible that in the southeastern United States, water availability is not as limiting to tree growth as is nutrient availability due to ample average rainfall (>1200 mm y^{-1}). Other potential factors include the presence of sandy soils and the related rooting patterns of trees, allowing access to water deeper in the soil profile or to water in shallow aquifers (Teskey et al. 1994, Barron-Gafford et al. 2003).

In a given system, limitations in nutrient availability typically manifest in suppressed growth rates (Chapin et al. 1986). The underlying causes of sub-optimal productivity in nitrogen-limited systems are shifts in the allocation of assimilated carbon, and factors associated with a diminished capacity for carbon fixation (decreased rates of photosynthesis or decreased quantities of photosynthetic tissues, i.e. foliage). By definition, a system is nutrient-limited if the addition of that particular nutrient leads directly to increases in productivity (Chapin et al. 1986). A study in two-year-old Sitka spruce (*Picea sitchensis* (Bong.) Carr.) seedlings sought to determine how nitrogen deficiencies limited productivity in nitrogen-deprived treatments by observing the responses of needle growth, shoot growth, and photosynthesis to increases in nitrogen supply (Chandler and Dale 1995). Not surprisingly, this study found that the lengths of shoots and needles grown in nitrogen-deprived treatments were significantly less than in control treatments. After refertilization, lengths of shoots and needles grown in nitrogen-deficient treatments were either equal to or greater than lengths of shoots and needles not grown under nutrient deprivation. Likewise, refertilization increased leaf chlorophyll concentration and net photosynthetic rates to levels either equal to or greater than in control treatments (Chandler and Dale 1995). Another study in fertilized loblolly pine stands (*Pinus taeda* L.) sought to determine the role of nutrients in growth limitations that occurred at higher planting densities (Barron-Gafford et al. 2003). Nitrogen, phosphorous, and potassium concentrations and contents were measured in stems, leaves, and fine roots to determine if the acquisition of any of these resources fell below levels considered to be critical for satisfactory growth (Barron-Gafford et al. 2003). While the authors found that phosphorous and potassium did not consistently differ with planting density, nitrogen concentration in all measured tree components decreased significantly in higher density treatments (Barron-Gafford et al. 2003). Furthermore, foliar nitrogen concentration was found to have dropped below established critical levels in the highest density treatments (Barron-Gafford et al. 2003). These results led the authors to conclude that nitrogen deficits in the higher planting densities may have been a significant contributory factor to diminished growth rates (Barron-Gafford et al. 2003).

There is evidence in the literature to suggest considerable similarities between density-induced and age-induced competition for growing space in forest systems, specifically in regard to nutrient limitations. Similar to increases in stand-level biomass associated with higher density stands, older stands often accumulate large quantities of standing biomass. The net effect is an intensification of nutrient limitations through a potentially greater demand for nutrients, and through the sequestration of nutrient resources on the forest floor and in standing biomass (Pearson et al. 1987, Ryan et al. 1997, Richter et al. 2000). For example, Binkley et al. (1995) reported that older stands of lodgepole pine (*Pinus contorta* Dougl.) exhibited greater nutrient limitations that were responsible, at least in part, for restrictions to growth.

Planting density and tree growth

The manipulation of planting density as a means of altering the dynamics of competition for growing space between individuals, thereby altering growth and yield in forest stands, has been studied extensively (e.g., Ware and Stahelin 1950, Sjolte-Jorgenson 1967, Dahms 1973, Schmidt et al. 1976, Seidel 1984, Evert 1971, Shepard 1971, Whitsell 1974, Balmer 1975, Harms and Langdon 1976, Pollack et al. 1990, Harms et al. 1994, Clark et al. 1994, Smith et al. 1997, Harms et al. 2000, Burkes et al. 2003). Studies typically find a consistent inverse relationship between planting density and tree size attributable to density-induced intraspecific competition for growing space, and reflected primarily by differences in stem diameter growth rather than height growth (e.g. Whitsell 1974, Balmer 1975, Harms and Langdon 1976, Harms et al. 1994, Harms et al. 2000). A study by Harms et al. (2000) found that 11-year-old stands of loblolly pine (*Pinus taeda* L.) had a quadratic mean diameter that was 51% greater in the lowest density treatment compared to the highest density treatment. This negative response to density was consistent for every measurement made throughout the 34-year study period (stand ages 4, 7, 11, 20, 25, 26, and 34). There are a few studies in very young forest plantations that show positive responses of individual tree diameter and height to planting density (Helmers 1948, Cameron et al. 1989, Gilbert et al. 1995, Knowe and Hibbs 1996, Ritchie 1997, Scott et al. 1998, Woodruff et al. 2002). In a study on the response of young Douglas-fir plantations (*Pseudotsuga menziesii* (Mirb.) Franco var. menziesii) to planting density, Woodruff et al. (2002) found that mean rates of stem diameter growth were greater in high density treatments compared to low density treatments (2960 trees ha^{-1} and 300 trees ha^{-1}) for the first five growing seasons. During the second and third growing seasons, mean diameter increment was 65% and 54% greater, respectively, in the high density versus the low density treatment. However, like other studies that report similar early-stage responses (e.g. Cameron et al. 1989, Scott et al. 1998), the positive effect of planting density on growth did not last. Density-induced intraspecific competition for growing space eventually led to a decrease in annual growth rate (Woodruff et al. 2002), a response that is consistent with the overwhelming majority of the literature dealing with planting density and growth (Evert 1971, Smith et al. 1997). Woodruff et al. (2002) suggest that the inversion of stem diameter growth response to density over time (from a positive to a negative relationship) is perhaps attributable to a mechanism that functions only in the early stages of seedling growth. It is also possible that this mechanism is still functioning when stands are older, but is overshadowed by the deleterious effects of increasing intraspecific competition on individual tree growth (Woodruff et al. 2002).

Planting density and stand growth

Despite the negative growth response of individual tree size to density-induced competition, there is an overall positive response in stand-level growth (e.g. Ware and Stahelin 1950, Mann and Dell 1971, Shepard 1971, Whitsell 1974, Balmer et al. 1975, Harms and Langdon 1976, Shelton 1984, Harms et al. 1994, Quicke et al. 1999, Harms et al. 2000, Burkes et al. 2003). This is primarily due to a greater number of stems per unit area, and the capacity of higher planting densities to acquire and use a greater proportion of available site resources such as nutrients, water, and light. A study in loblolly pine stands (*Pinus* taeda L) in the Piedmont physiographic region of Alabama found that an increase in planting density from 800 to 2200 trees ha^{-1} resulted in an increase of 150% and 93% in stand basal area and standing stemwood volume, respectively (Quicke et al. 1999). Similarly, Burkes et al. (2003) found that for loblolly (*Pinus taeda* L.) and slash (*Pinus elliottii* Engelm.) pine stands in the Coastal Plain of southern Georgia, stand-level stem biomass growth increased from roughly 5000 to roughly 17,500 kg ha^{-1} y^{-1} with an increase in stand density from 740 to 3700 trees ha^{-1}. The study by Harms et al. (2000) found that after four growing seasons, basal area and standing stemwood volume increased by 181% and 275%, respectively as stand density increased from 725 to 1585 trees ha^{-1}.

Burkes et al. (2003) found that increases in stem biomass were not directly proportional to increases in planting density. They reported that with a 300% increase in stand density, there was only a 250% increase in stem biomass growth (Burkes et al. 2003). Furthermore, with an increase in stand density of 500%, stem biomass growth increased by only 350% (Burkes et al. 2003). This result is common in planting density studies that measure stand-level growth and yield (e.g. Mann and Dell 1971, Harms and Langdon 1976, Shelton 1984, Harms et al. 1994, McCrady and Jokela 1996, Will et al. 2001, Barron-Gafford 2003) and indicates the presence of resource limitations in higher density stands perhaps brought about by full site occupancy and utilization of growing space.

Up to a certain planting density, stand-level stem growth increases with density due to the more efficient acquisition and use of site resources. If density is increased further, stem growth rates plateau, then decline as trees approach and exceed total consumption of growing space (e.g. Shelton 1984, Harms et al. 1994, McCrady and Jokela 1996). If density is increased yet further, trees occupying the site will require more resources than the site is capable of delivering, thereby leading to mortality as a means of releasing growing space for the remaining trees (Dean and Baldwin 1996). The density at which growing space is fully occupied (i.e. maximum growth rate) varies depending on site quality, stand age, and other environmental variables, with better sites capable of supporting greater planting densities and therefore greater stand-level stem growth rates (Harms et al. 1994). In general, stand growth rates are initially higher in more dense stands than in less dense stands. Over time, as individual trees become larger and require more growing space, growth rates in the less dense stands approach and then exceed growth rates of more dense stands. The point at which the total volumes carried by stands of different densities converge represents the upper limit of productivity for a given site. Better quality sites and sites with more intensive inputs of silvicultural treatments reach this point of convergence more quickly, and are capable of carrying greater total volumes at higher densities than poorer quality sites (Mann and Dell 1971, Harms et al. 1994).

Planting density and biomass partitioning

The limitations to stem growth resulting from density-induced intraspecific competition may be caused by shifts in the allocation of photosynthate between aboveground (stemwood, branches, foliage) and belowground (coarse roots, fine roots) components (Pearson et al. 1984, Nilsson and Albrektson 1993, Puri et al. 1993, McCrady and Jokela 1996, Burkes et al. 2003). Biomass partitioning is significantly influenced by site quality and nutrient amendments (Gower et al. 1995, Haynes and Gower 1995, Albaugh et al. 1998, Wang et al. 1998). Typically, stands growing on sites with greater nutrient and water availability require less extensive root systems. Conversely, stands on lower quality sites often have a higher proportion of assimilated carbon allocated belowground to procure these necessary resources (Keyes and Grier 1981, Gower

1992, Albaugh et al. 1998, Ibrahim 1998). A study in low and high productivity sites of 40-year-old Douglas-fir stands (*Pseudotsuga menziesii* (Mirb.) Franco) found that fine root biomass accounted for only 8% of net primary productivity (NPP) in high productivity sites, while accounting for 36% of NPP in low productivity sites (Keyes and Grier 1981). Similarly, the proportion of NPP allocated belowground versus aboveground decreased with fertilization in Rocky Mountain Douglas-fir stands (P. *menziesii* var. *glauca*) from 46% in control treatments to 23% in fertilized treatments (Gower et al. 1992). It has been suggested that stem biomass growth has a lower priority regarding the allocation of carbon relative to resource-acquiring components such as foliage and fine root biomass (Oliver and Larson 1990). In higher density stands, greater competition for growing space may cause trees to shift allocation of photosynthate away from stemwood production toward foliage and roots in order to acquire more resources. However, there is evidence for both increases (Puri et al. 1993), and decreases (Pearson et al. 1984) in the proportion of biomass allocated belowground with increasing density. In their study, Burkes et al. (2003) hypothesized that greater intraspecific competition for light, water, and nutrients associated with increases in stand density would result in a greater proportion of photosynthate allocated to foliage and fine root biomass. On the contrary, they found that higher density stands partitioned more biomass to stemwood production, with both stem production per unit foliage and stem production per unit fine root biomass increasing in higher density treatments (Burkes et al. 2003). Given the lack of consensus in the literature, it is not clear whether there is a specific or consistent pattern in biomass partitioning due to density-induced intraspecific competition. However, there is ample evidence of effects from gradients in site quality and nutrient amendments on carbon partitioning to roots.

Leaf area, growth, and planting density

The productivity of a forest stand is directly related to the amount of leaf area in the canopy and the efficiency with which this leaf area converts light and other resources to photosynthate (Gholz 1982, Vose and Allen 1988, Long and Smith 1990, Dalla-Tea and Jokela 1991, Gower et al. 1992, Coyea and Margolis 1994, Beets and Whitehead 1996, Fassnacht and Gower 1997, Albaugh et al. 1998, Burkes et al. 2003). This is primarily attributable to the role of the canopy as the principal exchange surface between the plant and the surrounding atmosphere; therefore making leaf area a dominant factor in the dynamics of light interception, water fluxes, and carbon dioxide exchange. In general, studies indicate that leaf area can explain between 80% and 90% of the variation in aboveground net primary production (ANPP) of forest stands (Gholz 1982, Gower et al. 1992, Fassnacht and Gower 1997).

Planting density is a factor in the accumulation of leaf area only until the point of canopy closure, after which leaf area index comes to an equilibrium level (Moller 1947, Marks and Bormann 1972, Turner and Long 1975, Shelton 1984, Long and Smith 1984, Long and Smith 1990). In the cited studies, although stands of differing planting densities eventually reached the same level of equilibrium for maximum sustainable leaf area, stands with higher initial densities reached this level more quickly than less dense stands. There is also evidence of species differences in the relationship between leaf area index and stand density. In a study on two species with different growth characteristics, lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), Jack and Long (1991) found that lodgepole pine had leaf area index (LAI) values that were generally constant over a wide range of densities. In subalpine fir, however, LAI values increased significantly with density (Jack and Long 1991). The authors suggest that these results are due to a difference in the plasticity of mean leaf area per tree between the two species (Jack and Long 1991). In other words, there was a different response of mean leaf area per tree to stand density by the two species. The authors attribute this to differences in relative shade tolerance and the resulting effects of decreased inter- and intra-canopy light levels on competitive interactions at higher densities (Jack and Long 1991).

Another study on lodgepole pine (*Pinus contorta*) also found that leaf area was independent of density for this species, with low density stands supporting the same total leaf area as high density stands (Long and Smith 1990). This study found a positive correlation between the rate of stand growth and leaf area. However, there was a significant degree of unexplained residual variation ($r^2 = 0.45$) (Long and Smith 1990). The authors attributed this variation to the influence of stand structure, noting that the distribution of leaf area in stands of differing densities varied, with low density stands consisting of a fewer number of trees with larger crowns (large mean leaf area per tree) and higher density stands consisting of more trees with smaller crowns (low mean leaf area per tree). They suggest that stands with similar leaf areas may display large degrees of variation in growth rate based on differences in canopy structure, with low density stands having lower overall growth rates due to the greater respiration requirements of non-photosynthetic tissues in the canopy (i.e. branches) relative to higher density stands (Long and Smith 1990).

Water availability (Grier and Running 1977, Gholz 1982, Long and Smith 1990, Burton et al. 1991, Sampson and Allen 1998), and nutrient availability (Vose and Allen 1988, Gower et al. 1992, Sampson and Allen 1998, Smethurst et al. 2002) are considered to be significant factors in determining maximum sustainable leaf area for a given site. Increases in leaf area resulting from higher levels of available water and nutrients may stem from the improved capacity to produce foliage, or from an increase in the allocation of photosynthate to the foliage from belowground components. A study by Sampson and Allen (1998) exemplifies the positive effect of increased water and nutrient availability on leaf area. In this work, irrigated and fertilized treatments of 14-year-old loblolly pine (*Pinus taeda* L.) displayed more than double the LAI of the control treatment. Vose and Allen (1988) similarly found that nitrogen fertilization increased the LAI of loblolly pine by as much as 60%, with larger responses of LAI to fertilization in lower quality sites. In regard to water limitations to leaf area, a study by Osorio et al. (1998) found that leaf area of *Eucalyptus globulus* seedlings decreased by 50% when exposed to moderate drought stress.

Intercepted radiation, growth, and planting density

Intercepted photosynthetically active radiation (PAR) is a measure of the amount of solar energy that is absorbed by a forest canopy for use in photosynthesis. This value represents the amount of usable energy a canopy intercepts over a given area and time (e.g. MJ m^{-2} y^{-1}). Similar to the relationship between leaf area and stand growth, there have been numerous studies that show a significant positive linear relationship between PAR capture and stand productivity (e.g. Monteith 1977, Cannell et al. 1987, Grace et al. 1987, Harrington and Fownes, 1995, Landsberg and Waring 1997, Will et al. 2001, Allen 2003). A value that is sometimes used as a surrogate for PAR capture is intercepted radiation (proportion or percent), which can be valuable in determining 'spot' (not time-integrated) measurements of radiation intercepted by the canopy. A study in three-year-old loblolly pine (*Pinus taeda* L.) found that the proportion of radiation intercepted by stands was highly correlated to the rate of stem volume growth, with 70% of variation explained with linear regression (Will et al. 2001). Another study in loblolly pine similarly found PAR capture to be highly correlated to stem volume growth (linear regression,

r^2=0.78) (Allen 2003). This study also examined the relationship between LAI and stem volume growth and found that, although still highly correlated, there was a higher level of unexplained variation (r^2 = 0.65) between these two variables than between PAR capture and growth (Allen 2003). The author suggests that PAR capture is a better predictor of stand productivity because measurements of LAI do not take into account differences in canopy structure that affect the efficiency with which photosynthetically active radiation (PAR) is intercepted by the canopy (Allen 2003).

Leaf area and PAR capture are inherently related. That is, stands that have greater leaf area are intrinsically capable of absorbing more PAR than stands with less leaf area. Therefore, factors that affect leaf area, such as resource availability and planting density, will likewise affect PAR capture. The quantity of PAR that can be absorbed by a given amount of leaf area varies depending primarily on foliage duration and canopy architecture, which refers to how foliage (photosynthetic biomass) and branches (non-photosynthetic biomass) are distributed both vertically and horizontally within the canopy. The efficiency of PAR capture by leaf area is a function of the resulting display of foliage and is strongly influenced by canopy attributes such as leaf angle and canopy density (Kozlowski et al. 1991).

In a study on loblolly pine (*Pinus taeda* L.), Vose and Allen (1988) examined the relationship between stand productivity and increasing levels of LAI (projected) stemming from site nutrient amendments. The study found that increases in LAI were proportional to increases in growth until LAI reached a value of 3.5 (Vose and Allen 1988). At LAI values greater than 3.5, incremental increases in LAI no longer led to corresponding increases in stand volume growth (Vose and Allen 1988). Vose and Allen (1988) suggest that the decrease in the response of stand growth to LAI at higher values resulted from relatively small gains in intercepted radiation (5%) with comparatively large gains in LAI (28%). Similarly, a study of 14-year-old loblolly pine (*Pinus taeda* L.) reported that with an increase of more than 200% in LAI with fertilization, PAR capture increased by only by 40% (Sampson and Allen 1998). The differential increases in LAI and intercepted radiation with fertilization in these studies likely stem from increased rates of self-shading in the canopies with higher leaf areas. In a study of young loblolly pine stands (*Pinus taeda* L.) of differing planting densities, Will et al. (2001) found a strong correlation between intercepted radiation and stand volume growth across all density treatments. They also found that increases in stand growth were not proportional to planting density in the higher density treatments (Will et al. 2001). The authors propose that the rate of stand volume growth was not proportional to increasing density because of limitations to the amount of radiation that could be intercepted by stands in the higher density treatments stemming from greater self-shading within the canopy associated with large quantities of leaf area (Will et al. 2001).

