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# Relationship between intercepted radiation, net photosynthesis, respiration, and rate of stem volume growth of *Pinus taeda* and *Pinus elliottii* stands of different densities

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**Abstract**

Intercepted radiation, net photosynthesis, foliar respiration, stem respiration, and foliar nitrogen concentrations were measured to determine how changes in physiology that occur with increasing stand density affect the rate of stem volume growth. Intensively managed *Pinus taeda* L. (loblolly pine) and *Pinus elliottii* Engelm. (slash pine) stands in their third and fourth growing seasons planted at densities of 740, 2220, and 3700 trees $ha^{-1}$ on the lower coastal plain of the southeastern United States were sampled. During the third growing season, stem volume growth was not proportional to stocking density with smaller increases in stem volume growth occurring as stand density is increased. The proportion of radiation intercepted by the canopies during the period of maximum leaf area was linearly related to the rate of stem volume growth. Stem respiration was greater for the trees planted at 740 trees $ha^{-1}$ than for trees at the other densities on a stem surface area basis, but not on a stem volume basis. Foliar respiration and net photosynthesis were not different between the trees growing at different densities even though foliar nitrogen concentration decreased with increasing stocking density. One difference between the species was that the specific leaf area ($m^2$ $kg^{-1}$ of leaf) of *P. elliottii* was significantly lower than *P. taeda*, with the result that area-based comparisons of foliar gas exchange were similar between *P. taeda* and *P. elliottii*, but on a mass basis, *P. elliottii* gas exchange was lower than *P. taeda*. For both species, specific leaf area increased with increasing stocking density. These results indicate that differences in net photosynthesis or respiration rates among stocking densities, or between species, were minimal and did not explain differences in stand growth rates. Instead, growth was well correlated with intercepted radiation and trees in the different density treatments appeared to modify their leaf morphology to improve canopy light interception. 

*Keywords:* Spacing; *Pinus taeda*; *Pinus elliottii*; Respiration; Photosynthesis; Intercepted radiation

## 1. Introduction

In an effort to determine the best planting density to optimize stem volume growth for different products, researchers have repeatedly examined the question of how planting density affects stand growth rate and yield. Empirical evidence describing the effect of planting density on *Pinus taeda* L. (loblolly pine) and *Pinus elliottii* Engelm. (slash pine) growth has been gathered from the 1930s and continues to the present (e.g., Ware and Stahelin, 1950; Worst, 1964; Mann and Dell, 1971; Shepard, 1971; Whitsell, 1974; Balmer et al., 1975; Harms and Langdon, 1976; Shelton, 1984; Harms et al., 1994; McCrady and

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Jokela, 1996). These studies have indicated that, initially, stand growth rate increases due to the greater number of stems per unit of land area (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). At a certain density, stand growth rate reaches a maximum and declines with additional trees. The density associated with the greatest growth rate depends on stand age, site quality, and environmental conditions, but in general, the greatest annual stem growth occurs initially in the densest stands and later, in less dense stands. The net effect is that total volume of stands with different stocking densities converges with age. This convergence represents the upper limit of productivity for the given site and environmental conditions.

The number of years required for convergence of stem volume between stands planted at differing initial density depends greatly on site quality. Better sites or more intensive silvicultural inputs accelerate stand development and the progression of volume convergence among the different densities (Harms et al., 1994). However, the total volumes carried by stands planted on better sites occur at higher densities than for stands planted on lower quality sites (Mann and Dell, 1971; Harms et al., 1994). Although much empirical evidence has been compiled which shows consistent, albeit site-specific results (e.g., Ware and Stahelin, 1950; Worst, 1964; Mann and Dell, 1971; Shepard, 1971; Whitsell, 1974; Balmer et al., 1975; Harms and Langdon, 1976; Shelton, 1984; Harms et al., 1994; McCrady and Jokela, 1996), the physiological mechanisms that control the responses of stand growth rate to stand density have received little attention. The literature examining the mechanisms controlling the growth responses of stands planted at different densities is sparse, with a few notable exceptions such as the report by Shelton (1984) which examined the biomass and nutrient allocation of *P. taeda* stands with different densities and that by McCrady and Jokela (1996) which examined the canopy dynamics of stands of young *P. taeda* families planted at two spacings.

