Biomass Partitioning and Growth Efficiency of Intensively Managed *Pinus taeda* and *Pinus elliottii* Stands of Different Planting Densities

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ABSTRACT. The effect of planting density (740, 2,220, 3,700, and 4,440 trees/ha^{-1}) on growth efficiency and biomass partitioning was examined in intensively managed stands of 4-yr-old loblolly (*Pinus taeda* L.) and slash pine (*Pinus elliottii* Engelm.) stands on the Coastal Plain of southern Georgia. The primary objective of this study was to determine whether decreased partitioning of biomass to stem relative to other tree components limits stem biomass growth on a per hectare basis as stand density increases. Fourth growing season stem biomass production did not increase proportionally with planting density, indicating that stem biomass growth was limited at the higher stand densities. For both species, growth efficiency (stem biomass growth produced during the fourth growing season per unit of leaf biomass) was significantly lower for stands planted at 740 trees/ha^{-1} compared to the other stand densities. Similarly, the ratio of stem biomass growth:fine root biomass was significantly lower for the 740 trees/ha^{-1} stand. Within sites, planting density had no effect on the ratio of fine root biomass: leaf biomass for either species. Overall, these results indicate that partitioning to stem growth increased relative to foliage or fine roots as stand density increased. Therefore, the limitation in stem biomass growth on a per hectare basis that occurred as stand density increased was not due to changes in partitioning, but probably due to a limitation in net primary production. FOR. SCI. 47(2):224–234.

Key Words: Biomass partitioning, fine root biomass, growth efficiency, leaf biomass, *Pinus elliottii, Pinus taeda.*

GROWTH AND YIELD OF A FOREST STAND are a function of net primary production (NPP) and the partitioning of biomass to stem relative to other stand components. Increasing the planting density of trees on a site generally increases the acquisition and use of resources such as light, nutrients, and water. As a result, total stem growth rate of stands (i.e., annual stem growth on a per hectare basis), increases with stand density even though the growth rate of

individual trees decreases. At higher planting densities, however, total stem growth rate of a stand reaches a maximum or may even decline (e.g., Shelton 1984, Harms et al. 1994, McCrady and Jokela 1996). The net effect is that total stem growth rates of higher density stands converge at a maximum that represents the upper limit of productivity for the given site and environmental conditions. This convergence in total stem growth rate of high density stands could be related to a

limitation in stand NPP, a smaller proportion of NPP partitioned to the stem, or a combination of both.

It has been proposed that a hierarchy in the priority of biomass partitioning exists whereby stem growth has a lower priority than foliage and fine root (Waring and Schlesinger 1985, Oliver and Larson 1996). As planting density increases, both aboveground and belowground intraspecific competition increases, potentially changing partitioning priorities. For example, higher density stands may increase biomass partitioning to fine roots to better compete for water and nutrients, or may increase partitioning to foliage to better compete for light.

Site quality and nutrient amendments alter the biomass partitioning of forest stands (e.g., Gower et al. 1995, Haynes and Gower 1995, Albaugh et al. 1998, Wang et al. 1998). Relatively less is known about how stand density affects biomass partitioning. Biomass partitioning to stem relative to other aboveground components may increase with increasing stand density (Nilsson and Albrektson 1993, Puri et al. 1993). However, increasing stand density may decrease growth efficiency (stem produced per unit of leaf) (Waring1983). Increasing stand density may decrease (Pearson et al. 1984) or increase (Puri et al. 1993) the proportion of biomass partitioned belowground. For loblolly pine (*Pinus taeda* L.), high planting density decreased growth efficiency during early stand development (Shelton 1984). However, when measured at age 25, NPP, leaf biomass, stem biomass produced per unit foliage, branch biomass produced per unit foliage, and total biomass produced per unit foliage were almost identical between stands planted at wide (1,200 trees ha^{-1}) and close (4,300 trees ha^{-1}) spacings (Shelton 1984). In an experiment examining intensively managed, 4-yr-old loblolly pine stands, McCrady and Jokela (1996) found that trees planted at 2,986 trees ha^{-1}, that had four times the growing space compared to stands planted at 11,814 trees ha^{-1}, had only 2.7 times more branch and foliage biomass production per tree. Although the amount of branch and foliage differed between the spacings, the amount of branch per foliage was fairly constant.