Photosynthetic capacity, foliar nitrogen status, and planting density

Intuitively, it is reasonable that the rate of growth in a forest stand is largely dependent on its capacity to photosynthesize. Indeed, much of the literature indicates that increases in growth rates are associated with increases in photosynthetic capacity for both deciduous and coniferous species (e.g. Walters and Reich 1989, Polley et al. 1997, Ellis et al. 2000, Jose et al. 2003). However there are also a few studies that have found little or no effect of photosynthetic rates on stand growth (e.g. Ellis et al. 2000, Samuelson et al. 2001, Will et al. 2001). For example, in their study on loblolly pine (*Pinus taeda* L.), Will et al. (2001) found that although relative rates of stand growth decreased with increasing planting density, light saturated photosynthetic rates remained consistent across all densities. This apparent incongruity between findings likely results from observations made over a variety of taxonomic levels; i.e., it is likely that the relationship between photosynthetic capacity and growth is highly variable when observed between different species or functional groups, while consistent when observed within a single species or group. Despite species differences in its relationship with growth, photosynthetic capacity remains an important parameter with far-reaching implications in ecophysiological processes ranging from the leaf level up through the landscape level (Dang et al. 1997).

There are many factors thought to influence the photosynthetic capacity of forest stands including ambient temperature, ambient carbon dioxide levels, light availability, water availability, and nutrient availability. The availability of nitrogen plays a particularly significant role since nitrogen is a primary constituent in many components including enzymes, pigments, and electron-transport compounds that make up the photosynthetic machinery in foliage (Evans 1989). In addition, foliar nitrogen distribution in the canopy is often well correlated with light availability (DeJong and Doyle 1985, DeJong et al. 1989, Ellsworth and Reich 1993, Niinemets 1997). Rubisco (ribulose biphosphate (RuBP) carboxylase/oxygenase), the enzyme in chloroplasts responsible for assimilating atmospheric carbon for the synthesis of essential organic compounds for the process of photosynthesis, is the largest single reservoir of nitrogen in plants, comprising up to 25% of nitrogen in foliage (Portis 1998). Typically, leaves with high nitrogen concentrations have higher rates of photosynthesis than leaves with low nitrogen concentrations (Tissue et al. 1993, Chandler and Dale 1995, Reich et al. 1995, Murthy et al. 1996, Samuelson 1998, Wang et al. 1998, Schoettle and Smith 1999, Clearwater and Meinzer 2001, Cordell et al. 2001, Jose et al. 2003). A study of nine-year-old loblolly pine stands (*Pinus taeda* L.) found that decreases in the foliar nitrogen concentration of one-year-old foliage coincided with concurrent decreases in light saturated net photosynthesis (Murthy et al. 1996). In another study, Schoettle and Smith (1999) found that foliar nitrogen concentration was significantly correlated with light saturated net photosynthesis in mature stands of lodgepole pine (*Pinus contorta* Dougl. ssp. *latifolia* Engelm.) for young needles (1-4 years old), but not for middle aged (5-8 years old) or old needles (9-15 years old). A study of nine conifer species by Reich et al. (1995) found similar positive relationships between foliar nitrogen concentration and light saturated net photosynthesis in young leaves.

There are also several studies that failed to find significant relationships between foliar nitrogen concentration and photosynthetic rate (Teskey 1994, Samuelson 1998, 2001, Will et al. 2001, Maier et al. 2002, Munger et al. 2003). For southern pine species, studies that found significant relationships between these two variables involved treatments with relatively low nitrogen concentrations or sites that were otherwise nutrient deficient (e.g. Tissue et al. 1993, Chandler and Dale 1995, Murthy et al. 1996), whereas studies that found no significant relationship involved treatments with higher overall foliar nitrogen concentrations or better quality sites (e.g. Teskey et al. 1994, Samuelson et al. 2001, Will et al. 2001, Munger 2003). A study that examined the effects of competition control and nutrient amendments on the relationship between foliar nitrogen concentration and photosynthetic capacity in loblolly pine (*Pinus taeda* L.) found that neither fertilization nor competition control had any consistent impact on photosynthetic rate, despite a significant response of foliar nitrogen concentration to fertilization (Munger et al. 2003). Here, the authors suggested that three factors may affect the relationship between foliar nitrogen concentration and photosynthetic rate in loblolly pine: (1) stage of stand development – a positive relationship between foliar nitrogen concentration and photosynthetic rate is often observed in seedlings, but rarely in mature trees, (2) inherent site quality – the potential for a significant relationship is greater in infertile sites than in sites with higher levels of nutrient availability, and (3) duration of fertilization treatments – occurrences of significant relationships between photosynthetic capacity and foliar nitrogen concentration with fertilization decrease with the length of treatment (Munger et al. 2003). Generally, since foliage can be viewed as a storage pool for nitrogen, higher concentrations do not necessarily entail greater photosynthetic capacity given that nitrogen is not always stored in a form that is useful for photosynthesis. It is likely that in more fertile sites, a greater proportion of foliar nitrogen is stored in non-photosynthetic compounds, while less fertile sites commit more available nitrogen to photosynthesizing compounds such as chlorophyll, or rubisco.

The response of foliar nitrogen concentration (and many other physiological variables) to planting density is frequently congruous to its response to changes in stand nutrient availability (i.e. fertilization). In both cases, stands experience shifts in growing space, either brought about by the addition of nutrients, or by decreases in their relative availability stemming from increased intraspecific competition. In general, an increase in the availability of nitrogen, whether through fertilization or manipulations to planting density, leads to increases in foliar nitrogen concentration (e.g. Chandler and Dale, Fife and Nambiar 1997, Wang et al. 1998, Clearwater and Meinzer 2001, Cordell et al. 2001, Will et al. 2001, Barron-Gafford et al. 2003, Munger et al. 2003). For example, a study on seven-year-old Monterey pine (*Pinus radiata* (D. Don)) growing in Australia found increased foliar nitrogen concentrations with nitrogen fertilization, regardless of needle age (Fife and Nambiar 1997). Increases of foliar nitrogen concentration for fully elongated needles in this study were apparent within two months of fertilization (Fife and Nambiar 1997). Likewise, an investigation of foliar nitrogen response to planting density in loblolly pine stands (*Pinus taeda* L.) found that concentrations significantly increased in lower densities (greater relative nutrient availability) (Barron-Gafford et al. 2003).

There are examples in the literature, however, of studies reporting no observable relationship between nutrient availability and foliar nitrogen concentration. For example, one study investigating this relationship in seedlings of loblolly pine (*Pinus taeda* L.) and sweetgum (*Liquidambar styraciflua* L.) found no response of nitrogen concentration after two years of growth (Samuelson et al. 2001). This lack in apparent response of foliar nitrogen concentration to gradients in nutrient availability is perhaps attributable to a dilution effect resulting from a moderate increase in foliar nitrogen compared to a large increase in leaf area.

Radiation-use efficiency and planting density

The seminal work of Monteith (1977) established a linear relationship between annual aboveground dry matter production and PAR capture for several agricultural crops. Since then, there have been many studies confirming this relationship for other agricultural crops as well as for many tree species (Cannell et al. 1987, Grace et al. 1987, Dalla-Tea and Jokela 1991, Monteith 1994, Harrington and Fownes 1995). This simple model of net primary production is often referred to as the light-use efficiency model (Medlyn 1998), and states that time-integrated NPP (or ANPP) for a given system is equal to the product of radiation-use efficiency (ε) and time-integrated absorbed PAR:

$$\mathrm{NPP} = \varepsilon\ \mathrm{APAR}$$

The slope of the relationship between productivity and PAR capture, ε, represents all photosynthetic and respiratory processes occurring in the system, and can also be expressed as stemwood production (volume or biomass) per unit of PAR captured by a canopy (e.g. g MJ^{-1}). The value of ε within and between systems varies considerably, and is influenced by factors such as species, temperature, water availability, nutrient availability, and radiation environment (Sinclair and Muchow 1999).

Studies have shown significant increases in ε as a result of nutrient amendments (Landsberg and Wright 1989, Balster and Marshall 2000). It is therefore not surprising that ε has also been found to be positively correlated with photosynthetic capacity (Sinclair and Horie 1989, Sands 1996, Sinclair and Muchow 1999), foliar nitrogen concentration (Sinclair and Horie 1989, Sinclair and Shiraiwa 1993, Medlyn 1996, Sands 1996), and water availability (Phillips and Riha 1993, Harrington and Fownes 1995). In their study in young loblolly (*Pinus taeda* L.) and slash (*Pinus elliottii* Engelm.) pine stands, however, Dalla-Tea and Jokela (1991) found no impact on ε from intensive cultural treatments. This result is perhaps attributable to a lack of correlation between nitrogen status and photosynthetic capacity for this species. There is very little in the literature that addresses the specific effects of planting density on ε. One exception is a study in soybean (*Glycine max* (L.) Merr.) by Purcell et al. (2002) that found significant decreases in ε with increases in planting density. This result seems appropriate given the substantial evidence in the literature regarding the direct association between ε and resource availability, and the fact that increases in planting density would result in increased competition for available resources.

Growth efficiency and planting density

The rate of growth in a forest stand is a direct function of the amount of leaf area present in the canopy, the effectiveness of PAR capture by the leaf area, and the efficiency with which intercepted PAR is converted to biomass. The relative contributions of leaf area and PAR capture to growth are quantified by two physiological parameters: growth efficiency and radiation-use efficiency. Growth efficiency, sometimes referred to as production efficiency or leaf area efficiency, is a measure of stemwood production (volume or biomass), net primary production (NPP), or aboveground net primary production (ANPP) per unit leaf area (LAI or biomass).

Growth efficiency is an integrated value representing the efficacy of light capture by the canopy, and the resultant quantity of assimilated carbon that is partitioned to wood (Waring et al. 1983).

Although leaf area is well correlated with growth (Vose and Allen 1988, Long and Smith 1990, Dalla-Tea and Jokela 1991, Albaugh et al. 1998), stands with similar leaf areas often display considerable variation in productivity (e.g. Long and Smith 1990), a result attributable to differences in growth efficiency. Factors affecting the relationship between stand productivity and leaf area include resource availability (Balster and Marshall 2000, Xiao et al. 2003), planting density (Waring 1983, Shelton 1984, Burkes et al. 2003), stand age (Ryan et al. 1997, Jokela and Martin 2000, Will et al. 2002), and differences in canopy structure (Smith and Long 1989, Long and Smith 1990). In general, stand age has a negative impact on growth efficiency (Colbert et al. 1990, Jokela and Martin 2000, Will et al. 2002). In a study by Will et al. (2002), decreases in growth efficiency with stand age were attributed to decreases in photosynthetic capacity per leaf area, increases in biomass partitioning belowground, or to increases in respiration associated with older, larger trees. In regard to the effects of stand structure on growth efficiency, Smith and Long (1989) found that in stands of similar total leaf areas, trees with large, deep crowns were inherently less efficient than trees with small, shallow crowns. The authors suggest this result is due to a greater ratio of respiratory tissue to photosynthetic tissue in large deep-crowned canopies relative to small shallow-crowned canopies (Smith and Long 1989). There are several conflicting reports in the literature regarding the response of growth efficiency to nutrient amendments (Vose and Allen 1988, Colbert et al. 1990, Beets and Whitehead 1996, Albaugh et al. 1998, Balster and Marshall 2000, Jokela and Martin 2000, Samuelson et al. 2001, Will et al. 2002). For studies that found positive responses to nitrogen fertilization (Colbert et al. 1990, Albaugh et al. 1998, Balster and Marshall 2000, Will et al. 2002), increases in growth efficiency were attributed to shifts in biomass partitioning and to a more efficient assimilation of carbon by the canopies. In studies that found no relationship between growth efficiency and nutrient amendments (Vose and Allen 1988, Beets and Whitehead 1996, Samuelson et al. 2001), results were attributed to increased self-shading within the canopy leading to less efficient PAR capture by the foliage, or to greater losses of carbon stemming from an increase in respiring tissues (Vose and Allen 1988).

A study by Burkes et al. (2003) sought to determine the source of limitations to stand volume growth with increasing planting density by investigating the effects of density on the growth efficiency and biomass partitioning of young loblolly (*Pinus taeda* L.) and slash (*Pinus elliottii* Engelm.) pine stands. The authors hypothesized that growth efficiency would decrease with stand density because of a reduced priority of carbon partitioning to stemwood, and lower light availability resulting from increased self-shading (Burkes et al. 2003). This hypothesis is supported by results from Waring (1983) and Shelton (1984) that found stem production per unit foliage to be greater in stands of low planting density, in part due to greater light availability in these stands. Instead, Burkes et al. (2003) found that growth efficiency increased with density, thereby negating the possibility of its contribution to density limitations to growth. The increase of growth efficiency with planting density was attributed to differences in canopy structure between stands of different densities, with low density treatments having a greater proportion of branch to foliage biomass than high density treatments, and to increases in the partitioning of biomass to stemwood relative to other tree components (Burkes et al. 2003).

Literature Cited

Albaugh, T.J., Allen, H.L., Dougherty, P.M., Kress, L.W., King, J.S. 1998. Leaf area and above- and belowground responses of loblolly pine to nutrient and water additions. Forest Science 44:317-328.

Allen, C.B. 2003. The effect of water and nutrient availability on canopy dynamics and radiation conversion of four tree species. M.S. Thesis, University of Georgia, Athens, GA.

Balmer, W.E., Owens, E.G., Jorgensen, J.R. 1975. Effects of various spacings on loblolly pine growth 15 years after planting. USDA Forest Service Research Note SE-211. Southeastern Forest Experiment Station.

Balster, N.J., and Marshall, J.D. 2000. Eight-year responses of light interception, effective leaf area index, and stemwood production in fertilized stands of interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca*). Canadian Journal of Forest Research 30:733-743.

Barron-Gafford, G.A., Will, R.E., Burkes, E.C., Shiver, B., Teskey, R.O. 2003. Nutrient concentrations and contents, and their relation to stem growth, of intensively managed *Pinus taeda* and *Pinus elliottii* stands of different planting densities. Forest Science 49(2):291-300.

Beets P.N., Whitehead, D. 1996. Carbon partitioning in *Pinus radiata* stands in relation to foliar nitrogen status. Tree Physiology 16:131-138.

Binkley, D., Smith, F.W., Son, Y. 1995. Nutrient supply and decline in leaf area production in lodgepole pine. Canadian Journal of Forest Research 25:621-628.

Burkes, E.C., Will, R.E., Barron-Gafford, G.A., Teskey, R.O., Shiver, B. 2003. Biomass partitioning and growth efficiency of intensively managed *Pinus taeda* and *Pinus elliottii* stands of different planting densities. Forest Science 49(2):224-234.

Burkholder, P.R. 1952. Cooperation and conflict among primitive organisms. American Scientist 40:601-631.

Burton, A.J., Pregitzer, K.S., Reed, D.D. 1991. Leaf area and foliar biomass relationships in northern hardwood forests located along an 800 km acid deposition gradient. Forest Science 37(4):1011-1059.

Cameron, D.M., Rance, S.J. Jones, R.M. Charles-Edwards, D.A., Barnes, A. 1989. Project STAG: an experimental study in agroforestry. Australian Journal of Agricultural Research 40:699-714.

Cannell, M.G.R., Milne, R., Sheppard, L.J., Unsworth, M.H. 1987. Radiation interception and productivity of willow. Journal of Applied Ecology 24:261-278.

Chandler, J.W., Dale, J.E. 1995. Nitrogen deficiency and fertilization effects on needle growth and photosynthesis in Sitka spruce (*Picea sitchensis*). Tree Physiology 15:813-817.

Clark, A.I., Saucier, J.R., Baldwin, V.C., Rower, D.R. 1994. Effect of initial spacing and thinning on lumber grade, yield and strength of loblolly pine. Forest Products Journal 44:14-20.

Clearwater, M.J., Meinzer, F.C. 2001. Relationships between hydraulic architecture and leaf photosynthetic capacity in nitrogen-fertilized *Eucalyptus grandis* trees. Tree Physiology 21:683-690.

Clements, F.E., Weaver, J.E., Hanson, H.C. 1929. Plant Competition: An analysis of community functions. Carnegie Institution of Washington.

Colbert, S.R., Jokela, E.J., Neary, D.G. 1990. Effects of annual fertilization and sustained weed control on dry matter partitioning, leaf area, and growth efficiency of juvenile loblolly and slash pine. Forest Science 36:995-1014.

Cordell, S., Goldstein, G., Meinzer, F.C., Vitousek, P.M. 2001. Morphological and physiological adjustment to N and P fertilization in nutrient-limited *Meterosideros polymorpha* canopy trees in Hawaii. Tree Physiology 21:43-50.

Coyea, The historical reconstruction of growth efficiency and its relationship to tree mortality in balsam fir ecosystems affected by spruce budworm. Canadian Journal of Forest Research 24:2208-2221.

Dahms, W.G. 1973. Tree growth and water use response to thinning in a 47-year-old lodgepole pine stand. USDA Forest Service Research Note PNW-194. Pacific Northwest Forest and Range Experiment Station.

Dalla-Tea, F., Jokela, E.J. 1991. Needlefall, canopy light interception, and productivity of young intensively managed slash and loblolly pine stands. Forest Science 37:1298-1313.

Dang, Q.-L., H.A. Margolis, M. Sy, M.R. Coyea, G.J. Collatz, and C.L. Walthall. 1997. Profiles of PAR, nitrogen and photosynthetic capacity in the boreal forest: implications for scaling from leaf to canopy. Journal of Geophysical Research 102(D24):28845-28860.

Dean, T.J., Baldwin Jr., V.C. 1996. Crown management and density. In: Carter, Mason C., ed. Growing trees in a greener world: industrial forestry in the 21st century; 35th LSU forestry symposium. Baton Rouge, LA: Louisiana State University Agricultural Center, Louisiana Agricultural Experiment Station: 148-159a-e.

DeJong, T.M., Day, K.R., Johnson, R.S. 1989. Partitioning of leaf nitrogen with respect to within carbon light exposure and nitrogen availability in peach (*Prunus persica*). Trees 3:89-95.

DeJong, T.M., Doyle, J.F. 1985. Seasonal relationships between leaf nitrogen content (photosynthetic capacity) and leaf canopy light exposure in peach (*Prunus persica*). Plant, Cell, and Environment 8:701-706.

Elliott, K.J., Vose, J.M. 1995. Evaluation of the competitive environment for white pine (*Pinus strobus* L.) seedlings planted on prescribed burn sites in the southern Appalachians

Elliott, K.J., White, A.S. 1987. Competitive effects of various grasses and forbs on ponderosa pine seedlings. Forest Science 33:356-366. Forest Science 41(3):513-530.