The rate of stem volume growth may be limited as stocking density increases due to changes in the rates of carbon gain and carbon loss. For instance, photosynthetic capacity on a leaf area basis may decrease as stocking density increases due to decreased nutrient or water availability, or due to lower canopy light levels. Increased foliar respiration also may contribute to the convergence of stem volume growth as stocking density increases. For a given stand volume, denser stands with more, smaller trees will have a greater amount of stem surface area than stands planted at a wider spacing with fewer, larger trees. This may result in greater respiratory losses that may negatively affect growth. Alternatively, canopy carbon gain may be limited principally by the amount of radiation intercepted. Identification and understanding of the processes that limit the rate of stem volume growth as stocking density and site occupancy increase are critical for the development of management strategies that will manipulate key resources and mechanisms to increase stand growth rates.

The overall goal of this study was to determine how planting density impacts the capacity of the canopies to intercept radiation and how planting density impacts the capacity for carbon gain and carbon loss. These impacts of density were then related to the rate of stem volume growth. Specific objectives of this study were to determine: (1) the relationship between the rate of stem volume growth and the amount of radiation intercepted by *P. taeda* and *P. elliottii* stands of different densities, (2) how stand density affects the light saturated photosynthetic capacity of *P. taeda* and *P. elliottii* and relates any changes to foliar nitrogen status, and (3) how stand density affects foliar and stem respiration rates of *P. taeda* and *P. elliottii*.

## 2. Methods

This study was conducted on four sites in the lower coastal plain of the southeastern United States. Plots were planted in spring of 1996 with *P. taeda* and *P. elliottii* seedlings at densities of 740, 2220, and 3700 trees $ha^{-1}$ (24 plots total). All of the plots used in this study were intensively managed, with bedding, complete interspecific competition control throughout the study, tip moth control during their first two growing seasons, fertilization at planting with 500 kg $ha^{-1}$ 10–10–10 NPK, and fertilization again during their second growing season with 500 kg $ha^{-1}$ 10–10–10 NPK plus micronutrients. Genetic composition of the study was controlled, in that one half-sib

family of *P. taeda* and one half-sib family of *P. elliottii* were planted at all sites. Depending on planting density, plots ranged in size from 0.12 to 0.20 ha. Although the soils at all four sites are primarily sand, they represent a wide range in soil types within the region. The site locations and soil characteristics were Rincon, GA (32°15′N, 81°16′W) — no spodic horizon, argillic horizon, high water table; Lake Park, GA (30°38′N, 83°09′W) — no spodic horizon, argillic horizon, low water table; Swamp, GA (31°00′N, 82°23′W) — spodic horizon, argillic horizon, high water table; Atkinson, GA (31°11′N, 81°50′W) — spodic horizon, no argillic horizon, high water table.

The rate of stem volume growth during the third growing season was determined from height and diameter measurements made in consecutive dormant seasons (February 1998 and February 1999). Diameters of all trees in the measurement plots and a subsample of heights, one-half to one-fourth of all trees present depending on density, were measured. Height of the remaining trees was estimated using plot-specific height vs. diameter relationships. Stem volume in 1998 was estimated by assuming that the stems were cone shaped. This was a reasonable assumption for these young, fast growing trees that was borne out by subsequent taper measurements. Stem volume in 1999 was determined using plot-specific volume equations.

Intercepted radiation was measured during peak leaf area in the summer of 1998 between August 16 and August 21. Intercepted radiation was measured between 10:00 and 16:00 h during cloud-free periods using the SunScan Canopy Analysis System (Delta-T, UK). Measurements within the canopy were compared to measurements recorded in a clearing using a photosynthetically active radiation (PAR) sensor connected to a data logger. Because intercepted radiation is affected by sun angle, the measurements were standardized to a sun angle of 60° from horizon using species- and spacing-specific empirically derived relationships between sun angle and intercepted radiation. The reflectance of *P. taeda* and *P. elliottii* are similar with no distinction being made between the two species in previous studies (Carter et al., 1996; Carter, 1998).