The objectives of this study were to determine how increasing planting density affects the partitioning of biomass to different tree components of intensively managed loblolly pine and slash pine (*Pinus elliottii* Engelm.) stands to determine whether the limitation in stem growth rate of forest stands that occurs at higher planting densities is related to changes in biomass partitioning, and whether a functional relationship between foliage and fine root biomass exists. Initial hypotheses regarding the limitation of total stem growth rate with stand density were that (1) growth efficiency would decrease with stand density, (2) partitioning of biomass to fine roots relative to stem biomass would increase with stand density, (3) the relationship between fine root biomass and foliar biomass would not be affected by planting density, but would vary between study sites.

Our first two hypotheses were based on the premise that carbon partitioning to stem would be a lower priority than foliage or fine root as intraspecific competition intensified for light, water, and nutrients as a result of increasing stand density. In addition, we expected growth efficiency to decrease as stand density increased due to lower light availability per unit of foliage within the higher density stands resulting in a decrease in photosynthate-produced per unit foliage. Our third hypothesis was based on the premise that a functional relationship between fine roots and foliage exists regardless of stand density such that there is a constant proportion between standing biomass of fine roots and foliage at a given site. This was part of a larger study examining the biology of fast growing, densely planted stands and the potential mechanisms that limit stem biomass growth. A previous paper described the effects of stand density on gas exchange and intercepted radiation (Will et al. 2001) and another study examined the nutrient dynamics (Barron-Gafford et al. accepted for publication).

Materials and Methods

This study was conducted at four locations on the Coastal Plain of southeastern Georgia. The soils on all sites were sandy, but varied in terms of the presence and absence of spodic and argillic horizons. The site in Effingham County had an argillic, no spodic horizon, and a high water table. The site in Lowndes County had an argillic, no spodic horizon, but a lower water table. The site in Charlton County had both an argillic and spodic horizon and a high water table. The site in Brantley County had a spodic horizon, but no argillic horizon. Each site was bedded in June of 1995. The sites were kept free of competing vegetation with a broadcast mixture of herbicides applied in the fall of 1995 and the spring of 1996. Thereafter, sites were kept free from competing vegetation with periodic, directed applications using backpack sprayers. At the time of planting (January 1996), 561 kg ha^{-1} of 10-10-10 NPK was applied. Before the third growing season (spring 1998), 673 kg ha^{-1} 10-10-10 NPK + micronutrients and 131 kg ha^{-1} ammonium nitrate was applied. Before the fourth growing season (spring 1999), an additional 131 kg ha^{-1} of ammonium nitrate was applied.

One replication of the factorial combination of species (loblolly and slash) and density (740, 2,220, and 3,700 trees ha^{-1}) was planted at each site in January 1996. An additional stand density of 4440 trees ha^{-1} was planted for loblolly pine. Seedlings of loblolly pine half-sib family 7–56 (North Carolina State Tree Improvement Cooperative) and slash pine family 5–61 (Rayonier and International Paper Co.) were hand-planted at all locations. Survival was excellent, averaging 95% after 3 yr. Gross plot size was 0.23 ha for the 740 trees ha^{-1} density and 0.12 ha for the other stand densities. Measurement plots within these gross plots were 0.13 ha for the 740 trees ha^{-1} and 0.05 ha for the other stand densities.