Ellis, A.R., Hubbell, S.P., Potvin, C. 2000. In situ field measurements of photosynthetic rates of tropical tree species: a test of the functional group hypothesis. Canadian Journal of Botany 78:1336-1347.

Ellsworth, D.S., Reich, P.B. 1993. Canopy structure and vertical patterns of photosynthesis and related leaf traits in a deciduous forest. Oecologia 96:169-178.

Evans, J.R. 1989. Photosynthesis and nitrogen relationships in leaves of C_3 plants. Oecologia 78:9-19.

Evert, F. 1971. Spacing studies – a review. Canadian Forestry Service, Forest Management Institute, Information Report FMR-X-37.

Fassnacht, K.S., Gower, S.T. 1997. Interrelationships between the edaphic and stand characteristics, leaf area index, and aboveground net primary production of upland forest ecosystems in north central Wisconsin. Canadian Journal of Forest Research 27:1058-1067.

Fife, D.N., Nambiar, E.K.S. 1997. Changes in the canopy and growth of *Pinus radiata* in response to nitrogen supply. Forest Ecology and Management 93:137-152.

Gholz, H.L. 1982. Environmental limits on aboveground net primary production, leaf area, and biomass in vegetation zones in the Pacific Northwest. Ecology 53:469-481.

Gilbert, I.R., Seavers, G.P., Jarvis, P.G., Smith, H. 1995. Photomorphogenesis and canopy dynamics. Phytochrome-mediated proximity perceptions accounts for the growth dynamics of canopies of *Populus trichocarpa* x *deltoides* ‘Beaupre’. Plant, Cell and Environment 18:478-497.

Gower, S.T., Vogt, K.A., Grier, C.C. 1992. Carbon dynamics of Rocky Mountain Douglas-fir: Influence of water and nutrient availability. Ecological Monographs 62:43-65.

Grace, J.C., Jarvis, P.G., Norman, J.M. 1987. Modelling the interception of solar radiant energy in intensively managed stands. New Zealand Journal of Forestry Science 17:193-209.

Grier, C.C., Running, S.W. 1977. Leaf area of mature northwestern coniferous forests: relation to site water balance. Ecology 58:893-899.

Harms, W.R., DeBell, D.S., Whitsell, C.D. 1994. Stand and tree characteristics and stockability in *Pinus taeda* plantations in Hawaii and South Carolina. Canadian Journal of Forest Research 24:511-521.

Harms, W.R., Langdon, O.G. 1976. Development of loblolly pine in dense stands. Forest Science 22:331-337.

Harms, W.R., Whitsell, C.D., DeBell, D.S. 2000. Growth and development of loblolly pine in a spacing trial planted in Hawaii. Forest Ecology and Management 126:13-24.

Harper, J.L. 1977. Population Biology of Plants. Academic Press, New York.

Harrington, R.A., Fownes, J.H. 1995. Radiation interception and growth of planted and coppice stands of four fast-growing tropical trees. Journal of Applied Ecology 32:1-8.

Haskel, E.F. 1949. A clarification of social science. Main Currents in Modern Thoughts 7:45-51

Haynes, B.E., Gower, S.T. 1995. Belowground carbon allocation in unfertilized and fertilized red pine plantations in northern Wisconsin. Tree Physiology 15:317-325.

Helmers, A.E. 1948. Early results from thinning seed spots. USDA Forest Service Research Note 48.

Hutchings M.J., and Budd, C.S.J. 1981. Plant competition and its course through time. Bioscience 31:640-645.

Ibrahim, L., Proe, M.F., Cameron, A.D. 1997. Main effects of nitrogen supply and drought stress upon whole-plant carbon allocation in poplar. Canadian Journal of Forest Research 27: 1413-1419.

Ibrahim, L., Proe, M.F., Cameron, A.D. 1998. Interactive effects of nitrogen and water availabilities on gas exchange and whole-plant carbon allocation in poplar. Tree Physiology 18:481-487.

Jack, S.B., Long, J.N. 1991. Response of leaf area index to density for two contrasting tree species. Canadian Journal of Forest Research 21:1760-1764.

Jokela, E.J., Martin, T.A. 2000. Effects of ontogeny and soil nutrient supply on production, allocation, and leaf area efficiency in loblolly and slash pine stands. Canadian Journal of Forest Research 30:1511-1524.

Jose, S., Merritt, S., Ramsey, C.L. 2003. Growth, nutrition, photosynthesis, and transpiration responses of longleaf pine seedlings to light, water, and nitrogen. Forest Ecology and Management 180:335-344.

Keyes, M.R., Grier, C.C. 1981. Above- and below-ground net production in 40-year-old Douglas-fir stands on low and high productivity sites. Canadian Journal of Forest Research 11:533-605.

Kikuzawa, K., Umeki, K. 1996. Effects of canopy structure on degree of asymmetry of competition in two forest stands in northern Japan. Annals of Botany 77(6):565-571.

Knowe, S.A., Hibbs, D.E. 1993. Stand structure of young red alder as affected by planting density. Forest Ecology and Management 82:69-85.

Kozlowski, T.T., Kramer, P.J., Pallardy, S.G. 1991. The Physiological Ecology of Woody Plants. *In* Physiological Ecology Ed. H.A. Mooney. Academic Press, Inc., London, Great Britain. 657 p.

Landsberg, J.J., Waring, R.H. 1997. A generalized model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. Forest Ecology and Management 95:209228.

Landsberg, J.J., Wright, L.L. 1989. Comparison among *Populus* clones and intensive culture conditions, using an energy-conversion model. Forest Ecology and Management 27:129-147.

Lieffers, V.J., Mugasha, A.G., MacDonald, S.E. 1993. Ecophysiology of shade needles of *Picea glauca* saplings in relation to removal of competing hardwoods and degree of prior shading. Tree Physiology 12(3):271-280.

Long, J.N., Smith, F.W. 1984. Relation between size and density in developing stands: a description and possible mechanisms. Forest Ecology and Management 7:191-206.

Long, J.N., Smith, F.W. 1990. Determinants of stemwood production in *Pinus contorta* var. *latifolia* forests: The influence of site quality and stand structure. Journal of Applied Ecology 27:847-856.

Maier, C.A., Johnson, K.H., Butnor, J., Kress, L.W, Anderson, P.H. 2002. Branch growth and gas exchange in 13-year-old loblolly pine (*Pins taeda*) trees in response to elevated carbon dioxide concentration and fertilization. Tree Physiology 22:1093-1106.

Mann Jr., W.F., Dell, T.R. 1971. Yields of 17-year-old loblolly pine planted at a cutover site at various spacings. USDA Forest Service Research Paper SO-70. Southern Forest Experiment Station.

Marks, P.L., Bormann, F.H. 1972. Revegetation following forest cutting: mechanisms for return to steady-state nutrient cycling. Science 176:914-915.

McCrady, R.L., Jokela E.J. 1996. Growth phenology and crown structure of selected loblolly pine families planted at two spacings. Forest Science 42:46-57.

McGuire, J.P., Mitchell, R.J., Moser, E.B., Pecot, S.D., Gierstad, D.H., Hedman, C.W. Gaps in a gappy forest: plant resources, longleaf pine regeneration, understory response to tree removal in longleaf pine savannas. Canadian Journal of Forest Research 31(5):765-778.

McMurtrie, R.E., Benson, M.L., Linder, S., Running, S.W., Talsma, T., Crane, W.J.B., Myers, B.J. 1990. Water/nutrient interactions affecting the productivity of stands of *Pinus radiata*. Forest Ecology and Management 30:415-423.

Medlyn, B.E. 1998. Physiological basis of the light use efficiency model. Tree Physiology 18:167-176.

Messier, C., Parent, S., Chengaou, M., Beaulieu, J. 1999. Juvenile growth and crown morphological plasticity of eastern white pines (*Pinus strobus* L.) planted along a natural light gradient: results after six years. The Forestry Chronicle 75(2):275-279.

Moller, C. 1947. The effect of thinning, age, and site on foliage, increment, and loss of dry matter. Journal of Forestry 45:393-404.

Monteith, J.L. 1977. Climate and the efficiency of crop production in Britain. Philosophical Transactions of the Royal Society of London 281:277-294

Monteith, J.L. 1994. Validity of the correlation between intercepted radiation and biomass. Agriculture and Forest Meteorology 68:213-220.

Morris, L.A., Moss, S.A., Garbett, W.S. 1993. Competitive interference between selected herbaceous and woody plants and *Pinus taeda* L. during two growing seasons following planting. Forest Science 39:166-187.

Munger, G.T., Will, R.E., Borders, B.E. 2003. Effects of competition control and annual nitrogen fertilization on gas exchange of different-aged *Pinus taeda*. Canadian Journal of Forest Research 33:1076-1083.

Murthy, R., Dougherty, P.M., Zarnoch, S.J., Allen, H.L. 1996. Effects of carbon dioxide, fertilization, and irrigation on photosynthetic capacity of loblolly pine trees. Tree Physiology 16:537-546.

Nambiar, E.K.S., Sands, R. 1993. Competition for water and nutrients in forests. Canadian Journal of Forest Research 23:1955-1968.

Niinemets, Ü., 1997. Role of foliar nitrogen in light harvesting and shade tolerance of four temperate deciduous woody species. Functional Ecology 11:518-531.

Nilsson, U., Albrektson, A. 1993. Productivity of needles and allocation of growth in young Scots pine trees of different competitive status. Forest Ecology and Management 62:173-187.

Oliver, C.D., Larson, B.C. 1990. Forest Stand Dynamics. McGraw-Hill, Inc., New York.

Osorio, J., Osorio, M.L., Chavez, M.M., Pereira, J.S. 1998. Water deficits are more important in delaying growth than in changing patterns of carbon allocation in *Eucalyptus globulus*. Tree Physiology 18:363-373.

Pearson, J.A., Fahey, T.J., Knight, D.H. 1984. Biomass and leaf area in contrasting lodgepole pine forests. Canadian Journal of Forest Research 14:259-265.

Pearson, J.A., Knight, D.H., Fahey, T.J. 1987. Biomass and nutrient accumulation during stand development in Wyoming lodgepole pine forests. Ecology 68:1966-1973.

Phillips, J.G., Riha, S.J. 1993. Canopy development and solar conversion efficiency in *Acacia auriculiformis* under drought stress. Tree Physiology 12:137-149.

Pollack, J.P., van Theinen, F., LePage, P. 1990. The Influence of Initial Espacement on the Growth of a 27-year-old Sitka Spruce Plantation. British Columbia Ministry of Forests, Research Note 104.

Polley, H.W., Johnson, H.B., Mayeux, H.S. 1997. Leaf physiology, production, water use, and nitrogen dynamics of the grassland invader *Acacia smallii* at elevated CO_2 concentrations. Tree Physiology 17:89-96.

Portis, A.R. 1998. Rubisco. *In* Nature Encyclopedia of Life Sciences. Nature Publishing Group, London, Great Britain.

Purcell, L.C., Ball, R.A., Reaper III, J.D., Vories, E.D. 2002. Radiation use efficiency and biomass production in soybean at different population densities. Crop Science 42:172-177.

Puri, S., Singh, V., Bhushan, B., Singh, S. 1993. Biomass production and distribution of roots in 3 stands of *Populus deltoides*. Forest Ecology and Management 65:135-147.

Quicke, H., Glover, G., Glover, R. 1999. Loblolly pine growth response to herbaceous vegetation control at different planting densities. Canadian Journal of Forest Research 29:960-967.

Reich, P.B., Kloeppel, B.D., Ellsworth, D.S., Walters, M.B. 1995. Different photosynthesis-nitrogen relations in deciduous hardwood and evergreen coniferous tree species. Oecologia 104:24-30.

Richter, D.D., Markewitz, D., Heinz, P.R., Jin, V., Raikes, J., Tian, K., Wells, C.G. 2000. Legacies of agriculture and forest regrowth in the nitrogen of old-field soils. Forest Ecology and Management 138:233-248.

Ritchie, G.A. 1997. Evidence for red : far red signaling and photomorphogenic response in Douglas-fir (*Pseudotsuga menziesii*) seedlings. Tree Physiology 17:161-168.

Ryan, M.G., Binkley, D., Fownes, J.H. 1997. Age-related decline in forest productivity: Pattern and process. Advances in Ecological Research 27:213-262.

Sampson, D.A., Allen, H.L. 1998. Light attenuation in a 14-year-old loblolly pine stands as influenced by fertilization and irrigation. Trees 13:80-87.

Samuelson, L.J. 1998. Influence of intensive culture on leaf net photosynthesis and growth of sweetgum and loblolly pine seedlings. Forest Science 44:308-316.

Samuelson, L.J. 2000. Effect of nitrogen on leaf physiology and growth of different families of loblolly and slash pine. New Forests 19:95-107.

Samuelson, L.J., Stokes, T., Cooksey, T., McElmore, P. 2001. Production efficiency of loblolly pine and sweetgum in response to sour years on intensive management. Tree Physiology 21:369-376.

Sands, P.J. 1996. Modelling canopy production. III. Canopy light-utilisation efficiency and its sensitivity to physiological and environmental variables. Australian Journal of Plant Physiology 23:103-114.

Schmidt, W.C., Shearer, R.C., Roe, A.L. 1976. Ecology and silviculture of western larch forests. U.S. Department of Agriculture Technical Bulletin. 1520.

Schoettle, A.W., Smith, W.K. 1998. Interrelationships between light, photosynthesis and nitrogen in the crown of mature *Pinus contorta* ssp. *Latifolia*. Tree Physiology 19:13-22.

Scott, W., Meade, R., Leon, R., Hyink, D., Miller, R. 1998. Planting density and tree-size relations in coast Douglas-fir. Canadian Journal of Forest Research 28:74-78.

Seidel, K.W. 1984. A western larch – Engelmann spruce spacing study in eastern Oregon: results after 10 years. USDA Forest Service Research Note PNW-409. Pacific Northwest Forest and Range Experiment Station.

Shelton, M.G., 1984. Effects of the initial spacing of loblolly pine plantations on production and nutrition during the first 25 years. Ph.D. Dissertation, Mississippi State University, Starkville, MS.

Shepard, R.K. 1971. The development of loblolly pine planted at various initial spacings. Louisiana Agriculture 15:8-11.

Sinclair, P.J., Shiraiwa, T. 1993. Soybean radiation-use efficiency as influenced by non-uniform specific leaf nitrogen distribution and diffuse radiation. Crop Science 33:808-812.

Sinclair, T.R., Horie, T. 1989. Leaf nitrogen, photosynthesis, and crop radiation use efficiency: A review. Crop Science 29:90-98.

Sinclair, T.R., Muchow, R.C. 1999. Radiation use Efficiency. Advances in Agronomy 65:215-265.

Sjolte-Jorgensen, J. 1967. The influence of spacing in the growth and development of coniferous plantations. International Review of Forest Research 2:43-94.

Smethurst, P, Baillie, C., Cherry, M., Holz, G. 2002. Fertilizer effects on LAI and growth of four *Eucalyptus nitens* plantations. Forest Ecology and Management 176:531-542.

Smith, D.M., Larson, B.C., Kelty, M.J., Ashton, P.M.S. 1997. The practice of silviculture. 9th ed. John Wiley and Sons, New York.

Smith, D.M., Larson, B.C., Kelty, M.J., Ashton, P.M.S. 1997. The practice of silviculture. 9th ed. John Wiley and Sons, New York.

Smith, F.W., Long, J.N. 1989. The influence of canopy architecture on stemwood production and growth efficiency of *Pinus contorta* var. *latifolia*. Journal of Applied Ecology 26:681-691.

Tansley, A.G. 1920. The classification of vegetation and the concept of development. Journal of Ecology 8:118-149.

Teskey, R.O., Gholz, H.L., Cropper Jr., W.P. 1994. Influence of climate and fertilization on net photosynthesis of mature slash pine. Tree Physiology 14:1215-1227.

Tissue, D.T., Thomas, R.B., Strain, B.R. 1993. Long-term effects of elevated CO_2 and nutrient s on photosynthesis and rubisco in loblolly pine seedlings. Plant, Cell and Environment 16:859-865.

Turner, J., Long, J.N. 1975. Accumulation of organic matter in a series of Douglas-fir stands. Canadian Journal of Forest Research 5:681-690.

Vose, J.M., Allen, H.L. 1988. Leaf area, stemwood growth, and nutrient relationships in loblolly pine. Forest Science 34:547-563.

Walters, M.B., Reich, P.B. 1989. Response of *Ulmus americana* seedlings to varying nitrogen and water status. I. Photosynthesis and growth. Tree Physiology 5:159-172.

Wang, J.R., Hawkins, C.D.B., Letchford, T. 1998. Relative growth rate and biomass allocation of paper birch (*Betula papyrifera*) populations under different soil moisture and nutrient regimes. Canadian Journal of Forest Research 28:44-55.

Ware, L.M., Stahelin, R. 1950. Growth of southern pine plantations at various spacings. Journal of Forestry 50:267-274.

Waring, R.H. 1983. Estimating forest growth and efficiency in relation to canopy leaf area. Advances in Ecological Research 13:327-354.

Whitsell, C.D. 1974. Effects of spacing on loblolly pine planted in Hawaii after 11 years. USDA Forest Service Research Note PSW-295. Pacific Northwest Forest and Range Experiment Station.

Will, R.E., Barron, G.A., Burkes, E.C., Shiver, B., Teskey, R.O. 2001. Relationship between intercepted radiation, net photosynthesis, respiration, and rate of stem volume growth of *Pinus taeda* and *Pinus elliottii* stands of different densities. Forest Ecology and Management 154:155-163.

Will, R.E., Munger, G.T., Zhang, Y., Borders, B.E. 2002. Effects of annual fertilization and complete competition control on current annual increment, foliar development, and growth efficiency of different aged *Pinus taeda* stands. Canadian Journal of Forest Research 32:1728-1740.

Woodruff, D.R., Bond, B.J., Ritchie, G.A., Scott, W. 2002. Canadian Journal of Forest Research 32:420-427.

Xiao, Y., Jokela, E.J., White, T.L. 2003. Species differences in crown structure and growth performance of juvenile loblolly and slash pine. Forest Ecology and Management 174:295-313.

Zedaker, S.M. 1982. The competition-release enigma: adding apples and oranges and coming up with lemons. *In* Proc., Second Biennial Southern Silviculture Research Conference, Atlanta, GA. USDA Forest Service, Southeastern Forest Experiment Station, Athens, GA. Technical Report SE-24.