Foliar maintenance respiration was measured on the first flush of the 1998 growing season with an LI-6400 portable photosynthesis system (Li-Cor, Lincoln, NE). Respiration rates were measured during the dormant season to prevent confounding growth and maintenance respiration. Measurements were conducted on one site per day, 17–21 February 1999, between 10:00 and 16:00 h. Measurements were made on clipped branches (Ginn et al., 1991) from three trees per plot for both *P. taeda* and *P. elliottii* planted at 740, 2220, and 3700 trees $ha^{-1}$. All samples were obtained from the upper third of the canopy. Three fascicles were placed in the cuvette for measurement. The three measurements within plots were subsamples and were averaged to obtain the experimental unit for the plot. Measurements were conducted in three groups. Each group contained one tree of each species and planting density measured in random order. Leaf temperature was controlled by the cuvette so that it was constant within a group of measurements but was changed between measurement groups and between days to reflect changing ambient temperature conditions. By measuring three groups, each containing a sample from both species and all spacings in random order, the effects of diurnal environmental changes were balanced between the different plot means. All foliage was kept in the dark for approximately 10 min before measurement.

Stem respiration was measured concurrently with foliar respiration using an open gas exchange system consisting of an LI-6252 infrared gas analyzer (Li-Cor, Lincoln, NE), a mass flow controller, and a cuvette with 120 $cm^2$ surface area made of PVC pipe, an internal fan for mixing, and a gasket made of closed-cell neoprene foam. Differential readings took between 5 and 15 min to stabilize. Stem temperature was measured with a thermocouple during the respiration measurement. Three trees per plot from the *P. taeda* and *P. elliottii* plots planted at 740, 2220, and 3700 trees $ha^{-1}$ were measured at each site. Stem respiration measurements also were completed in three groups with each group containing one tree of both species and each spacing measured in random order.

Light saturated net photosynthesis was measured in the summer of 1999, in both *P. taeda* and *P. elliottii* using the same plots in which respiration was measured. All samples were obtained from the upper third of the canopy. One site was measured per day on June 29, June 30, July 13, and July 15. Net photosynthetic rates were measured using an LI-6400 portable

photosynthesis system in the same manner that respiration measurements were conducted with the exception that two flushes, the second flush of 1998 and the first flush of 1999, were measured. Irradiance was kept constant at 1600 μmol $m^{-2}$ $s^{-1}$ by a red/blue LED light source attached to the cuvette (Li-Cor, Lincoln, NE). Following the photosynthetic measurements, the leaf area of the fascicles used for the measurements was determined, the samples were dried, ground, and their nitrogen concentration determined using an NC2100 CNS analyzer (CE Elantech, Lakewood, NJ). All-sided specific leaf areas were determined in the process.

For all analyses, site served as the blocking variable and multiple measurements within plots were averaged to obtain the experimental unit. To analyze respiration, species and spacing were analyzed using a two-way ANOVA. For the analysis of net photosynthesis, nitrogen concentration, and specific leaf area, where two flushes were measured, data were analyzed with a split plot analysis with the factorial combination of spacing and species serving as the whole plot factors, and flush as the split plot factor. Stem volume growth during the third growing season was regressed with the percent intercepted radiation to determine the relationship between the two variables.

## 3. Results

The repeated fertilization and complete interspecific competition control resulted in rapid tree growth and stand development. At the end of the third growing season, average tree height for *P. taeda* was 4.5 m and for *P. elliottii* was 3.4 m. During the third growing season, the rate of stand volume growth did not increase in proportion to stand density. Rather, the rate of stand volume growth increased less with additional trees as density increased. For *P. taeda*, stem volume growth during the third growing season increased from 9.0 to 19.1 $m^3$ $ha^{-1}$ $year^{-1}$ with an increase in density from 740 to 2220 trees $ha^{-1}$, but increased to only 24.4 $m^3$ $ha^{-1}$ $year^{-1}$ with a similar sized increase in planting density to 3700 trees $ha^{-1}$. A similar response was measured in *P. elliottii*, with stem volume growth during the third growing season of 6.0, 11.4, and 13.2 $m^3$ $ha^{-1}$ $year^{-1}$ for the stands planted at 740, 2220, and 3700 trees $ha^{-1}$, respectively. This decreased growth response with increasing density indicated that the rate of stem volume growth was becoming limited by some factor or factors as stocking density increased.