Height and diameter at breast height (dbh) were measured during the winter of 1998/1999 and 1999/2000. In 1999/2000, every dbh and every other tree height was measured. In 1998/1999 every dbh was measured, but the number of heights measured varied with density. Height was measured for every other tree in the 740, every third tree in the 2,220, and every fourth tree in the 3,700 and 4,400 trees ha^{-1} plots. Heights of the trees not measured were predicted using site-specific regression equations developed from the measured

height-dbh pairs. The average r^2 for these relationships are presented in Table 1.

Stem volumes at age 3 (following the 1998 growing season) and age 4 (following the 1999 growing season) were estimated using taper information measured in the summer of 1999 from 15 trees per plot that captured the range of tree sizes. At 1 m intervals, including dbh, the diameter and bark thickness were measured from groundline up to a 2.5 cm diameter top. Total tree height also was measured. From these measurements, volume for each meter segment was calculated and summed to find the total tree volume and percent bark by volume. These volumes, along with their measured dbh and total height, were used to generate plot-specific volume equations based on height and outside bark dbh. The average r^2 for these relationships are presented in Table 1. Stem wood specific gravity was determined from 15 5 mm diameter cores per plot taken 0.91 m above groundline. Cores were stored on ice, brought to the lab, soaked in water, and their displacement measured to calculate volume. Cores were then dried at 60°C for several days and weighed. Stem biomass of each plot was calculated by multiplying the specific gravity by total stem volume. Up to and throughout the fourth growing season, all stem wood was juvenile so the cores give a good estimate of overall stem specific gravity.

Eight soil cores (5.2 cm diameter × 30 cm length) per plot were taken in August 1999. Four cores were taken on the beds, and four were taken between beds. The cores were stored in a freezer until processed. The samples were washed using a hydropneumatic root elutriator to separate roots from soil and organic debris. Root biomass was estimated using a line intercept technique. In this technique, eight 10 × 10 cm grids consisting of 100 1 cm^2 individual cells were laid out in a plastic tray. The washed samples were evenly distributed over the grids. Four grids were selected at random and the number of intersections between the roots and gridlines were counted. Only live roots less than 0.5 mm in diameter were counted. A subsample of 50 cm of fine root from each sample was oven dried at 60°C for 72 hours and specific root length was calculated. To predict fine root length from the number of grid-line intersections, a regression equation ($r^2 = 0.99$) was developed using known lengths of 0.5 mm diameter monofilament cut into small pieces. Fine root biomass was calculated using the total root length of samples and specific root length. This technique provides a more accurate estimate of fine root biomass than separating, sorting, and weighing fine roots (Hendrick and Pregitzer 1993). In addition, live roots can be separated from dead by optical determination during the counting process. Fine root biomass was scaled to the hectare basis using the soil surface area sampled by the cores.

Litterfall was collected in 0.46 m^2 circular traps that were randomly placed on plots. More traps were placed on the lower density stands to compensate for greater spatial heterogeneity in litter fall. Twelve, nine, seven, and six traps were placed on the 740, 2,220, 3,700, and 4,400 trees ha^{-1} plots respectively. Litter was collected at approximately 4 wk intervals between March 1999 and March 2001. An empirically derived correction factor was determined to convert the biomass of litter to that of foliage. The conversion factor was developed in April 2000 from first and second flush foliage from each plot. Paired foliage samples were collected from the mid-canopy of each plot and their surface area determined in the field by measuring radius with an SPI Scale Lupe 7× Optical Comparator (Structure Probe, Inc., West Chester, PA). One sample was placed on ice, transported to the lab, dried at 60°C for several days and weighed. The other sample from each plot was allowed to air-dry for several weeks to simulate changes that occur in needle weight during senescence and abscission, and then dried at 60°C and weighed. The conversion factor was calculated as the ratio of dry weight of fresh foliage to dry weight of air-dried foliage for equal areas of foliage. This technique is similar to that used by others (e.g., Dalla-Tea and Jokela 1991, Gholz et al.1991). No significant differences in the ratio were found between densities, flushes, or sites, so one conversion factor was used for each species. Loblolly and slash pine growing on the lower Coastal Plain retain their needles for about 18 months so the majority of foliage produced during one growing season remains on the trees until the end of the next growing season. Therefore, litter collected in this study represents foliage that developed during the 1998 growing season and was present on the trees throughout the 1999 growing season as well as foliage that developed during the 1999 growing season.