CHAPTER 3

MATERIALS AND METHODS

Field sites

The sites used in this study were located in the Piedmont and Upper Coastal Plain physiographic provinces of Georgia. All sites were established through a joint effort between the Plantation Management Research Cooperative (PMRC) based at the University of Georgia's Warnell School of Forest Resources, and forest industry partners. International Paper (formerly Union Camp Corporation) was responsible for the establishment of sites near Gough and Vidette (Burke County), Plum Creek Timber Co. was responsible for the establishment of the site near Union Point (Greene County), International Paper established the site near Sparta (Hancock County), and Weyerhaeuser was responsible for the Shady Dale site (Jasper County). Established in 1998, the sites comprised six plots of loblolly pine (*Pinus taeda* L.) that varied in planting density in equal increments from 740 to 4440 trees ha^{-1}. Each cooperating forest products company procured seedlings for sites in their ownership; therefore, while genetics were consistent between treatments at each study site, there were genetic differences in seedlings between most of the sites (the exception being the sites in Burke County, which were both established by Union Camp Corp.). Seedlings for the site in Greene County (Union Point, GA) were obtained from a bulk-lot-mix of several families grown in a second generation orchard operated by Plum Creek Timber Co. in the Piedmont of Georgia. These seedlings were grown from cones collected in 1992, and have moderate genetic gains for growth and rust resistance. The site in Hancock County (Sparta, GA) was stocked with 7-111 loblolly pine, while the sites in Burke County (Gough and Vidette, GA) were both stocked with 7-56 loblolly pine. Seedling genetics information was not available for the site established by Weyerhaeuser in Jasper County (Shady Dale, GA). Survival percentages ranged from a high of 100% in the 740 trees ha^{-1} treatments at Gough and Union Point and the 1480 trees ha^{-1} treatment at Sparta, to a low of 79% in the 740 trees ha^{-1} treatment at Vidette. Overall average survival rate for all sites and treatments was 96% (table 1).

The climate at all study locations typically consists of long, hot, humid summers with an average maximum July temperature of 32° C. Winters are cool and relatively short with an average minimum January temperature of 1.5° C. Average annual precipitation is approximately 1200 mm, of which about 650 mm falls between the months of April and October (table 2). Piedmont soil types were fine, kaolinitic, thermic Typic Kanhapludults or Rhodic Kandiudults, while Upper Coastal Plain soils were fine-loamy, kaolinitic, thermic Plinthic Kandiudults (table 2).

Site preparation

At planting, each site received 560 kg ha^{-1} of 10-10-10 fertilizer (56 kg ha^{-1} N). The same initial application of 560 kg ha^{-1} 10-10-10 fertilizer was again repeated one year after establishment (1999). All treatments were kept free of competing vegetation. During the early spring of the first growing season (1998), approximately 290 ml ha^{-1} of the herbicide Oust^{tm} (sulfometuron methyl, DuPont) was sprayed over the top of seedlings to control for interspecific competition. Directed spraying of non-soil active herbicides was permitted to control the establishment of hardwoods. Spring broadcast spraying of 290 ml ha^{-1} of Oust^{tm} in addition to directed sprays of Roundup^{tm} (glyphosate, Monsanto) and Garlon^{tm} (triclopyr amine, Dow

Agrosciences LLC) were applied as needed. In the fall of 2000, a mop-up application of 875 ml ha^{-1} of Arsenal^{tm} (imazapyr, BASF) was applied.

Leaf area index

Projected leaf area index (LAI) was estimated using litter trap sampling. Round traps, each 0.46 m^2 in area were placed throughout the study plots using a stratified sampling scheme designed to representatively sample areas at different distances from trees. The number of traps used varied by plot, with the greatest number of traps located in the lowest density plots to account for a greater degree of spatial heterogeneity and larger distance between trees. The plots contained 28, 14, 10, 8, 8, and 7 traps for the 740, 1480, 2220, 2960, 3700 and 4440 tree ha^{-1} plots, respectively. Litter was collected from these traps at approximately six-week intervals throughout the study period, from May 2001 to April of 2003. For each collection, leaf litter from each plot was placed into paper bags and dried at 60° C. Litterfall between May 2001 and April 2002 was used to estimate leaf area of previous-year, or 2000 age class foliage, with litterfall from May 2002 to April 2003 used to estimate current-year, or 2001 age class foliage. Specific litter area was used from measurements in loblolly pine stands of similar age and similar planting density (Burkes 2003) in the Lower Coastal Plain physiographic region of Georgia. All-sided LAI was then calculated from these data as follows:

All-sided LAI = (Specific litter area) (litter mass) (1.221) / total litter trap surface area

where the constant of 1.221 is an empirically derived correction factor to account for area shrinkage that occurs between fresh needles and those that are senesced and dried (Will et al. 2002). All-sided LAI was then converted to projected LAI by dividing by a factor of 3.14 (Grace 1987). All analyses pertaining to LAI were performed using the sum of both needle age cohorts (total projected LAI). Foliar biomass was estimated by dividing the summed mass of leaf litter by an empirically derived factor developed to account for biomass differences between fresh foliage and litter (Burkes et al. 2003). These values were then scaled to a hectare basis.

Foliar nitrogen

Foliar nitrogen concentration was estimated using a subsample of needles collected approximately every six weeks from August 2000 through April 2002. Samples comprised at least eight trees, with a separate sample taken for each combination of needle-age-class (one-year-old and current-year) and canopy position (upper, middle, and lower). Collections made prior to needle elongation in the spring consisted of only the previous year's cohort while all other collections consisted of both current-year and one-year-old foliage. Therefore, the maximum number of samples collected per plot was six (two age classes x three canopy positions). The methodology used to collect needles from each tree was intended to effectively represent the actual distribution of needles on each branch. Specifically, one, two, or three fascicles per flush were included in the sample depending on the relative length and density of flushes in each needle-age-class by canopy position combination. Canopy positions were defined as upper, middle, and lower with each position consisting of one-third the total vertical canopy height. Samples were placed in sealed plastic bags, kept chilled in a cooler, and transferred into paper bags for drying at 60° C. After drying, samples were ground using an SPEX CertiPrep 8000D Mixer/Mill (SPEX CertiPrep, Metuchen, NJ), and were analyzed for nitrogen concentration using a NA1500 C/N/H analyzer (CE Elantech Inc., Lakewood, NJ). Nitrogen concentration was scaled up to canopy nitrogen content for each needle age cohort using foliar biomass data derived from leaf litter traps. Total canopy nitrogen content was calculated as the sum of canopy nitrogen content in each foliar cohort.

PAR capture

Intercepted radiation was measured between 10:00 and 16:00 h during clear, cloud-free days using the SunScan Canopy Analysis System (Delta-T Devices Ltd., Cambridge UK). The proportion of solar radiation intercepted by the canopies in each plot was determined by comparing the amount of solar radiation measured within the canopy to measurements of solar radiation recorded in a clearing. To measure solar radiation under the canopy, seventy subsamples were measured in each plot using a spatially random sampling strategy to account for heterogeneity of leaf display. Intercepted radiation was measured a total of seven times from August 2000 and April 2002, with five of the sampling sessions taking place between January 2001 and January 2002. Percent intercepted radiation was corrected to a constant sun angle of 30° from zenith using spacing-specific, empirically derived relationships between sun angle and intercepted radiation to facilitate comparison between plots and between sites. This value (30° from zenith) was chosen for two reasons: (1) for the latitudes of these study sites, a large proportion of annual solar radiation that reaches the earth generally occurs with the sun at approximately 30° from zenith, and (2) at sun angles closer to zenith (<45°) there is less variation in incident solar radiation with incremental changes in sun angle.

To estimate annual PAR capture, percent intercepted radiation data was first interpolated between the seven collection dates assuming a constant rate of change between consecutive sampling dates. Next, total incident radiation estimates for these sites were obtained through the National Solar Radiation Database (Renewable Resource Data Center, U.S. Department of Energy) using a representative location and year (Augusta GA, 1975). Incident radiation values for this location and year were chosen based on similarities in average weather conditions (cloudy vs. cloudless days, mean annual temperature, precipitation) between Augusta, 1975 and the study sites in 2001. Total incident radiation was converted to PAR using a conversion factor of 0.5 (Monteith 1970, Cannell 1989). Total incoming PAR was then multiplied by the daily proportion of radiation intercepted by stands, normalized to a 30^{o} sun angle. The resulting estimates of daily PAR capture were summed for all days between January 1, 2001 and January 1, 2002, providing an estimate of total PAR absorbed by the canopy in each study plot for the year.

Stem volume growth

Stem taper was measured on a random sample of at least 10 trees per plot during the winter of 2000/2001 and again in early spring of 2002. Taper was determined by measuring stem diameter at breast height (DBH), and at one-meter increments starting from the base of the stem to the top of each tree. Stem volume was estimated assuming a series of stacked geometrical frustums from the base to the terminus, with the terminal section of the stem represented by a geometrical cone. Regression equations developed from taper data to predict stem volume using DBH were not significantly different between treatments, but did differ between sites. Therefore, site-specific regression equations were used to predict stem volume. Volume growth during the 2001 growing season was estimated using the change in plot volume between dormant seasons.

Statistical analysis

All analyses were performed using the SAS statistical software package (SAS Institute Inc., Cary, NC). LAI, annual PAR capture, previous- and current-year foliar nitrogen concentration (separately by cohort), and total canopy nitrogen content were each analyzed for density effects using ANOVA. Each response variable was analyzed using a randomized complete block design where site was a replicate (blocking variable), and planting density the treatment effect. For proportion of intercepted radiation, sampling date was also included as a factor. These analyses were performed using a blocked split-plot design where site served as the blocking variable, density the whole-plot effect, and sampling date the sub-plot effect. For nitrogen concentration, each year class of needles was analyzed separately with data analyzed with a split-split plot design using site (block), density treatment (whole-plot factor), canopy position (split-plot factor), and date (split-split plot factor). Regression analysis was used to determine the strength and nature of correlations between each response variable and the rate of stem growth. Relationships were tested for both linear and quadratic components, with the most appropriate regression used to fit the data.

Table 1. Percent of targeted planting density realized at each study site and for each planting density treatment after the fourth growing season.

Planting density (trees ha^{-1})	Gough	Sparta	Shady Dale	Union Point	Vidette
740	100%	88%	98%	100%	79%
1480	99%	100%	99%	99%	95%
2220	93%	97%	99%	97%	93%
2960	99%	98%	98%	98%	93%
3700	99%	95%	96%	99%	97%
4440	99%	97%	96%	95%	93%

Overall survival: 96%

Table 2. Location of study sites in Georgia (latitude and longitude, county), mean annual precipitation (mm), soil series, and physiographic province. Source for precipitation data is USDA Forest Service 20 km grid GIS (Northeastern Research Station). Soil series and physiographic province data is from the USGS State Soil Geographic (STATSGO) database.

Study site	Latitude	Longitude	County	Mean annual precipitation (mm)	Soil series	Physiographic province
Gough	33˚ 6’	82˚ 13’	Burke	1165	Tifton-Dothan-Grady[1]	Vidalia Uplands - Upper Coastal Plain
Sparta	33˚ 17’	83˚ 0’	Hancock	1202	Cecil-Madison-Pacolet[2]	Washington Slope -Piedmont
Shady Dale	33˚ 24’	83˚ 43’	Jasper	1210	Madison-Davidson-Pacolet[3]	Washington Slope -Piedmont
Union Point	33˚ 37’	83˚ 5’	Greene	1233	Cecil-Madison-Pacolet[2]	Washington Slope - Piedmont
Vidette	33˚ 0’	82˚ 14’	Burke	1167	Tifton-Dothan-Grady[1]	Vidalia Uplands - Upper Coastal Plain

[1] Fine-loamy, kaolinitic, thermic Plinthic Kandiudults
[2] Fine, kaolinitic, thermic Typic Kanhapludults
[3] Fine, kaolinitic, thermic Rhodic Kandiudults

CHAPTER 4

RESULTS

At the end of the fourth growing season (2001), overall average tree height was 5.1 m, with an average DBH of 7.5 cm and an average stand basal area of 10.5 m^2 ha^{-1} (table 3). Total mean standing stemwood volume was 35.5 m^3 ha^{-1}. Planting density had no significant effect on tree height ($p=0.91$), but did have a significant effect on DBH ($p<0.0001$) with mean stem DBH decreasing from 9.1 to 6.3 cm as density increased from 740 to 4440 trees ha^{-1}. Stand basal area increased significantly with planting density ($p<0.0001$) from 5.0 to 14.5 m^2 ha^{-1} in the least to most dense stands, respectively. Total mean standing stem volume was similarly affected by planting density ($p<0.0001$), with total standing stem volume increasing from 15.9 to 49.4 m^3 ha^{-1}, going from the least dense to most dense stands. Stem volume growth (current annual increment) during the 2001 growing season was 26.1 m^3 ha^{-1} y^{-1}, increasing from 12.0 to 35.2 m^3 ha^{-1} y^{-1} in the lowest to highest density treatments, respectively. Although stem growth increased with planting density, the rate of increase was not proportional (figure 1), resulting in a curvilinear relationship. This relationship had both a significant linear ($p<0.0001$) and quadratic ($p=0.02$) component, with a quadratic relationship explaining a larger degree of variation in stem growth ($r^2=0.84$) than a linear relationship ($r^2=0.79$). The increases in stem growth between each successive increase in density were 8.5, 4.4, 5.8, 2.4, and 2.1 m^3 ha^{-1} y^{-1}, respectively. The successively smaller increases in stem volume growth rate with increasing density suggests that as planting density increased, some resource, or combination of resources, was becoming limiting.

Previous-year foliar nitrogen concentration was significantly affected by canopy position ($p=0.0005$, table 4), with significantly greater nitrogen concentrations in the lower canopy compared to the middle or upper canopy. Nitrogen concentration in the lower, middle, and upper thirds of the canopy averaged 13.0, 12.4, and 12.5 mg g^{-1}, respectively (table 4). Current-year foliage was also significantly affected by canopy position ($p<0.0001$, table 4), with nitrogen concentrations increasing in roughly equal increments from 13.7 mg g^{-1} in the lower canopy to 15.7 mg g^{-1} in the upper canopy, a pattern that was reversed from that of the previous-year foliar cohort. For both cohorts, nitrogen concentration varied by sampling date ($p<0.0001$), with no significant interactions between date and canopy position ($p>0.10$).

Foliar nitrogen concentration in the previous-year needle age class was not significantly affected by density ($p =0.25$), and averaged 12.6 mg g^{-1} (table 5). Average nitrogen concentration in current-year foliage was 14.7 mg g^{-1}, and was significantly affected by density ($p=0.01$, table 5), decreasing from 15.3 to 13.9 mg g^{-1} in the least to most dense stands, respectively. The effects of density on current-year foliar nitrogen concentration, however, depended on canopy position (canopy position x density interaction $p=0.01$). When analyzed separately, density significantly affected nitrogen concentration in both the middle and lower portions of the canopy ($p=0.006$, and 0.0007), but had no effect on foliar nitrogen concentrations in the upper canopy ($p=0.39$, table 4).

Mean canopy nitrogen content (sum of previous-year and current-year foliage) was 100.9 kg ha^{-1} (table 5), and increased significantly from 67.0 to 107.3 kg ha^{-1} ($p<0.0001$) as density increased from 740 to 4440 trees ha^{-1}. However, given that foliar nitrogen concentration was either not affected (previous-year) or decreased (current-year) with increasing density, the significant positive response of canopy nitrogen content to increasing density was primarily driven by increases in stand-level foliar biomass. Total foliar biomass (sum of previous-year and current-year foliage) averaged 7311 kg ha^{-1}, and increased significantly from 4607 to 8146 kg ha^{-1} in the least to most dense stands, respectively ($p<0.0001$, table 5). On a per tree basis, however, both foliar biomass ($p<0.0001$) and nitrogen content ($p<0.0001$) decreased significantly with density. Foliar biomass decreased from a high of 6.23 kg tree^{-1} in the 740 trees ha^{-1} treatment to a low of 1.83 kg tree^{-1} in the 4440 trees ha^{-1} treatment. Likewise, nitrogen content per tree decreased from 92 g N tree^{-1} in the 740 trees ha^{-1} treatment to 24 g N tree^{-1} in the 4440 trees ha^{-1} treatment. Mean projected LAI (sum of previous-year and current-year foliage) averaged 4.00 across all densities, and was likewise significantly affected by planting density ($p<0.0001$), increasing from 2.52 to 4.46 in the least to most dense stands, respectively (table 5).

During the 2001 growing season, an average of 64% of incoming PAR (normalized to 30° sun angle) was intercepted by the canopies across all density treatments (table 5). The percentage of radiation intercepted by stands increased significantly with planting density ($p<0.0001$) from a seasonal average of 30% in the least dense stands to an average of 81% in the most dense stands. The percentage of radiation intercepted by the stands also differed significantly with sampling date ($p<0.0001$), averaging 54% and 73% of intercepted PAR for the first and last measurement dates of the 2001 growing season, respectively (figure 2). As the growing season progressed, there was a convergence in the proportion of radiation intercepted by the canopy in higher densities; however, the interaction between density and date was not significant ($p=0.10$).

Annual PAR capture had a mean value of 1852 MJ m^{-2} y^{-1}, and responded significantly to planting density ($p<0.0001$, table 5), increasing from 863 to 2345 MJ m^{-2} y^{-1} as density increased. Although both LAI and annual PAR capture increased significantly with density, increases were not proportional (figures 3 and 4). Both linear and quadratic components of the relationship between LAI and density were significant ($p=0.0003$, $p=0.0064$) and a quadratic relationship exhibited a lesser degree of unexplained variation ($r^2=0.62$) than did a linear relationship ($r^2=0.50$). Similarly the relationship between annual PAR capture and density had both a significant linear ($p<0.0001$) and quadratic ($p=0.0002$) component. Again, the quadratic relationship provided a better fit to the data ($r^2=0.85$) than did a linear relationship ($r^2=0.74$). The curvilinear relationships between LAI and density, and annual PAR capture and density, suggest the onset of treatment-induced limitations to LAI resulting in subsequent restrictions to annual PAR capture. The relationship between LAI and annual PAR capture was linear ($p<0.0001$, $r^2=0.69$; figure 5), indicating that self shading at higher leaf areas was not a factor in limiting the efficiency of PAR capture per unit LAI. When this relationship was examined further for density effects, PAR capture per unit LAI was found to increase significantly with density ($p=0.003$, figure 6), from 350 PAR LAI^{-1} (MJ m^{-2} y^{-1}) in the 740 trees ha^{-1} treatment to 532 PAR LAI^{-1} (MJ m^{-2} y^{-1}) in the 4440 trees ha^{-1} treatment.