Although the rate of stem volume growth did not increase linearly with stocking density, stem volume growth during the third growing season was linearly related to the proportion of radiation intercepted by the canopies. The relationship between the rate of stem volume growth and intercepted radiation was similar for both species (Fig. 1). When stem volume growth during the third growing season was correlated with the proportion of radiation intercepted, the relationship had an $r^2$ of 0.57. When one outlier was removed from the analysis (circled in Fig. 1), the $r^2$ improved to 0.70. This correlation indicated that even with variation due to species, site-specific edaphic and environmental variation, and random measurement errors, the rate of stem volume growth was well related to intercepted radiation.

Whether calculated on a leaf area or leaf weight basis, foliar respiration was not significantly affected by stocking density (Fig. 2a). Foliar respiration of *P. taeda* was significantly greater than that of *P. elliottii* on a leaf weight basis, but not on a leaf area basis ($P < 0.0002$) (Fig. 2b). The difference between area- and biomass-based measurements of respiration was due to lower specific leaf areas of *P. elliottii* compared to *P. taeda*.

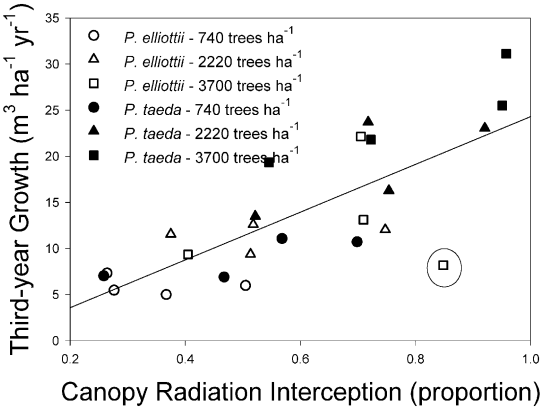


Fig. 1. The relationship between 3-year stem volume growth and the proportion of radiation intercepted by *P. taeda* and *P. elliottii* stands during peak leaf area. The $r^2$ for the regression is 0.59 with including the circled outlier and 0.70 without.

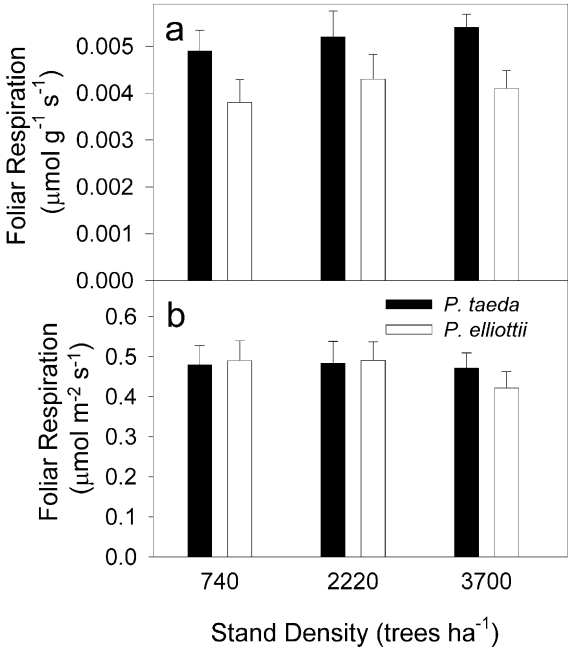


Fig. 2. Foliar respiration of 3-year-old *P. taeda* and *P. elliottii* planted at three densities: (a) respiration on a leaf weight basis and (b) respiration on a leaf area basis. Vertical bars represent the standard error of the mean.

In contrast to foliar respiration, stem respiration on a surface area basis was significantly affected by stocking density ($P < 0.03$). Stem respiration was greater in the 740 trees $ha^{-1}$ treatment than in the 2220 or 3700 trees $ha^{-1}$ treatments (Fig. 3). Rates

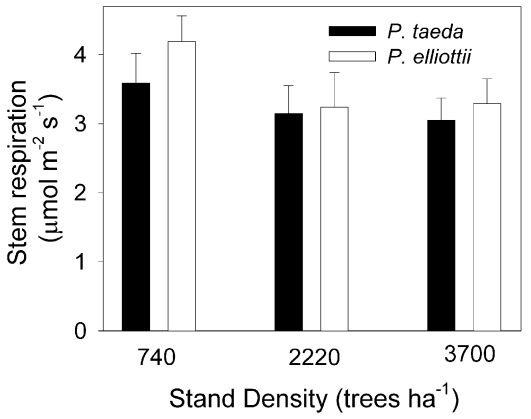


Fig. 3. Stem respiration of 3-year-old *P. taeda* and *P. elliottii* planted at three densities. Vertical bars represent the standard error of the mean.