Because two needle cohorts influence stem biomass growth in any given year, growth efficiency (GE) was calculated three ways; (1) the amount of stem biomass produced during the 1999 growing season per unit of leaf biomass that developed during 1998 and remained on the trees throughout the 1999 growing season, (2) the amount of stem biomass pro-

Table 1. Mean stand height (ht 98) and diameter at breast height (dbh 98) at the end of 1998 growing season, mean stand height (ht 99) and diameter at breast height (dbh 99) at end of 1999 growing season, mean r^2 from equations used to predict height from diameter at breast height (r^2 ht), and mean r^2 from equations used to predict volume (r^2 vol). Standard errors in parentheses.

Species	Density	ht 98		dbh 98		ht 99		dbh 99		r^2 ht		r^2 vol	
		m	SE	mm	SE	m	SE	mm	SE	mean	SE	mean	SE
Loblolly pine	740	2.78	(0.20)	35.0	(5.4)	4.37	(0.24)	79.3	(4.2)	0.68	(0.05)	0.90	(0.05)
	2,220	2.91	(0.21)	33.8	(5.4)	4.62	(0.34)	69.7	(5.3)	0.74	(0.07)	0.95	(0.01)
	3,700	2.90	(0.30)	31.1	(6.1)	4.63	(0.38)	63.3	(3.5)	0.59	(0.02)	0.97	(0.01)
	4,400	2.84	(0.27)	29.7	(6.2)	4.51	(0.19)	58.7	(3.8)	0.71	(0.03)	0.96	(0.01)
Slash pine	740	2.13	(0.14)	31.6	(4.8)	3.45	(0.26)	71.4	(4.2)	0.73	(0.05)	0.92	(0.02)
	2,220	1.99	(0.19)	27.9	(6.1)	3.33	(0.15)	63.5	(5.1)	0.66	(0.08)	0.96	(0.02)
	3,700	2.14	(0.14)	30.9	(4.7)	3.48	(0.18)	63.1	(2.0)	0.72	(0.03)	0.95	(0.02)

duced during the 1999 growing season per unit of leaf biomass that developed during 1999, and (3) the amount of stem biomass produced during the 1999 growing season per unit of leaf biomass that developed during 1998 and 1999 combined. The ratios of stem biomass growth:fine root biomass and fine root biomass:leaf biomass also were calculated.

Data were analyzed using a randomized complete block design with the factorial combination of species and stand density used to test the effects of species, planting density (740, 2,220, and 3,700 trees ha^{-1}), and the species × density interaction. Each site was a block and contained one replication of each species × density combination. Ratios were transformed using the natural logarithm before analysis. The slopes of the relationships between (1) leaf biomass and stem biomass growth, (2) fine root biomass and stem biomass growth, and (3) fine root biomass and leaf biomass for the different species and sites were analyzed to determine whether these allometric relationships differed between species or sites. An additional analysis for loblolly pine only included the stands planted 4,440 trees ha^{-1} to test the linear and quadratic components of the relationship between planting density and stem biomass growth. In addition, the linear relationship between stand density and average stem growth of the plots was compared to the quadratic relationship to determine which model fit the data better.

Results

Average tree height and diameter at breast height (dbh) for the different species and planting density combinations following the 1998 and 1999 growing seasons are presented in Table 1. At the end of the 1999 growing season, trees in the slash pine stands were significantly smaller than in the loblolly pine stands ($P < 0.05$) for height and diameter. Height was not significantly affected by stand density, but dbh decreased with increasing planting density for both species ($P < 0.01$).