Growth efficiency (stem growth LAI^{-1}), nitrogen-use efficiency (stem growth kg leaf N^{-1}), and radiation-use efficiency (stem growth PAR^{-1}) were each calculated on a stem volume (CAI) basis (table 6). Growth efficiency averaged 6.4 m^3 LAI^{-1}, and increased significantly with density from 4.8 to 8.0 m^3 LAI^{-1} ($p=0.003$). Nitrogen-use efficiency (NUE) also exhibited a positive response to planting density ($p=0.001$), increasing from 0.18 to 0.33 m^3 kg leaf N^{-1} with increasing density. As with canopy nitrogen content, the significant response of NUE to density was driven primarily by increases in foliar biomass and leaf area, rather than actual effects of foliar nitrogen status. Radiation-use efficiency (ε) was not significantly affected by planting density ($p=0.09$), and averaged 1.40 cm^3 MJ^{-1} over all treatments.

In all analyses for significant relationships between stem growth rate and measured variables, linear regression was used. The decision to employ linear regression analysis was based on results of significance tests of slope ($p<0.05$), and from evidence published in the literature (e.g. Monteith 1977, Landsberg and Waring 1997, Will et al. 2001, Barron-Gafford et al. 2003, Burkes et al. 2003). For canopy variables that were significantly related to stem growth rate, previous-year foliar nitrogen concentration, canopy nitrogen content (sum of previous-year and current-year foliage), leaf area index (sum of previous-year and current-year foliage), and annual PAR capture, there were no significant differences in slopes between sites. Growth was not significantly correlated to current-year foliar nitrogen concentration ($p=0.07$). Although the slope of the relationship between previous-year foliar nitrogen concentration and stem growth exhibited a significant negative relationship ($p=0.01$), there was a large amount of unexplained residual variation ($r^2=0.21$). Canopy nitrogen content was also significantly related to growth ($p<0.0001$), however as discussed, the relationship was a function of leaf area and biomass rather than of nitrogen status. This is evidenced by the fact that growth was better correlated to LAI ($p<0.0001$, $r^2=0.67$; figure 7) than to canopy nitrogen content ($r^2=0.55$, figure 8). Overall, stem growth was best correlated to annual PAR capture ($r^2=0.90$, figure 9). The strength of the relationships between growth and LAI, and growth and PAR capture suggests that these variables were of primary importance in controlling stem productivity in these stands.

Table 3. Mean diameter at breast height (DBH), tree height, stand basal area, standing stem volume, and current annual increment for each density treatment at the end of the fourth growing season. Values in parentheses represent standard error of the mean. Means in the same column with the same letter are not significantly different. (Duncan's multiple range test; $p<0.05$, $n=5$).

Planting density (trees ha^{-1})	DBH (cm)	Height (m)	Basal area (m^2 ha^{-1})	Standing stem volume (m^3 ha^{-1})	Current annual increment (m^3 ha^{-1} y^{-1})
740	9.1^a (0.56)	5.2 (0.31)	5.0^a (0.58)	15.9^a (1.80)	12.0^a (1.03)
1480	8.2^b (0.27)	5.1 (0.20)	8.0^b (0.49)	27.2^b (1.83)	20.5^b (1.00)
2220	7.4^c (0.25)	5.1 (0.27)	10.0^c (0.65)	33.1^c (2.22)	24.9^c (1.18)
2960	7.1^{cd} (0.27)	5.2 (0.22)	12.3^d (0.92)	41.8^d (3.72)	30.6^d (2.17)
3700	6.6^{de} (0.28)	5.1 (0.27)	13.2^d (1.07)	45.5^{de} (4.68)	33.1^{de} (2.57)
4440	6.3^e (0.21)	5.1 (0.22)	14.5^e (0.91)	49.4^e (4.00)	35.2^e (1.94)
Average:	**7.5**	**5.1**	**10.5**	**35.5**	**26.1**

Table 4. Mean nitrogen concentration (foliar [N]) for both previous and current-year foliage for each density treatment by canopy position. Values in parentheses represent the standard error of the mean. Means in the same column with the same letter are not significantly different (Duncan's multiple range test; $p<0.05$, n=5).

Planting density (trees ha^{-1})	Foliar [N] (mg g^{-1}) Previous-year			Current-year		
	Upper (p = 0.06)	Middle (p = 0.86)	Lower (p = 0.11)	Upper (p = 0.39)	Middle (p = 0.006)	Lower (p = 0.0007)
740	13.0 (0.36)	12.7 (0.42)	13.3 (0.23)	15.6 (0.89)	15.4^{a} (0.40)	15.0^{a} (0.31)
1480	12.0 (0.36)	12.4 (0.31)	13.1 (0.30)	15.8 (0.69)	14.9^{ab} (0.30)	14.3^{ab} (0.26)
2220	12.7 (0.50)	12.4 (0.29)	13.2 (0.57)	15.7 (0.25)	14.6^{bc} (0.36)	13.7^{bc} (0.48)
2960	12.4 (0.24)	12.7 (0.19)	13.1 (0.15)	16.3 (0.55)	15.0^{ab} (0.55)	13.7^{bc} (0.33)
3700	12.6 (0.52)	12.3 (0.56)	12.6 (0.43)	15.9 (0.31)	14.6^{bc} (0.31)	12.9^{c} (0.50)
4440	12.2 (0.49)	12.2 (0.47)	12.5 (0.43)	15.1 (0.18)	13.9^{c} (0.11)	12.8^{c} (0.33)
Average:	**12.5**	**12.4**	**13.0**	**15.7**	**14.7**	**13.7**

Table 5. Foliar nitrogen concentration (foliar [N]), canopy nitrogen content, foliar biomass, projected leaf area index (LAI), and photosynthetically active radiation (PAR) measured during the fourth growing season reported for each density treatment. Planting density had a significant effect ($p<0.05$) on all variables except for previous-year foliar [N]. Values in parentheses represent the standard error of the mean. Means in the same column with the same letter are not significantly different (Duncan's multiple range test; $p<0.05$, $n=5$).

Planting density (trees ha^{-1})	Previous-year foliar [N] (mg g^{-1})	Current-year foliar [N] (mg g^{-1})	Total canopy N content (kg ha^{-1})	Total foliar biomass (kg ha^{-1})	Total projected LAI (m^{2} m^{-1})	Mean PAR (Proportion)	Annual PAR capture (MJ m^{-2} y^{-1})
740	13.0 (0.32)	15.3^{a} (0.45)	67.0^{a} (9.1)	4607^{a} (357.6)	2.52^{a} (0.32)	0.30^{a} (0.03)	863^{a} (86.9)
1480	12.5 (0.31)	15.0^{ab} (0.36)	91.5^{b} (8.1)	6550^{b} (527.9)	3.58^{b} (0.29)	0.55^{b} (0.04)	1568^{b} (119.3)
2220	12.7 (0.44)	15.0^{ab} (0.23)	102.2^{bc} (9.9)	7394^{bc} (396.5)	4.05^{bc} (0.40)	0.66^{c} (0.04)	1887^{c} (127.1)
2960	12.7 (0.17)	14.7^{bc} (0.44)	114.7^{cd} (8.7)	8154^{cd} (425.6)	4.46^{cd} (0.28)	0.75^{d} (0.03)	2181^{d} (98.8)
3700	12.5 (0.45)	14.4^{cd} (0.09)	122.7^{d} (3.9)	9016^{cd} (321.4)	4.93^{d} (0.14)	0.78^{de} (0.04)	2270de (113.9)
4440	12.3 (0.44)	13.9^{d} (0.19)	107.3^{bcd} (5.3)	8147^{d} (235.9)	4.46^{cd} (0.28)	0.81^{e} (0.03)	2345^{e} (87.2)
Average:	**12.6**	**14.7**	**100.9**	**7311**	**4.00**	**0.64**	**1852**

Table 6. The effects of density on growth efficiency, nitrogen-use efficiency, and radiation-use efficiency for the fourth growing season calculated on a current annual increment (CAI) basis. Growth efficiency is the ratio of CAI to leaf area index, nitrogen-use efficiency is the ratio of CAI to canopy nitrogen content, and radiation-use efficiency is the ratio of CAI (in cm^3) to annual PAR capture. Values in parentheses represent the standard error of the mean. Means in the same column with the same letter are not significantly different. (Duncan's multiple range test; $p<0.05$).

Planting density ($trees\ ha^{-1}$)	Growth efficiency ($m^3\ LAI^{-1}$)	Nitrogen-use efficiency ($m^3\ kg\ N^{-1}$)	Radiation-use efficiency ($cm^3\ MJ^{-1}$)
	($p = 0.003$)	($p = 0.001$)	($p = 0.09$)
740	4.8^{a}	0.18^{a}	1.39
1480	5.7^{ab}	0.22^{ab}	1.31
2220	6.2^{b}	0.24^{ab}	1.32
2960	6.9^{bc}	0.27^{b}	1.40
3700	6.7^{bc}	0.27^{b}	1.46
4440	8.0^{c}	0.33^{c}	1.50
Average:	**6.4**	**0.25**	**1.40**

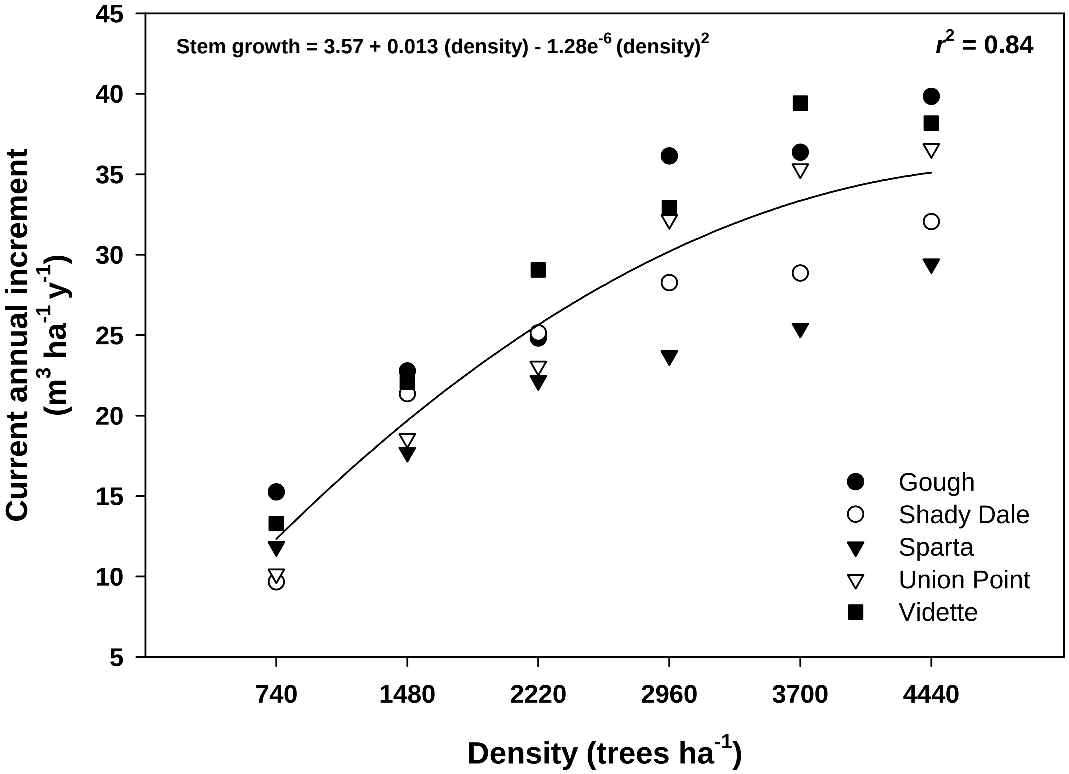

Figure 1. Quadratic regression representing the curvilinear relationship between planting density treatment and current annual increment during the fourth growing season. Symbols represent different sites (blocks).

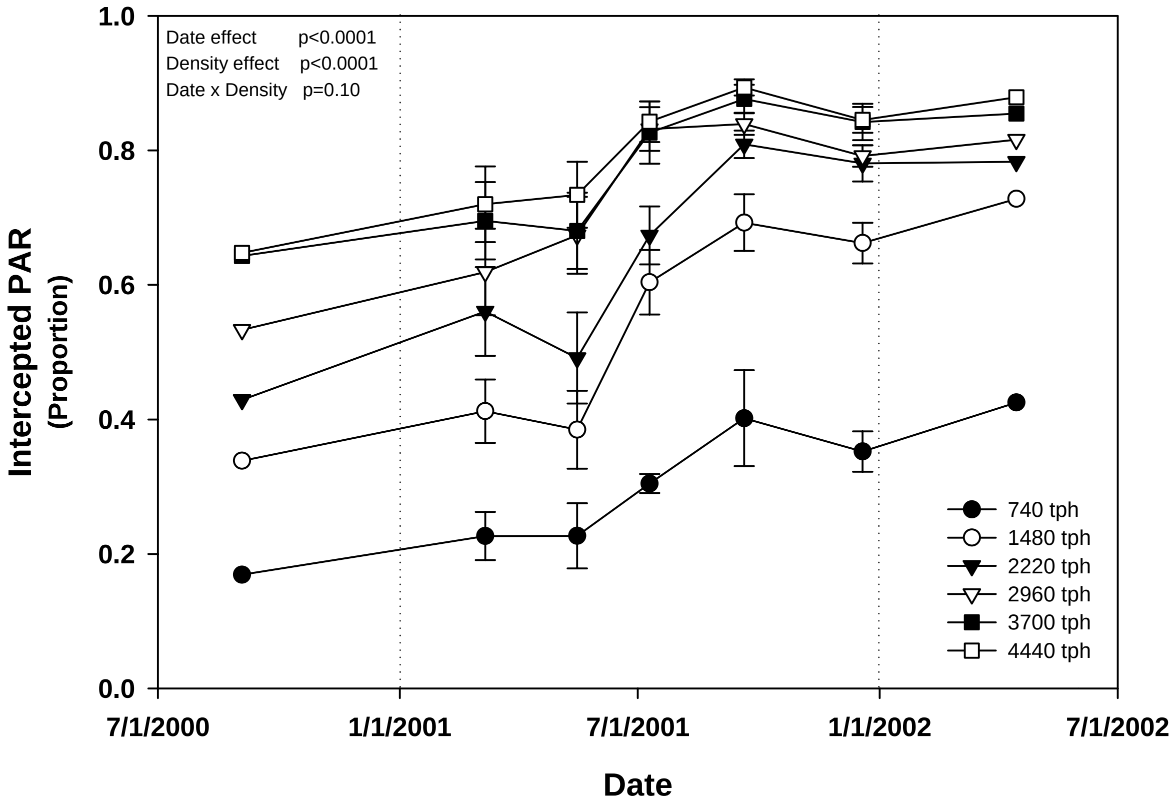

Figure 2. Proportion of photosynthetically active radiation (PAR) intercepted by stands over seven rounds of data collection. The vertical dotted lines demarcate the 2001 growing season. Symbols represent different planting density treatments. Error bars represent the standard error of the mean.

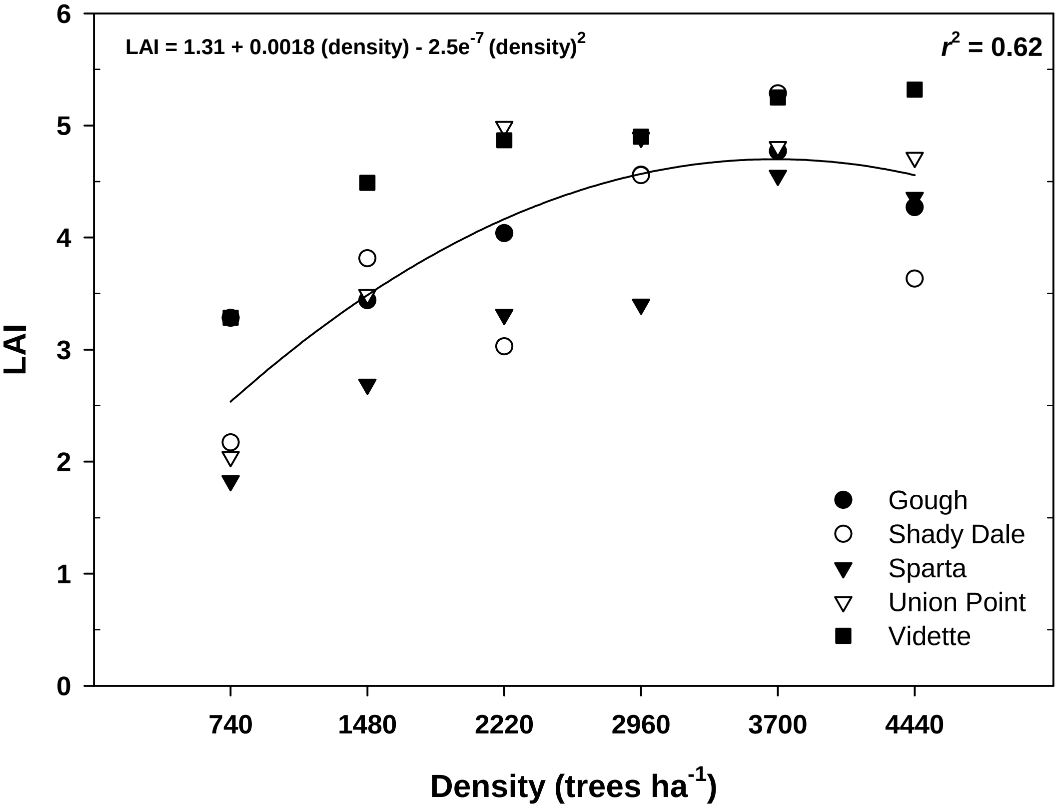

Figure 3. Quadratic regression representing the curvilinear relationship between planting density treatment and projected leaf area index (LAI) in the fourth growing season. Symbols represent different sites (blocks).