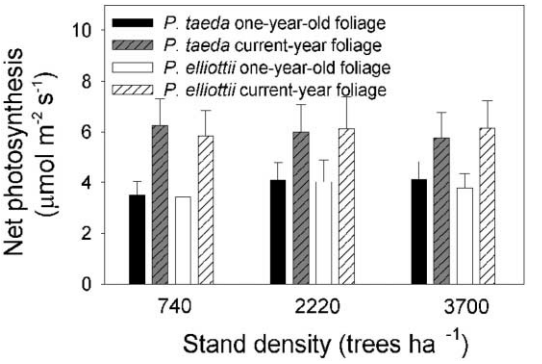


Fig. 4. Light saturated net photosynthesis measured during the third growing season on 1-year-old and current-year foliage of *P. taeda* and *P. elliottii* planted at three densities. Vertical bars represent the standard error of the mean.

of stem respiration of *P. taeda* and *P. elliottii* were not significantly different. The higher mean stem respiration rates of the trees growing at the wider spacing were not related to temperature. Stem temperature was not significantly different among the different treatments.

When measured in mid-summer, the net photosynthetic rates of the different species were similar regardless of planting density (Fig. 4). Net photosynthetic rates of the current-year flush were approximately 1.5–2 times greater than those of the 1-year-old foliage ($P < 0.0001$). There was no effect of stocking density on net photosynthetic rate even though the nitrogen concentration of the fascicles that were measured for photosynthesis decreased with increasing planting density ($P < 0.017$) (Fig. 5a). The effect of spacing on nitrogen concentration was consistent regardless of species or foliage age class such that no statistical interactions with spacing occurred. In addition to the effect of spacing on nitrogen concentrations, the nitrogen concentrations of *P. taeda* needles were significantly greater than those of *P. elliottii* needles ($P < 0.0005$) and the nitrogen concentrations of current-year foliage were significantly greater than the nitrogen concentrations of 1-year-old foliage ($P < 0.0001$).

When nitrogen was expressed on a needle area basis, the effect of stand density on nitrogen was highly significant. Nitrogen per unit leaf area of trees growing in the 740 trees $ha^{-1}$ treatment was significantly greater than for trees growing in the 2220 trees $ha^{-1}$ treatment,

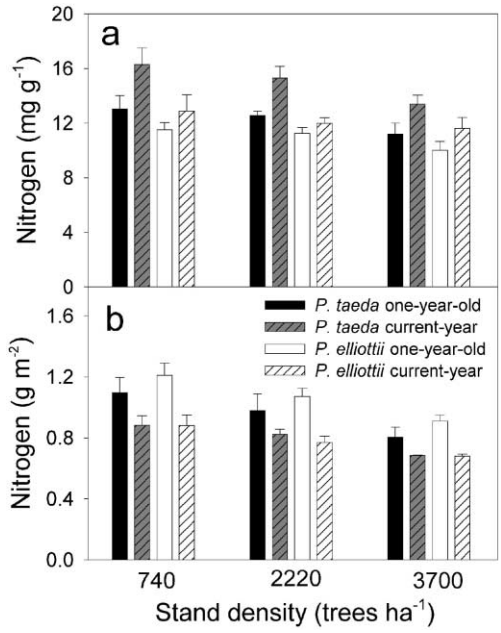


Fig. 5. Foliar nitrogen concentration measured during the third growing season on 1-year-old and current-year foliage of *P. taeda* and *P. elliottii* planted at three densities: (a) nitrogen concentration on a leaf weight basis and (b) nitrogen concentration on a leaf area basis. Vertical bars represent the standard error of the mean.

which in turn, was greater than trees growing in the 3700 trees $ha^{-1}$ treatment ($P < 0.0004$) (Fig. 5b). In contrast to nitrogen concentration on a weight basis, nitrogen on a leaf area basis was not significantly different between *P. taeda* and *P. elliottii* and was significantly greater for 1-year-old foliage than for current-year foliage ($P < 0.0001$). The differences in needle nitrogen expressed on a biomass and an area basis result from differences in specific leaf area between treatments. Specific leaf area significantly increased with planting density ($P < 0.001$), was significantly greater for *P. taeda* than for *P. elliottii* ($P < 0.0001$), and was significantly greater for current-year foliage than for 1-year-old foliage ($P < 0.0001$) (Fig. 6).