Fourth-year stem biomass growth of stands was not significantly different between loblolly and slash pine (unless specifically stated otherwise, stem biomass growth refers to fourth growing season stem biomass production at the stand level, i.e., kg ha^{-1} yr^{-1}). No significant interactions between species and stand density occurred for stem biomass growth or any of the other measured variables. Therefore, the main effects of stand density were examined using the combined
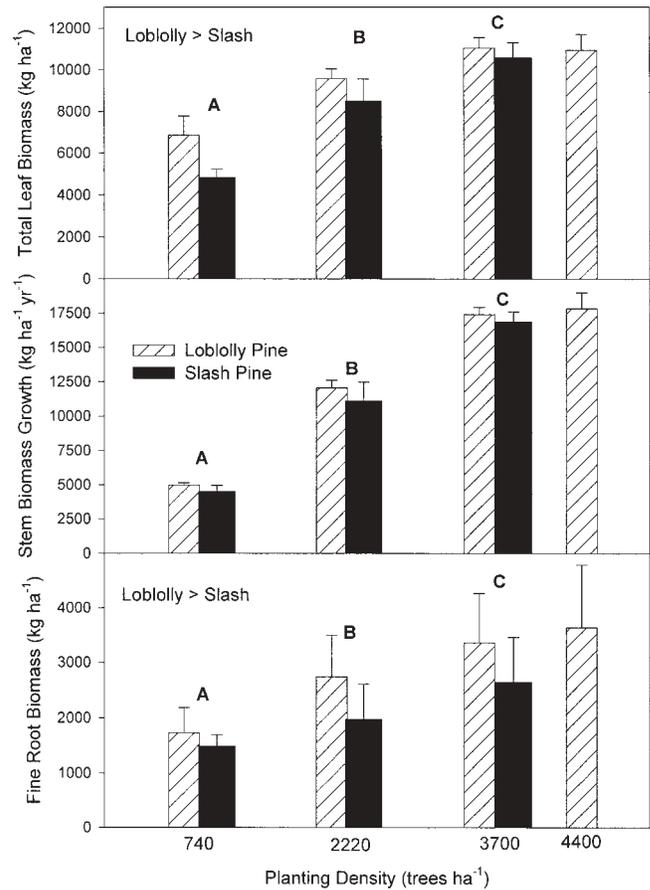

Figure 1. Total leaf biomass based on litterfall from the 1998 and 1999 foliage cohorts, stem biomass growth during the fourth growing season (1999), and fine root biomass measured during the middle of the fourth growing season of intensively managed loblolly and slash pine stands planted at different densities. Vertical bars represent one standard error. Different letters indicate a significant difference between planting densities (**P < 0.05**). A significant difference between loblolly and slash pine is noted on the graph when it occurred. Statistical significance was determined from a two-way ANOVA with site serving as the blocking variable.

responses of loblolly and slash pine. Stem biomass growth of stands significantly increased (Table 2) with stand density, but the increase was not proportional (Figure 1). Stem biomass growth during the fourth growing season increased approximately 2.5 times with a tripling of planting density from 740 to 2,200 trees ha^{-1}. Stem biomass growth increased only about 3.5 times with a five-fold increase in

Table 2. P values for the ANOVA based on a randomized complete block design with site serving as block (n = 4) and the factorial combination of species (loblolly pine vs. slash pine) and planting density (740, 2,220, and 3,700 tree ha^{-1}). Variables were standing fine root biomass in summer 1999 (FRB), stem biomass growth during 1999 growing season (SBG), leaf biomass of the 1998 cohort (LB98), leaf biomass of the 1999 cohort (LB99), leaf biomass of the 1998 and 1999 cohorts combined (LBT), the biomass of the 1998 cohort: biomass of the 1999 cohort (98:99), stem biomass growth during 1999: biomass of 1998 cohort (GE98), stem biomass growth during 1999: biomass of 1999 cohort (GE99), stem biomass growth during 1999: biomass of 1998 and 1999 cohort (GET), fine root biomass during summer 1999: stem biomass growth during 1999 (FR:ST), and fine root biomass during summer of 1999: leaf biomass of 1998 and 1999 cohorts (FR:LBT).