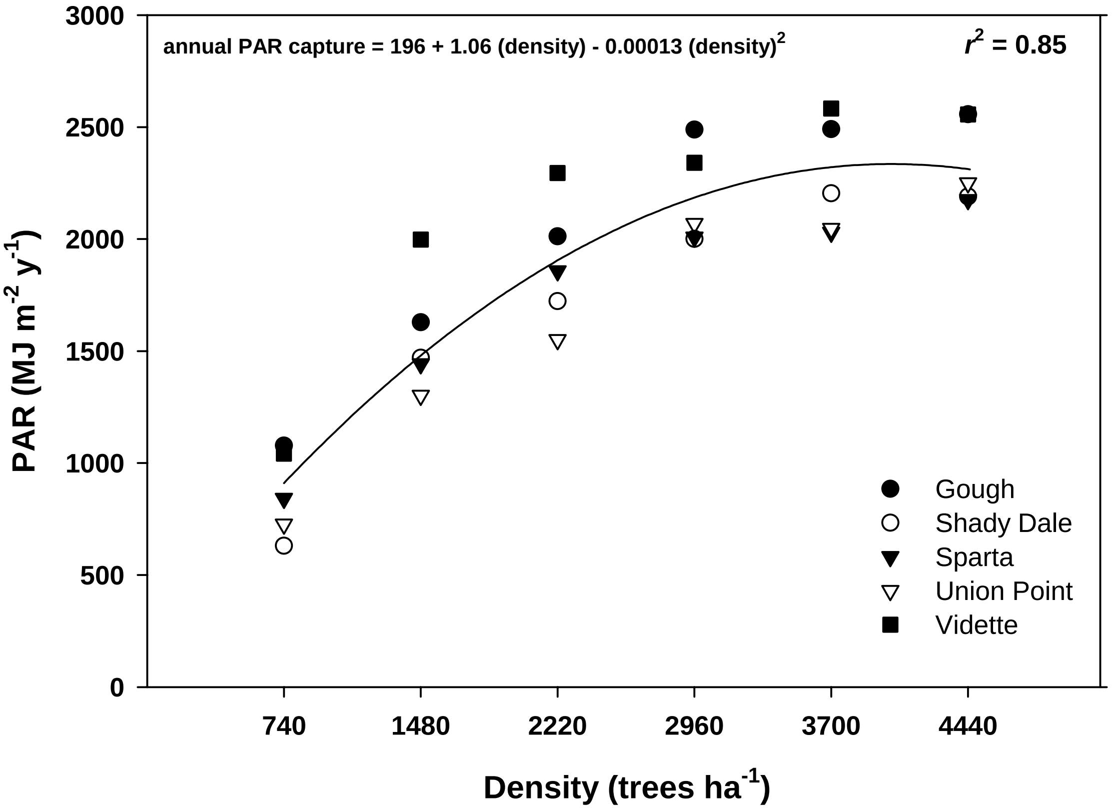

Figure 4. Quadratic regression representing the relationship between planting density treatment and annual PAR capture during the fourth growing season. Symbols represent different sites (blocks).

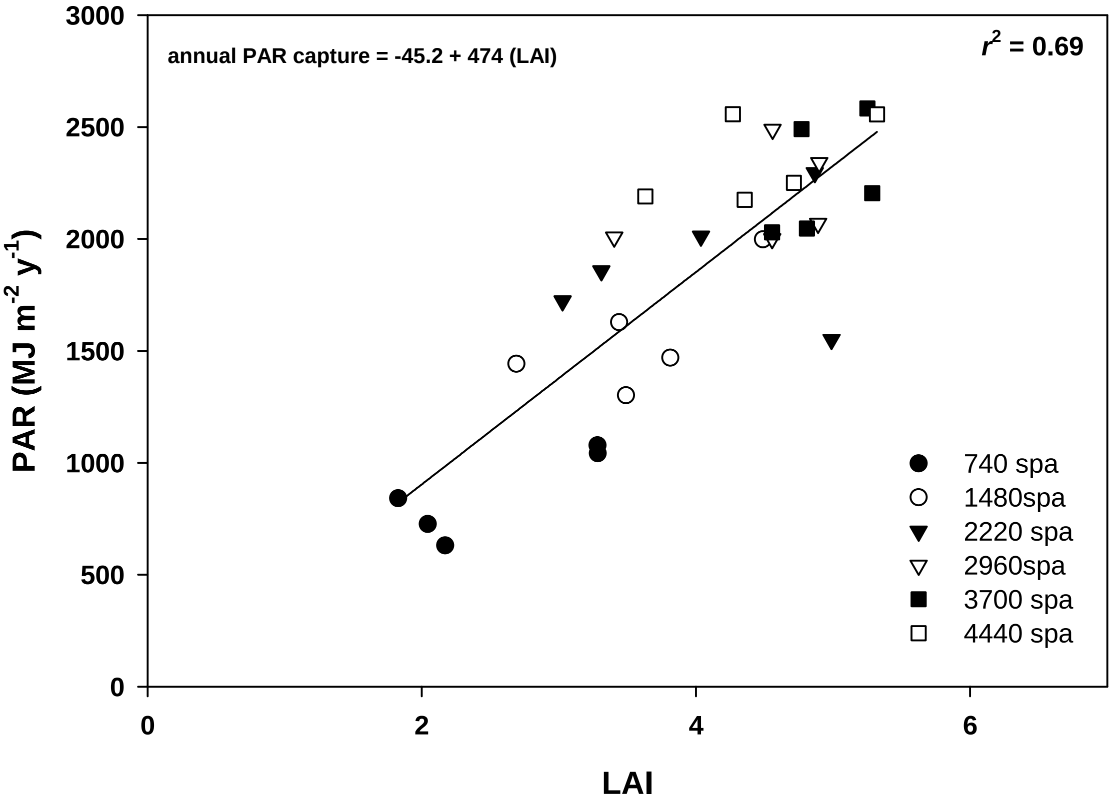

Figure 5. Linear regression representing the relationship between projected leaf area index and annual PAR capture during the fourth growing season. Symbols represent different planting density treatments.

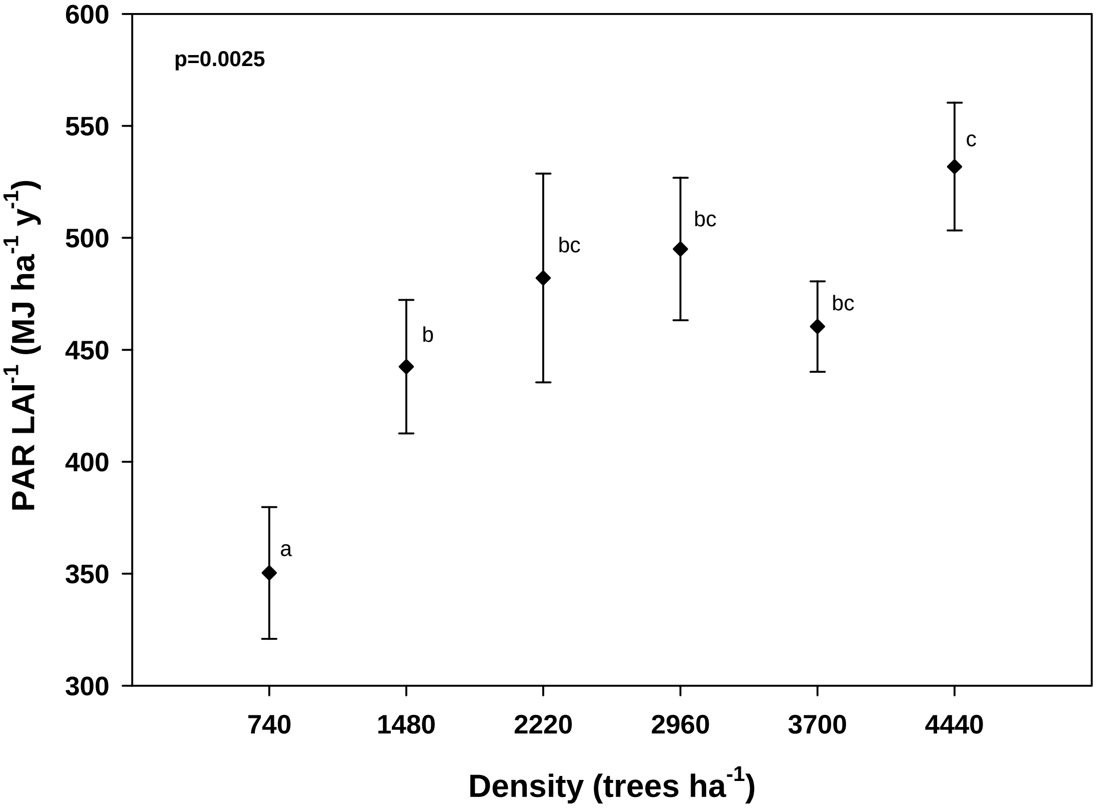

Figure 6. The effects of increasing planting density on the ratio of annual photosynthetically active radiation (PAR) capture to projected leaf area index (LAI). Error bars represent the standard error of the mean. Means with the same letter are not significantly different (Duncan's multiple range test; $p<0.05$).

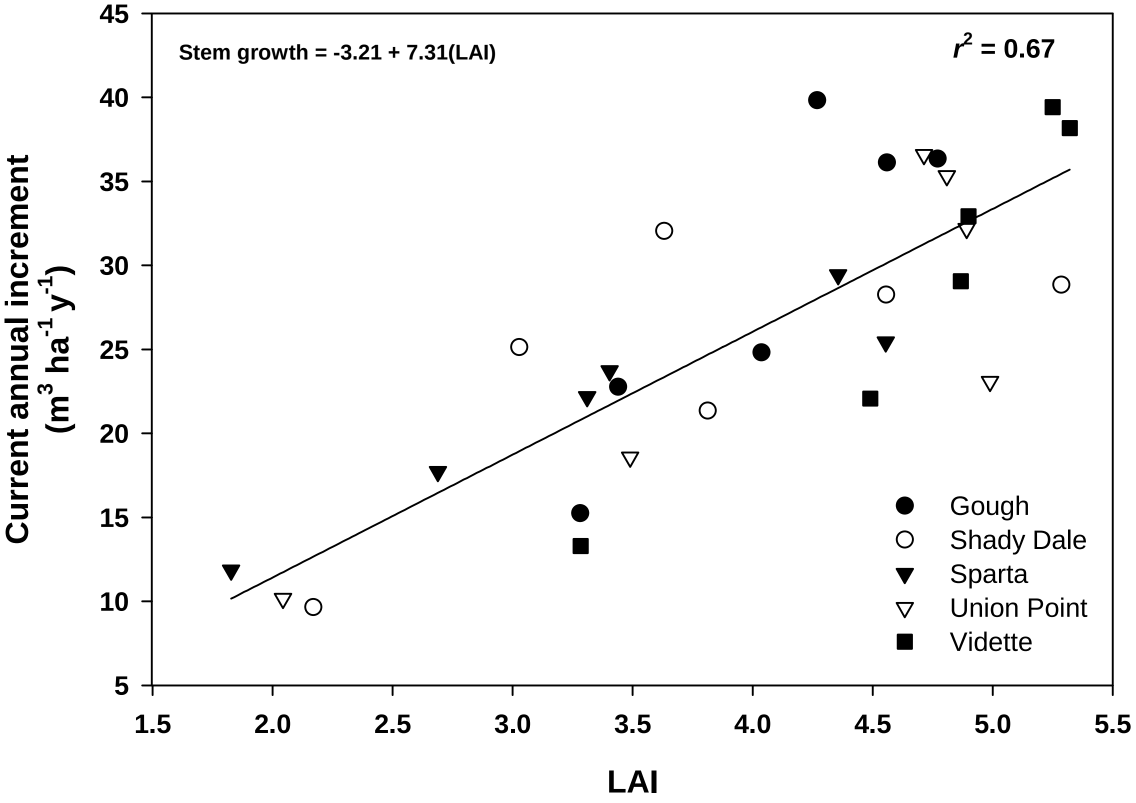

Figure 7. Linear regression representing the relationship between projected leaf area index (LAI) and current annual increment during the fourth growing season. Symbols represent different sites (blocks).

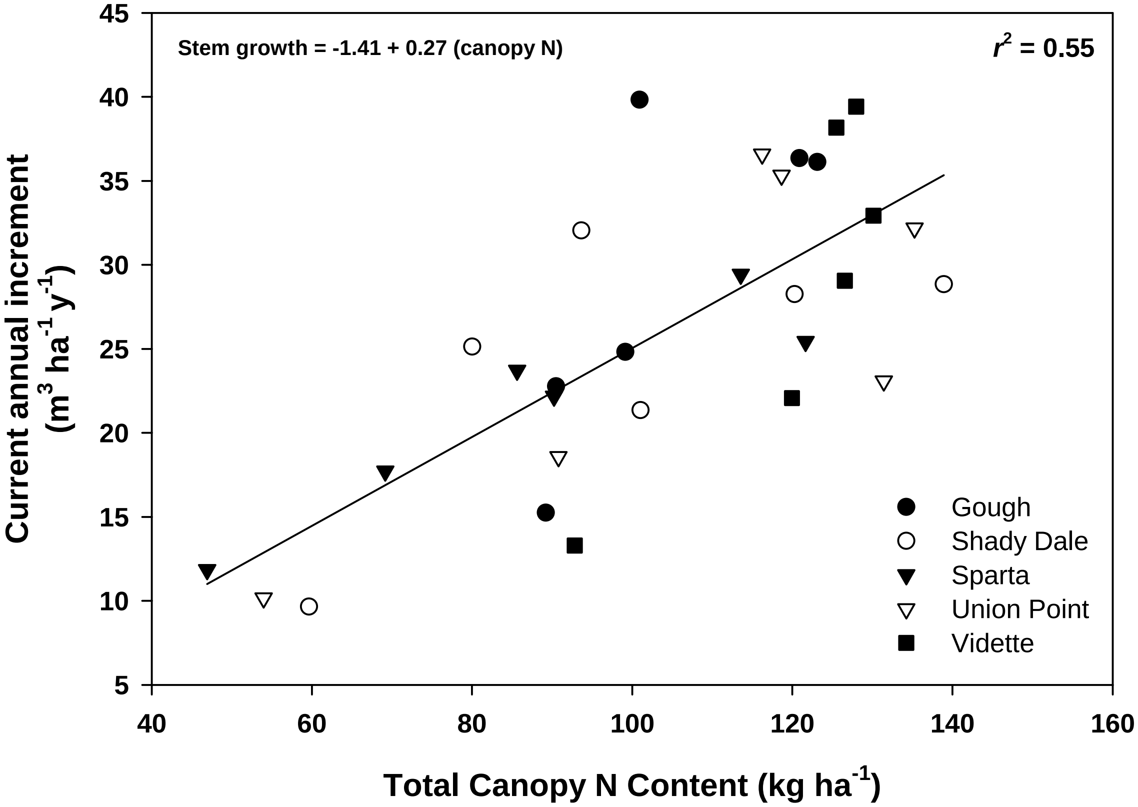

Figure 8. Linear regression representing the relationship between total canopy nitrogen content and current annual increment during the fourth growing season. Symbols represent different sites (blocks).

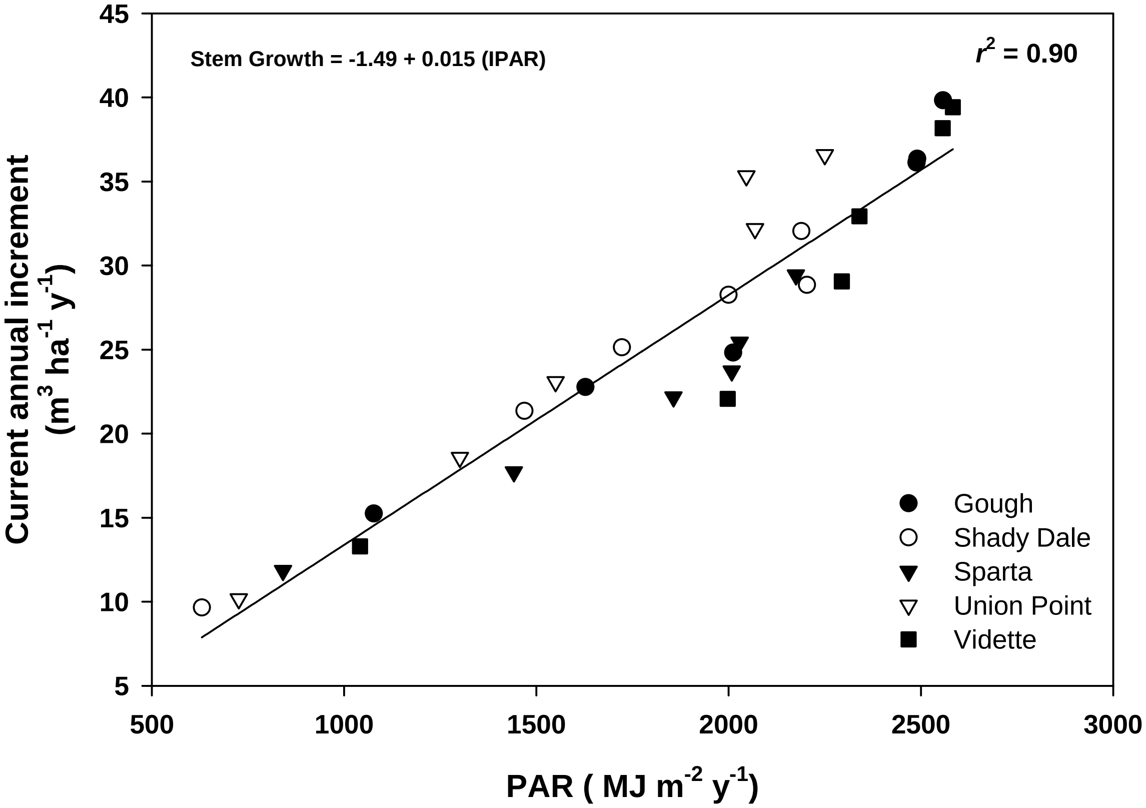

Figure 9. Linear regression representing the relationship between annual photosynthetically active radiation (PAR) capture and current annual increment during the fourth growing season. Symbols represent different sites (blocks).

CHAPTER 5

DISCUSSION

The effect of planting density on tree height and mean stem DBH in our study was consistent with the majority of the literature (e.g., Ware and Stahelin 1950, Sjolte-Jorgenson 1967, Dahms 1973, Schmidt et al. 1976, Seidel 1984, Evert 1971, Shepard 1971, Whitsell 1974, Balmer 1975, Harms and Langdon 1976, Pollack et al. 1990, Harms et al. 1994, Clark et al. 1994, Smith et al. 1997, Harms et al. 2000, Burkes et al. 2003). These studies show that as stand density increases, individual tree growth decreases due to the high level of intraspecific competition for resources (e.g., light, water, nutrients, growing space, etc.) in more dense stands. Specifically, these studies indicate that tree height is largely insensitive to density whereas diameter growth displays a significant inverse relationship with density (e.g., Lanner 1985, Harms et al. 2000, Burkes et al. 2003). For example, a study that quantified spacing effects on the growth and development of loblolly pine (*Pinus taeda* L.) in Hawaii showed no significant height response to spacing throughout the 34-year study period (Harms et al. 2000). However, the study indicated that as early as four years into stand development the widest spacings (3.7 m) had mean stem diameters (DBH) that were 18% larger than the closest spaced treatments (1.8 m). In the nine-year period between stand ages 11 and 20, trees in the 3.7 m spacing grew 7.0 cm in diameter, compared to 4.4 cm in trees in the 1.8 m spacing, a difference of 59% in growth (Harms et al. 2000). In our study, there was a 44% increase in mean stem DBH between the least and most dense stands after the fourth year of growth. The variation between the 18% difference in DBH in the study by Harms et al. and our 44% difference can be attributed to a greater difference in density between the least and most dense stands in our study compared to their study (4440 trees ha^{-1} vs. 2200 trees ha^{-1}). In a study of four-year old loblolly pine stands (*Pinus taeda* L.) of different planting densities in the Lower Coastal Plain of Georgia, mean DBH in the least dense stands (740 trees ha^{-1}) was 35% greater than DBH in the most dense stands (4440 trees ha^{-1}) (Burkes et al. 2003, Barron-Gafford et al. 2003).