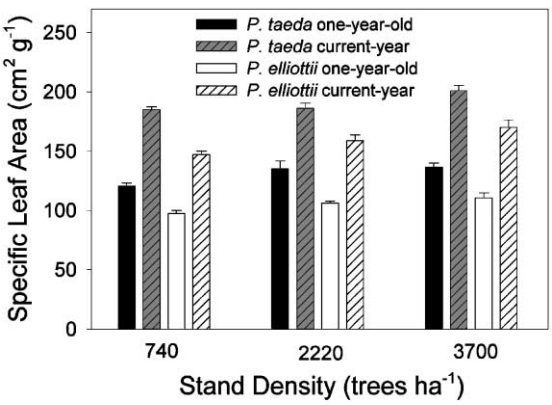


Fig. 6. Specific leaf area measured during the third growing season on 1-year-old and current-year foliage of *P. taeda* and *P. elliottii* planted at three densities. Vertical bars represent the standard error of the mean.

## 4. Discussion

Differences in the rate of stem volume growth in stands of different stocking densities could not be explained by rates of carbon gain and loss for either *P. taeda* or *P. elliottii*. Point measurements of light saturated net photosynthetic rates, stem respiration, and foliar respiration were similar among densities. Rather, radiation intercepted by the canopy was highly correlated to the rate of stem volume growth. Although this has not been reported before for different planting densities, intercepted radiation has been reported to be linearly related to dry matter production in a number of tree species (e.g., Cannell et al., 1987; Landsberg et al., 1996). Similarly, previous studies have found leaf area index to be strongly correlated with conifer stand growth rate across sites and treatments of differing resource availability (Beets and Whitehead, 1996; Fassnacht and Gower, 1997; Carlyle, 1998).

The relationship between the rate of stand volume growth during the third growing season and stand density was curvilinear, caused by a decrease in stand growth rate at higher densities. Neither a decrease in the photosynthetic capacity nor an increase in foliar respiration rate was related to the decrease in stem growth rate as stocking density increased. No change in foliar gas exchange rates occurred among the different stand densities even though nitrogen concentration expressed on either a needle weight or needle area basis decreased with stand density. A lack of correlation between nitrogen concentration and gas exchange has been previously documented in studies of *P. taeda* and *P. elliottii* (Cropper and Gholz, 1991; Teskey et al., 1994a; Samuelson, 1998). However, in

other studies where nitrogen concentrations were very low in some of the treatments, gas exchange and nitrogen concentration were correlated (Tissue et al., 1993; Thomas et al., 1994; Murthy et al., 1996).

The relationships between conifer photosynthesis and nitrogen, and respiration and nitrogen, have been reviewed several times before (e.g., Teskey et al., 1994b, 1995; Sprugel et al., 1995). The lack of correlation between nitrogen concentration and foliar gas exchange in this study may have resulted because the stands had been fertilized twice in 3 years and average nitrogen concentrations of the treatments were all greater than 10 mg $g^{-1}$. As Sprugel et al. (1995) point out, a nitrogen rich environment can result in a large amount of nitrogen occurring as amino acids rather than as proteins associated with respiration or photosynthesis. This could be why there was not a correlation between gas exchange and nitrogen concentration in this study or in other studies where nitrogen concentrations are above a critical threshold.

Stem respiration was greater when calculated on a stem area basis for the trees planted at the lowest density. However, the trees in the lowest density plots were larger and had greater stem volume under the cuvette during measurements (stem volume under the cuvette was calculated based on a wedge with an arc equal to the cuvette width). When these differences in tree size were taken into account, stand density had no effect on respiration expressed on a stem volume basis. This proportionality between stem respiration and stem volume suggests that a greater respiratory burden will not occur as planting density increases and stand volume shifts from fewer, large trees to more, smaller trees. Therefore, increased stem respiration does not appear to be limiting the rate of stem volume growth as stocking density increases. This relationship between stem volume and respiration rate is similar to the constancy of the relationship between stem respiration and sapwood volume in conifers discussed by Sprugel et al. (1995). In a study of *P. taeda* stem respiration, Maier et al. (1998) found that differences in respiration rate between fertilized and unfertilized treatments were closely related to stem nitrogen content. In our study, all stands received equal and high rates of fertilization, so no differences in stem nitrogen concentration should have existed. Therefore, stem nitrogen content can be expected to be proportional to stem volume and respiration.