There are a few studies on very young forest plantations that show positive relationships between mean stem DBH, tree height, and density (Helmers 1948, Cameron et al. 1989, Gilbert et al. 1995, Knowe and Hibbs 1996, Ritchie 1997, Scott et al. 1998, Woodruff et al. 2002). Woodruff et al. (2002) found that for young Douglas-fir seedlings (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) grown at initial planting densities of 300, 1360, and 2960 trees ha^{-1}, both diameter and height increased with density through the fourth growing season, with the greatest positive correlations between growth and density occurring in the second and third growing seasons. However, as is the case with most of the research that report similar early relationships, the positive effect of density on individual tree size did not last. By the seventh year, the positive response of growth to planting density had changed to a negative response, so that by then, the greatest diameter increments were occurring in the least dense stands (Woodruff et al. 2002). As Woodruff et al. (2002) suggest, this inversion in growth response to density over time could be attributed to a mechanism that functions only in the very early stages of seedling growth. It is also possible that this mechanism is still functioning when stands are older, but is overshadowed by the deleterious effects of increasing intraspecific competition on individual tree growth (Woodruff et al. 2002).

The majority of the literature indicates, as does our study, that despite the decline in productivity of individual trees with increasing planting density in developing stands, there is an overall increase in total stand volume and stand basal area (Ware and Stahelin 1950, Mann and Dell 1971, Whitsell 1974, Balmer et al. 1975, Harms et al. 1994, Quicke et al. 1999, Harms et al. 2000, Burkes et al. 2003). This can be attributed to a greater number of trees per hectare in high-density stands relative to low-density stands, and the associated capacity of more trees per unit area to acquire and use a greater proportion of available resources. In a study by Quicke et al. (1999), mean stand basal area and mean standing stemwood volume of loblolly pine stands under complete competition control showed significant positive growth responses to initial density. With an increase in density from 800 to 2200 trees ha^{-1}, basal area and standing stemwood volume was 150% and 93% greater in the higher density stands, respectively, after five years of growth (Quicke et al. 1999). Likewise, in the previously cited study by Harms et al. (2000), after four years of growth, basal area and standing stemwood volume increased by 181% and 275%, respectively as planting density increased from 725 to 1585 trees ha^{-1}. The findings from these two studies are similar to our results, where fourth-year mean stand basal area and mean standing stemwood volume increased by 190% and 210% respectively as density increased from 740 to 4440 trees ha^{-1}. The greater positive response of mean basal area and standing stemwood volume to planting density in our study is again attributable to a larger density differential between our highest and lowest stocked stands in comparison to the other studies. In a study of loblolly pine stands in the Lower Coastal Plain of Georgia (Burkes et al. 2003, Barron-Gafford et al. 2003), mean stand basal area increased by 230% with an increase in planting density from 740 to 4440 trees ha^{-1}.

The positive effect of planting density on stand basal area and standing stemwood volume in developing stands is likewise reflected in rates of stem volume growth (Shepard 1971, Whitsell 1974, Balmer et al. 1975, Harms and Langdon 1976, Harms et al. 1994, Will et al.

2001, Barron-Gafford et al. 2003, Burkes et al. 2003). Although current annual increment in our study displayed an overall positive response to planting density, the response was not proportional. For example, the increase in the rate of growth between the 740 and 1480 trees ha^{-1} stands was 8.5 m^3 ha^{-1} y^{-1}, whereas the increase in the rate of growth between the 3700 and 4440 trees ha^{-1} stands was only 2.1 m^3 ha^{-1} y^{-1}. This result is again consistent with much of the previously published literature (Mann and Dell 1971, Harms and Langdon 1976, Harms et al. 1994, Will et al. 2001, Barron Gafford et al. 2003, Burkes et al. 2003). The curvilinear response of current annual increment to increasing density (figure 1) indicates some type of limitation to stem volume accumulation in higher density stands.

In their study on loblolly and slash pine in the Coastal Plain physiographic region of Georgia, Burkes et al. (2003) sought to determine whether this observed restriction in the rate of stem growth with increasing density could be attributed to shifts in biomass partitioning between fine roots, stemwood, and foliage. It was their hypothesis that with increased planting density, a greater proportion of photosynthate would be partitioned to fine roots and foliage to compensate for greater intraspecific competition for above and belowground resources (e.g., light, water, nutrients, etc.), resulting in a net decrease of carbon allocation to the stem (Burkes et al. 2003). Instead, they discovered an increase in carbon partitioning to stemwood with increases in planting density, making it unlikely that limitations to the rate of stem growth with increasing planting density could be attributed to partitioning effects (Burkes et al. 2003). Using the same loblolly and slash pine stands, a separate study also investigated the restriction to stem growth rates with increased density by measuring certain physiological attributes that might contribute to this effect (Will et al. 2001). Foliar maintenance respiration, stem respiration, and light saturated net photosynthesis were measured to determine whether shifts in the rates of carbon gain and carbon loss might account for the limitation. Will et al. (2001) concluded that the decrease in the rate of stem volume growth with density was not due to a decrease in photosynthesis nor to an increase in respiration (Will et al. 2001). Since shifts in biomass partitioning and carbon balance do not seem to be factors in limitations to growth at high densities, perhaps factors associated with the size and efficiency of the canopy are responsible.

In our study, both previous and current-year foliar nitrogen concentrations varied significantly throughout the growing season, a result similar to previous findings (Munger et al 2003, Zhang and Allen 1996). This variation in foliar nitrogen concentration over time could be due to differences in nitrogen utilization and demand throughout the growing season, or to changes in rates of nitrogen uptake. For instance, early in the year large quantities of available nitrogen are being invested in the production of photosynthetic tissues for a new foliar cohort, a significant but temporary sink for nitrogen. Also, changes in meteorologic conditions throughout the course of the growing season (i.e. solar radiation, potential evapotranspiration, temperature) likely lead to considerable temporal fluctuations in rates of nitrogen uptake. A study on five- and six-year-old Redblush grapefruit trees (*Citrus paradisi* Macf.) by Syvertsen et al. (1997) found that whole-tree nitrogen uptake and tree evapotranspiration were positively correlated, providing some evidence for this hypothesis. Other significant factors causing variation in foliar nitrogen concentration over time are seasonal shifts in partitioning between photosynthetic proteins and forms of nitrogen that are more mobile (e.g., amino acids) for transportation to growing sinks (Maier 2002), and resorption and translocation of nutrients prior to leaf senescence (Del Arco et al. 1991, Killingbeck 1996).

Previous-year foliage from the lower canopy in our study had higher nitrogen concentrations than either the middle or upper portions of the canopy, whereas current-year foliage had its highest nitrogen concentrations in the upper canopy. Contrary to our results, several studies in both deciduous and coniferous species have reported no significant effect of canopy position on foliar nitrogen concentration (Ellsworth and Reich 1993, Zhang and Allen 1996, Ishida et al. 1999, Morecroft and Roberts 1999, Kazda et al. 2000, Maier 2002, Will et al. in press). Will et al. (in press), however, determined that canopy position played a role in several interactions resulting in higher nitrogen concentrations in the lower canopy for previous-year foliage. A study by Leal and Thomas (2003) showed congruous results for 1-year-old foliage in old growth *Pinus strobus* L., where the highest nitrogen concentrations were again associated with the lower canopy. In a pooled analysis of *Pinus ponderosa*, *Pseudotsuga menziesii*, and *Tsuga heterophylla*, Bond et al. (1999) found significantly higher foliar nitrogen concentrations as incident light levels increased upward through the canopy, similar to our results for current-year foliage. Another study by Niinemets (1997b) in *Picea abies* found the opposite effect of incident light for some needle age cohorts but not for others, with nitrogen concentrations in the affected foliage cohorts decreasing with increased levels of incident light. Leal and Thomas suggest that these conflicting results are perhaps due to large vertical gradients in leaf mass per unit area caused by morphological adaptations of foliage to light, thus differentially diluting or concentrating nitrogen in the foliage depending on, for example, species-specific light acclimation potential or gradients in biomechanical stress (Leal and Thomas 2003).

In our study, planting density did not significantly influence nitrogen concentration in previous-year foliage. Current-year concentration showed a negative response to density, but nitrogen concentration in both age cohorts remained well above established critical levels for loblolly pine (12.0 mg g^{-1}, Jokela et al. 1991). It is therefore unclear whether deficiencies in foliar nitrogen played a role in the restriction of stem volume growth rates with increasing density. Barron-Gafford et al. (2003) found similar negative trends between foliar nitrogen concentration and density in loblolly pine, but found that nitrogen concentrations fell below established critical levels in the higher densities and were therefore a possible contributory factor to limitations in stem volume growth.

There are numerous examples in the literature that show significant correlations between stand growth rates and photosynthetic capacity in both deciduous and coniferous species (e.g. Walters and Reich 1989, Polley et al. 1997, Jose et al. 2003), as well as several examples that have found no connection (Ellis et al. 2000, Samuelson et al. 2001, Will et al. 2001). There have also been several conflicting studies in pines regarding the relationship between photosynthetic capacity and foliar nitrogen concentration (Tissue et al. 1993, Teskey et al. 1994, Teskey et al. 1995, Murthy 1996, Samuelson 2001, Will et al. 2001, Munger et al. 2003). In pines, studies that found significant relationships between nitrogen concentration and gas exchange generally involved treatments with very low nitrogen concentrations (Tissue et al. 1993, Murthy et al. 1996), whereas studies that found no significant relationship had higher foliar nitrogen concentrations (Teskey et al. 1994, Samuelson 2001, Will et al. 2001). Although no measurements of gas exchange were made in the current study, given previous research it is unlikely that decreases in foliar nitrogen concentration with density significantly influenced photosynthetic capacity. The negative response of foliar nitrogen to density was likely a result of density-induced limitations to nitrogen availability, or perhaps was a function of increased foliar biomass and the associated dilution of nitrogen within canopies of higher density treatments.

Current-year foliage in our study showed a significant canopy position by density interaction, where density negatively impacted foliar nitrogen concentrations in the lower and middle canopy positions, but had no influence on the upper canopy. One possible explanation for this interaction is the translocation of nitrogen from the lower and middle canopy to the upper canopy in attempt to economize available resources for photosynthesis as nitrogen and light availability were constrained by increasing planting density. It is also possible that this effect was due to shifts in leaf mass per unit area, differentially affecting foliage in separate canopy positions as inter- and intra-canopy light environments changed with increasing planting density (Bond et al. 1999).

Nitrogen content of both previous and current-year foliage in our study increased significantly with planting density. Barron-Gafford et al. (2003) found similar responses of nitrogen content to stand density for 1-year-old foliage. Although in their study current-year foliar nitrogen content also increased with density, the effect was not statistically significant (Barron-Gafford et al. 2003). The positive response of nitrogen content to planting density in the current study was not due to changes in foliar nitrogen concentration (since [N] actually decreased with density); rather, it was attributable to increases in foliar biomass and LAI brought about by the increased acquisition of resources in higher density stands, a result also found by Barron-Gafford et al. (2003). Like canopy nitrogen content, LAI showed a significant positive response to density. However, it is clear that LAI was approaching maximum sustainable values in higher density treatments as evidenced by the disproportional increases in LAI with increases in density (figure 3). This may be an indication that full site occupancy and utilization of growing space was approaching, or had already been reached in some of these treatments (Mohler et al. 1978, Long and Smith 1992, Dean and Baldwin 1996). As Dean and Baldwin (1996) describe, full site occupancy is characterized by the achievement of maximum supportable LAI, a reduction to minimum of tree-level growth, and a concurrent achievement of maximum stand productivity since the acquisition of available resources has reached its peak.

The significant temporal effect on intercepted PAR in our study was directly related to the progression of canopy development toward closure, in addition to normal seasonal changes in the canopy (e.g. generation of current year foliar cohort, full needle development, senescence of previous year cohort). The proportion of radiation intercepted by the stands was at a minimum early in the growing season (April 2001), and increased steadily for all density treatments through leaf senescence in the fall (October 2001). The convergence in intercepted radiation in the higher density treatments likely resulted from the imminence of full site occupancy and achievement of maximum LAI in these stands.

Growth efficiency in our stands significantly increased with planting density, a result also found by Burkes et al. (2003). Other studies, however, have reported opposite findings (Waring 1983, Shelton 1984). In these studies, lower density stands had greater growth efficiencies, results the authors attributed to greater light availability and photosynthetic rates in these stands (Waring 1983, Shelton 1984). In the study by Burkes et al. (2003), the authors reasoned that because increases in stand density would likely be associated with lower intra-canopy light levels and photosynthetic rates, increases in growth efficiency with density were likely the result of greater relative biomass partitioning to stemwood. This supposition was supported by their overall finding that biomass partitioning to the stem relative to other tree components did in fact increase with density (Burkes et al. 2003). Shifts in biomass partitioning may also have contributed to the positive response of growth efficiency to density in the current study; however, the fact that growth efficiency increased with density, but radiation-use efficiency did not seems to indicate that increases in growth efficiency may have resulted from increases in the efficiency of PAR capture per unit LAI in higher density treatments. In other words, since growth per unit leaf area was greater in high density stands, and growth per unit PAR capture stayed the same across all densities, it follows that there may have been an increase in the amount of PAR captured per unit leaf area in the high density stands.

Like LAI, annual PAR capture increased significantly with planting density. Also like LAI, increases were not proportional to density, an indication of density-induced limitations to energy capture. The similarity in the responses of LAI and annual PAR capture to density is not unexpected given the inherent association between them. In general, factors that play a role in restrictions to LAI with density (e.g. resource availability, full site occupancy) also impact PAR capture. Examination of the relationship between these two variables found that annual PAR capture increased linearly with leaf area throughout the range of LAI (figure 5). This result differs from the curvilinear relationship often reported between these variables in the literature (e.g. Vose and Allen 1988, Sampson and Allen 1998, Allen 2003). In the cited studies, PAR capture seemed to increase linearly with leaf area up to a certain LAI. Beyond this, decreases in light availability associated with greater self-shading within the canopy led to decreases in PAR capture per unit leaf area, the result being an overall curvilinear relationship. For example, in a study in fertilized 12-year-old loblolly pine stands (*Pinus taeda* L.), Vose and Allen (1988) reported that beyond an LAI of 3.5, PAR capture increased only marginally (5%) in response to a substantial increase (28%) in LAI. Similarly, Sampson and Allen (1998) found that an overall doubling of leaf area in 14-year-old loblolly pine stands increased PAR capture by only 40%. The disparity between our findings and those reported in the cited studies is possibly a function of differences in stand age and canopy development. That is, older stands with closed canopies are perhaps more likely to experience increases in self-shading with greater LAI than stands that are yet to fully achieve canopy closure; however, LAI in this study exceeded the point at which LAI and PAR capture became nonlinear in other studies. Another explanation for the difference in observed relationships involves the potential variability in canopy structure stemming from the substantial range of planting densities (and intra-canopy light levels) in our stands; i.e., it is possible that PAR capture maintained a linear relationship with LAI in our stands, even at high levels of LAI, because of density-induced compensatory changes in canopy structure. Further investigation of this relationship showed that the ratio of annual PAR capture to LAI significantly increased with planting density. This response indicates that adjustments in canopy architecture, foliar display, or other morphological adaptations of foliage stemming from greater planting density or greater competition for available light did in fact result in the more efficient capture of energy by existing leaf area in higher density stands (Ford 1992, Bond et al. 1999, Will et al. 2001).

It is important to note that while measures of stand-level stem volume, stem growth rate, canopy nitrogen content, LAI, and PAR capture were all significantly greater in higher planting density treatments, differences in these measures will likely diminish with age. For example, when stands in the lesser planting density treatments begin to approach full canopy closure and canopy development, LAI in these stands (and therefore PAR capture and canopy nitrogen content) will likely be very similar to LAI, PAR capture, and canopy nitrogen content in higher planting density treatments. Likewise, growth rates will eventually begin to taper off over time in higher density treatments because of increasing intraspecific competition for resources associated with larger trees and larger resource requirements. At that time, stands in the lower planting densities will continue to grow at constant rates, thus leading to a convergence in standing stem volume and stem growth rates between all density treatments. While the aforementioned canopy variables will likely converge to common measures over time, there are other canopy attributes that will remain distinct between planting density treatments. Specifically, canopy dimensions and characteristics of canopy architecture will continue to be much different in stands planted at these different spacings. Canopies of stands planted at low densities will generally have greater vertical height (from the bottom of the canopy to the top of the canopy) than stands planted at higher densities. This would likely lead to a greater potential for self-shading in these lower density stands. In addition, the size of individual branches will continue to vary considerably between plating densities over time, with larger diameter branches in lower density treatments than in higher density treatments. These differences in branch characteristics would likely lead to a smaller ratio of photosynthetic tissues to woody biomass in the canopies of lower density stands compared to higher density stands.

There was no clear relationship between foliar nitrogen concentration and current annual increment with increasing density. However, growth rates were significantly correlated to canopy nitrogen content, LAI, and annual PAR capture. The relationship between nitrogen content and current annual increment was primarily a function of leaf area, since foliar nitrogen concentrations actually decreased with density; therefore, growth rates were best correlated with LAI and annual PAR capture. The relationship between leaf area and productivity is well documented (Gholz 1982, Vose and Allen 1988, Albaugh et al. 1998, Samuelson et al. 2001, Burkes et al. 2003), and is generally attributed to the role of leaf area as the principal exchange surface between the canopy and the surrounding atmosphere, thereby affecting the dynamics of energy absorption, water fluxes, and gas exchange. Although the relationship between growth rate and LAI in the current study was highly significant, there was still a relatively large degree of unexplained residual variation (r^2=0.67). Growth rate was, however, extremely well correlated to annual PAR capture, with simple linear regression accounting for approximately 90% of residual variation. A study by Allen (2003) in irrigated and fertilized loblolly pine stands (*Pinus* *taeda* L.) similarly found that growth rate was highly correlated to annual PAR capture, with linear regression accounting for 78% of residual variation. In another study, Will et al. (2001) found that intercepted radiation was the primary factor in density-induced limitations to growth rate, accounting for 70% of the variation in growth.

There have been many studies over the years that have shown similarly strong relationships between stand volume growth and PAR capture (Monteith 1977, Cannell et al. 1987, Grace et al. 1987, Landsberg and Waring 1997, Will et al. 2001). Monteith (1977) was one of the first to discuss the linear relationship between PAR capture and growth in agricultural crops. In that work, it was proposed that the productivity of a given system is directly proportional to the amount of radiation intercepted by the canopy, with the slope of the relationship governed by the efficiency (ε) with which intercepted radiation is converted to biomass. Since then, there have been many studies that have confirmed the nature of this relationship for agricultural crops and forest tree species alike (Cannell et al. 1987, Grace et al. 1987, Dalla-Tea and Jokela 1991, Monteith 1994, Harrington and Fownes 1995, Will et al. 2001, Allen 2003). While there is very little in the literature that addresses the specific effects of planting density on radiation-use efficiency (ε), the current study found that ε was not significantly affected by density gradients. As previously discussed, the fact that ε was not affected by density while growth efficiency increased with density provides some interesting insights into the relative contributions of, and interactions between LAI and annual PAR capture: With increases in planting density, a given amount of leaf area was able to intercept a greater amount of PAR, the cause being possible compensatory changes in canopy structure and foliar display. Also, increases in LAI resulted in proportional increases in annual PAR capture throughout the range of LAI. Finally, PAR capture was more closely related to growth than LAI.

Overall, annual PAR capture was a better predictor of current annual increment than was LAI because of two principal factors: First, PAR capture is a more direct measure of resource availability than is LAI. Specifically, estimates of LAI do not account for differences in energy capture associated with variations in canopy architecture and foliar display. Second, like current annual increment, annual PAR capture is an integrated metric that represents both temporal and spatial variations in factors impacting productivity.

CHAPTER 6

SUMMARY AND CONCLUSIONS

Planting density had a positive effect on foliar nitrogen content, LAI, PAR capture, and stand growth rate; a significant negative effect on foliar nitrogen concentration of current-year foliage; and no effect on foliar nitrogen concentration of previous-year foliage. Although foliar nitrogen content was found to increase significantly with planting density, the effect was due to increases in leaf biomass. All variables that increased with density did so because of a greater number of trees per area and a greater resultant capacity to acquire and utilize site resources. However, increased intraspecific competition for growing space in the higher density treatments was clearly beginning to limit stand growth rates. Limitations to LAI and PAR capture, likely related to limitations in stand growth rates, were similarly observed in higher planting densities. The adverse impact of increased planting density on current-year foliar nitrogen concentration was apparently caused by a dilution effect stemming from the distribution of nitrogen over greater leaf area. It is uncertain whether foliar nitrogen concentration played a role in limitations to growth despite the fact that concentrations remained well above established critical thresholds (Jokela et al. 1991); i.e., while foliar nitrogen concentrations below these critical values indicate a nitrogen deficiency, values above these thresholds do not necessarily ensure maximum growth rates.

Previous-year foliage in the lower canopy had higher nitrogen concentrations than foliage in the middle or upper portions of the canopy. Conversely, nitrogen concentrations in current-year foliage were greatest in the upper canopy, decreasing in roughly equal increments with canopy height. Planting density effects on current-year foliar nitrogen concentrations depended on canopy position, with concentrations significantly influenced by density in the middle and lower canopies, but not in the upper canopy. This result was potentially attributable to the retranslocation of nitrogen from the lower and middle canopy positions (i.e. lower light availability) to the upper canopy (greater light availability) as intraspecific competition for nitrogen increased, so that trees could most effectively utilize available nitrogen. The inconsistent trends in foliar nitrogen concentrations between age classes and canopy positions could also be attributed to large vertical gradients in leaf mass per unit area caused by morphological adaptations to light, differentially diluting or concentrating nitrogen in the foliage (Leal and Thomas 2003).

PAR capture per unit LAI was linear for all LAI, with no evidence of increased self-shading with high LAI. When analyzed for density effects, PAR capture per unit LAI increased significantly with density. This could have been due to substantial differences in canopy architecture, foliar display, and other morphological adaptations of foliage between density treatments driven by increased competition for available light, or inherent structural differences associated with different planting densities. Evidence for disparities in canopy characteristics was also provided by the fact growth efficiency significantly increased with density, while radiation-use efficiency did not. Further research is necessary to conclusively determine the specific drivers of observed increases in PAR capture efficiency by LAI in higher density treatments.

It is evident from the results of this study that restrictions to the rate of stem growth with increasing density were attributable primarily to limitations in LAI and annual PAR capture. Limitations to LAI with increasing density likely stemmed from the progression of stands in high density treatments toward full site occupancy and utilization of growing space, resulting in the pending achievement of maximum LAI in these stands. The plateau reached by LAI in these stands in turn limited PAR capture. Current annual increment was well correlated with LAI (r^2=0.67), and best correlated with annual PAR capture (r^2=0.90). Overall, annual PAR capture was a better predictor of stemwood growth than LAI because annual PAR capture is an integrated metric that represents temporal and spatial variations in factors impacting productivity. Secondly, LAI did not account for differences in energy capture associated with variations in canopy architecture and foliar display.

The results of this work provide further evidence regarding the importance of canopy dynamics in controls to productivity. This study also provides evidence confirming the considerable effects of planting density on canopy architecture and foliar display, particularly in regard to resultant differences in the efficiency of PAR capture by LAI. Forest managers may be able to use the general predictive relationships found between these canopy variables to write silvicultural prescriptions that seek to more effectively maximize annual PAR capture of a forest stand throughout its harvest rotation. The highly significant correlation between current annual increment and annual PAR capture found in this study can likewise benefit the development or refinement of physiology-based process models.

CHAPTER 7

LITERATURE CITED

Albaugh, T.J., Allen, H.L., Dougherty, P.M., Kress, L.W., King, J.S. 1998. Leaf area and above- and belowground responses of loblolly pine to nutrient and water additions. Forest Science 44:317-328.

Balmer, W.E., Owens, E.G., Jorgensen, J.R. 1975. Effects of various spacings on loblolly pine growth 15 years after planting. USDA Forest Service Research Note SE-211. Southeastern Forest Experiment Station.

Barron-Gafford, G.A., Will, R.E., Burkes, E.C., Shiver, B., Teskey, R.O. 2003. Nutrient concentrations and contents, and their relation to stem growth, of intensively managed *Pinus taeda* and *Pinus elliottii* stands of different planting densities. Forest Science 49(2):291-300.

Bond, B.J., Farnsworth, B.T., Coulombe, R.A., Winner, W.E. 1999. Foliage physiology and biochemistry in response to light gradients in conifers with varying shade tolerance. Oecologia 120:183-192.

Burkes, E.C., Will, R.E., Barron-Gafford, G.A., Teskey, R.O., Shiver, B. 2003. Biomass partitioning and growth efficiency of intensively managed *Pinus taeda* and *Pinus elliottii* stands of different planting densities. Forest Science 49(2):224-234.

Cameron, D.M., Rance, S.J. Jones, R.M. Charles-Edwards, D.A., Barnes, A. 1989. Project STAG: an experimental study in agroforestry. Australian Journal of Agricultural Research 40:699-714.

Cannell, M.G.R., Milne, R., Sheppard, L.J., Unsworth, M.H. 1987. Radiation interception and productivity of willow. Journal of Applied Ecology 24:261-278.

Clark, A.I., Saucier, J.R., Baldwin, V.C., Rower, D.R. 1994. Effect of initial spacing and thinning on lumber grade, yield and strength of loblolly pine. Forest Products Journal 44:14-20.

Dahms, W.G. 1973. Tree growth and water use response to thinning in a 47-year-old lodgepole pine stand. USDA Forest Service Research Note PNW-194. Pacific Northwest Forest and Range Experiment Station.

Dean, T.J., Baldwin Jr., V.C. 1996. Crown management and density. In: Carter, Mason C., ed. Growing trees in a greener world: industrial forestry in the 21st century; 35th LSU forestry symposium. Baton Rouge, LA: Louisiana State University Agricultural Center, Louisiana Agricultural Experiment Station: 148-159a-e.

del Arco, J. M., Escudero, A., Garrido, M.V. 1991. Effects of site characteristics on nitrogen retranslocation from senescing leaves. Ecology 72:701-708.

Ellis, A.R., Hubbell, S.P., Potvin, C. 2000. In situ field measurements of photosynthetic rates of tropical tree species: a test of the functional group hypothesis. Canadian Journal of Botany 78:1336-1347.

Ellsworth D.S., Reich, P.B. 1993. Canopy structure and vertical patterns of photosynthesis and related leaf traits in a deciduous forest. Oecologia 96:169-178.

Evert, F. 1971. Spacing studies – a review. Canadian Forestry Service, Forest Management Institute, Information Report FMR-X-37.

Ford, D.E. 1992. The control of tree structure and productivity through the interaction of morphological development and physiological processes. International Journal of Plant Sciences 153(3):S147-S162.

Gilbert, I.R., Seavers, G.P., Jarvis, P.G., Smith, H. 1995. Photomorphogenesis and canopy dynamics. Phytochrome-mediated proximity perceptions accounts for the growth dynamics of canopies of *Populus trichocarpa* x *deltoides* 'Beaupre'. Plant, Cell and Environment 18:478-497.

Grace, J.C., Jarvis, P.G., Norman, J.M. 1987. Modelling the interception of solar radiant energy in intensively managed stands. New Zealand Journal of Forestry Science 17:193-209.

Haase, D.L., Rose, R. 1995. Vector analysis and its use for interpreting plant nutrient shifts in response to silvicultural treatments. Forest Science 41:54-66.

Harms, W.R., Langdon, O.G. 1976. Development of loblolly pine in dense stands. Forest Science 22:331-337.

Harms, W.R., DeBell, D.S., Whitsell, C.D. 1994. Stand and tree characteristics and stockability in *Pinus taeda* plantations in Hawaii and South Carolina. Canadian Journal of Forest Research 24:511-521.

Harms, W.R., Whitsell, C.D., DeBell, D.S. 2000. Growth and development of loblolly pine in a spacing trial planted in Hawaii. Forest Ecology and Management 126:13-24.

Helmers, A.E. 1948. Early results from thinning seed spots. USDA Forest Service Research Note 48.

Ishida, A., Uemura, A., Koike, N., Matsumoto, Y., Hoe, A.L. 1999. Interactive effects of leaf age and self shading on leaf structure, photosynthetic capacity and chlorophyll fluorescence in the rain forest tree, *Dryobalanops aromatica*. Tree Physiology 19:741-747.

Jokela, E.J., Allen, H.L., McFee, W.W. 1991. Fertilization of southern pines at establishment. p. 263-277 *in* Forest regeneration manual, Duryea, M.L. and P.M. Dougherty (eds.). Kluwer Academic Publishers, The Netherlands.

Jose, S., Merritt, S., Ramsey, C.L. 2003. Growth, nutrition, photosynthesis, and transpiration responses of longleaf pine seedlings to light, water, and nitrogen. Forest Ecology and Management 180:335-344.

Kazda, M., Salzer, J. Reiter, I. 2000. Photosynthetic capacity in relation to nitrogen in the canopy of a *Quercus robur*, *Fraxinus angustifolia* and *Tilia cordata* flood plain forest. Tree Physiology 20:1029-1037.

Killingbeck, K. 1996. Nutrients in senesced leaves: keys to the search for potential resorption and resorption proficiency. Ecology 77:1716-1727.

Knowe, S.A., Hibbs, D.E. 1993. Stand structure of young red alder as affected by planting density. Forest Ecology and Management 82:69-85.

Landsberg, J.J., Waring, R.H. 1997. A generalized model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. Forest Ecology and Management 95:209228.

Lanner, R.M. 1985. On the insensitivity of height growth to spacing. Forest Ecology and Management 13:143-148.

Leal, D.B., Thomas, S.C. 2003. Vertical gradients and tree-to-tree variation in shoot morphology and foliar nitrogen in old-growth *Pinus strobus* stand. Canadian Journal of Forest Research 33:1304-1314.

Long, J.N., Smith, F.W. 1992. Volume increment in *Pinus contorta* var. *latifolia*: the influence of stand development and stand dynamics. Forest Ecology and Management 53:53-64.

Maier, C.A., Johnson, K.H., Butnor, J., Kress, L.W, Anderson, P.H. 2002. Branch growth and gas exchange in 13-year-old loblolly pine (*Pins taeda*) trees in response to elevated carbon dioxide concentration and fertilization. Tree Physiology 22:1093-1106.

Mann Jr., W.F., Dell, T.R. 1971. Yields of 17-year-old loblolly pine planted at a cutover site at various spacings. USDA Forest Service Research Paper SO-70. Southern Forest Experiment Station.

Mohler, C.L., Marks, P.L., Sprugel, D.G. 1978. Stand structure and allometry of trees during self-thinning of pure stands. Journal of Ecology 66:599-614.

Monteith, J.L. 1977. Climate and the efficiency of crop production in Britain. Philosophical Transactions of the Royal Society of London 281:277-294

Morecroft, M.D., Roberts, J.M. 1999. Photosynthesis and stomatal conductance of mature canopy Oak (*Quercus robur*) and Sycamore (*Acer pseudoplatanus*) trees throughout the growing season. Functional Ecology 13:332-342.

Munger, G.T., Will, R.E., Borders, B.E. 2003. Effects of competition control and annual nitrogen fertilization on gas exchange of different-aged *Pinus taeda*. Canadian Journal of Forest Research 33:1076-1083.

Murthy, R., Dougherty, P.M., Zarnoch, S.J., Allen, H.L. 1996. Effects of carbon dioxide, fertilization, and irrigation on photosynthetic capacity of loblolly pine trees. Tree Physiology 16:537-546.

Niinemets, Ü., 1997. Acclimation to low irradiance in *Picea abies*: influences of past and present light climate on foliage structure and function. Tree Physiology 17:723-732.

Pollack, J.P., van Theinen, F., LePage, P. 1990. The Influence of Initial Espacement on the Growth of a 27-year-old Sitka Spruce Plantation. British Columbia Ministry of Forests, Research Note 104.

Polley, H.W., Johnson, H.B., Mayeux, H.S. 1997. Leaf physiology, production, water use, and nitrogen dynamics of the grassland invader Acacia smallii at elevated CO2 concentrations. Tree Physiology 17:89-96.

Quicke, H., Glover, G., Glover, R. 1999. Loblolly pine growth response to herbaceous vegetation control at different planting densities. Canadian Journal of Forest Research 29:960-967.

Ritchie, G.A. 1997. Evidence for red : far red signaling and photomorphogenic response in Douglas-fir (*Pseudotsuga menziesii*) seedlings. Tree Physiology 17:161-168.

Samuelson, L.J., Stokes, T., Cooksey, T., McElmore, P. 2001. Production efficiency of loblolly pine and sweetgum in response to sour years on intensive management. Tree Physiology 21:369-376.

Schmidt, W.C., Shearer, R.C., Roe, A.L. 1976. Ecology and silviculture of western larch forests. U.S. Department of Agriculture Technical Bulletin. 1520.

Scott, W., Meade, R., Leon, R., Hyink, D., Miller, R. 1998. Planting density and tree-size relations in coast Douglas-fir. Canadian Journal of Forest Research 28:74-78.

Seidel, K.W. 1984. A western larch – Engelmann spruce spacing study in eastern Oregon: results after 10 years. USDA Forest Service Research Note PNW-409. Pacific Northwest Forest and Range Experiment Station.

Shepard, R.K. 1971. The development of loblolly pine planted at various initial spacings. Louisiana Agriculture 15:8-11.

Sjolte-Jorgensen, J. 1967. The influence of spacing in the growth and development of coniferous plantations. International Review of Forest Research 2:43-94.

Smith, D.M., Larson, B.C., Kelty, M.J., Ashton, P.M.S. 1997. The practice of silviculture. 9th ed. John Wiley and Sons, New York.

Syvertsen, J.P., Smith, M.L., Lloyd, J., Farquhar, G.D. 1997. Net carbon dioxide assimilation, carbon isotope discrimination, growth, and water-use efficiency of Citrus trees in response to nitrogen status. Journal of the American Society for Horticultural Science 122(2):226-232.

Teskey, R.O., Gholz, H.L., Cropper Jr., W.P. 1994. Influence of climate and fertilization on net photosynthesis of mature slash pine. Tree Physiology 14:1215-1227.

Teskey, R.O., Sheriff, D.W., Hollinger, D.Y., Thomas, R.B. 1995. External and internal factors regulating photosynthesis. In: Smith, W.K., Hinckley, T.M. (eds.), Resource Physiology of Conifers: Acquisition, Allocation, and Utilization. Academic Press, New York. p. 105-140.

Tissue, D.T., Thomas, R.B., Strain, B.R. 1993. Long-term effects of elevated CO_2 and nutrient s on photosynthesis and rubisco in loblolly pine seedlings. Plant, Cell and Environment 16:859-865.

Vose, J.M., Allen, H.L. 1988. Leaf area, stemwood growth, and nutrient relationships in loblolly pine. Forest Science 34:547-563.

Walters, M.B., Reich, P.B. 1989. Response of Ulmus americana seedlings to varying nitrogen and water status. I. Photosynthesis and growth. Tree Physiology 5:159-172.

Ware, L.M., Stahelin, R. 1950. Growth of southern pine plantations at various spacings. Journal of Forestry 50:267-274.

Whitsell, C.D. 1974. Effects of spacing on loblolly pine planted in Hawaii after 11 years. USDA Forest Service Research Note PSW-295. Pacific Northwest Forest and Range Experiment Station.

Woodruff, D.R., Bond, B.J., Ritchie, G.A., Scott, W. 2002. Canadian Journal of Forest Research 32:420-427.

Will, R.E., Barron, G.A., Burkes, E.C., Shiver, B., Teskey, R.O. 2001. Relationship between intercepted radiation, net photosynthesis, respiration, and rate of stem volume growth of *Pinus taeda* and *Pinus elliottii* stands of different densities. Forest Ecology and Management 154:155-163.

Will, R.E., Gafford-Barron, G.A., Teskey, R.O., Shiver, B.D. In Press. Within and between canopy variability of foliar nitrogen concentration for loblolly and slash pine stands planted at different densities. *In* Proc., Twelfth Biennial Southern Silviculture Research Conference, Biloxi, MS. USDA Forest Service, General Technical Report.

Xiao, Y., Jokela, E.J., White, T.L. 2003. Growth and leaf nutrient responses of loblolly and slash pine families to intensive silvicultural management. Forest Ecology and Management 183:281-295.

Zhang, S., Allen, H.L. 1996. Foliar nutrient dynamics of 11-year-old loblolly pine (*Pinus taeda*) following nitrogen fertilization. Canadian Journal of Forest Research 26:1426-1439.