The gas exchange measurements in this study represent a few points in time and may not be indicative of the entire growing season. However, gas exchange measurements were carefully conducted to get as good an estimate as possible. For instance, respiration was conducted during the dormant season to prevent confounding growth and maintenance respiration. Photosynthetic measurements were conducted during mid-summer, the time of year that tree nitrogen use is at a maximum, so that the any potential effects of nitrogen stress on photosynthesis should occur at this time. Additionally, a less extensive set of photosynthesis measurements were conducted in the winter with similar results to the summer measurements (data not shown).

The proportion of intercepted radiation was well correlated to stand volume growth. Other studies found a linear relationship between intercepted radiation and stand growth rate (e.g., Monteith, 1977; Linder, 1985; Grace et al., 1987; Harrington and Fownes, 1995; Landsberg et al., 1996; Landsberg and Waring, 1997). In this study, intercepted radiation was measured once during the period of peak leaf area and standardized to one sun angle. Therefore, we cannot calculate growth efficiency. The data from this study can be used as a relative index and shows that, as in other studies, the rate of stand volume growth is well correlated to the amount of radiation intercepted by the canopy. From this, it can be surmised that the rate of stem volume growth was not proportional to stocking density at the higher densities because the amount of radiation intercepted by the stands was beginning to limit stem volume growth as leaf area began to reach high levels. Although light saturated net photosynthesis of individual leaves did not decrease with increasing stand density, the integrated photosynthetic rate of the canopy did become limiting as the amount of intercepted radiation reached a plateau and as the amount of self-shading probably increased.

As stand density increased, the amount of radiation intercepted per unit of leaf area most likely decreased due to greater amounts of self-shading. However, the relationship between intercepted radiation and the rate of stand volume growth was linear among stocking densities, perhaps in part because needle morphology adjusted to differences in irradiance. In this study, specific leaf area increased with increasing stand

density thus indicating that at higher densities, needles of the same surface area weighed less. The result of this increase in specific leaf area is that more radiation can be intercepted per unit of needle biomass or unit of nitrogen and may have helped to offset the effects of increased self-shading. Increased specific leaf area is a common response of southern pines to decreased irradiance (McLaughlin and Madgwick, 1968; Shelton and Switzer, 1984; McCrady and Jokela, 1996; Baldwin et al., 1997; Zhang et al., 1997). Given that there was no change in light saturated photosynthetic capacity and a decrease in needle nitrogen concentration as stand density increased, the morphological change in specific leaf area may have been a means to increase the efficiency of nitrogen use and radiation interception.

Foliar respiration of *P. taeda* was greater than for *P. elliottii* when expressed on a needle biomass basis, but foliar respiration and photosynthesis were similar when expressed on a needle area basis. This discrepancy was due to the lower specific leaf area of *P. elliottii*. A similar relationship occurred for nitrogen concentration. Therefore, the differences between *P. taeda* and *P. elliottii* occurred mainly in needle morphology. Given the good correlation between intercepted radiation and the rate of growth, the greater growth of *P. taeda* in this study was due to the amount of needle area produced and the display of that needle area, not due to differences in needle physiology of the two species. Similarly, Dalla-Tea and Jokela (1991) concluded that growth of *P. taeda* was greater than for *P. elliottii* due to the amount and display of needle area.

In summary, differences in net photosynthesis and respiration among stocking densities, and between species, were minimal and did not explain differences in stand growth rate. Instead, growth rate was well correlated with a simple index of intercepted radiation. Trees in the different density treatments appeared to modify their leaf morphology to increase canopy light interception. Dewar (1996) noted that the physiological basis for a linear relationship between productivity and intercepted radiation has not yet been established. This study provides evidence that, at least for these species, the relationship holds because of consistency in net photosynthetic and respiratory capacities and adjustments of specific leaf area within the canopies to increase light interception.

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