Source	FRB	SBG	LB98	LB99	LBT	98:99	GE98	GE99	GET	FR:ST	FR:LBT
Site	<0.01	0.25	0.01	0.08	0.11	<0.01	0.25	0.04	0.43	<0.01	<0.01
Species	0.02	0.27	0.09	0.06	0.04	0.88	0.93	0.22	0.32	0.14	0.49
Spacing	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.57
Spec*Spac	0.59	0.93	0.60	0.56	0.51	0.97	0.82	0.78	0.79	0.29	0.14

planting density from 740 to 3,700 trees ha^1. For loblolly pine, a further increase in planting density from 3,700 to 4,400 trees ha^{-1} had very little effect, only increasing stem biomass growth from 17,400 to 17,800 kg ha^{-1}. The relationship between loblolly pine stem biomass growth and stand density had both a significant linear ($P < 0.0001$) and quadratic component ($P = 0.02$). A quadratic relationship ($y = 40.9 + 17.4x - 0.004x^2$, $r^2 = 0.94$) between planting density (trees ha^{-1}) and stem biomass growth (kg ha^{-1}) fit the data better than the linear relationship ($y = 3115 + 8.8x$, $r^2 = 0.91$).

Wood specific gravity was not affected by stand density, but was slightly, though significantly, greater ($P = 0.04$) for slash pine (0.37) compared to loblolly pine (0.35). The proportion of the total stem that bark composed did not differ between stands of different densities. Percent bark was significantly greater ($P = 0.02$) for slash pine (13%) than for loblolly pine (11%).

Loblolly pine stands had significantly more (Table 2) fine root biomass than slash pine stands (Figure 1). Fine root biomass significantly increased (Table 2) with stand density (Figure 1). Similar to stem biomass growth, fine root biomass of loblolly pine stands planted at 3,700 and 4,400 trees ha^1 was very similar, 3,360 vs. 3,640 kg ha^{-1}.

Total leaf biomass (1998 + 1999 foliage cohort) was significantly greater (Table 2) for loblolly pine than for slash pine stands (Figure 1). Total leaf biomass significantly increased (Table 2) as stand density increased from 740 to 3,700 trees ha^1 (Figure 1). Total leaf biomass of loblolly pine stands planted at 3,700 and 4,400 trees ha^{-1} was similar, 8,420 vs. 7,824 kg ha^{-1} (Figure 1). Leaf biomass of the 1998 foliage cohort significantly increased with each successive increase in stand density, but the difference between species was not significant (Table 2) (Figure 2). Similarly, leaf biomass of the 1999 foliage cohort increased as stand density increased from 740 to 2,220 tree ha^{-1}, but the difference between the stands planted at 2,220 and 3,700 trees ha^{-1} was not significant (Table 2) (Figure 2). When the biomass of the 1998 foliage cohort was divided by the biomass of the 1999 foliage cohort, the ratio significantly increased (Table 2) with increasing stand density (Figure 2), indicating that the relative increase in foliage between the 1998 and 1999 foliage cohorts was greater in the lower stand densities.

Regardless of how growth efficiency (GE) was calculated, mean growth efficiencies of loblolly and slash pine stands were not significantly different, and GE increased with increasing stand density (Table 2) (Figure 3). Growth efficiency calculated as the 1999 stem biomass growth:1998 cohort leaf biomass was significantly less (Table 2) for stands planted at 740 trees ha^{-1} than the other two densities (Figure 3). Growth efficiency calculated based on 1999 cohort leaf biomass or total leaf biomass significantly increased (Table 2) with each successive increase in stand density (Figure 3).

Slopes of the relationship between 1999 stem biomass growth and 1998 cohort leaf biomass for the different sites were not significantly different from each other, and the overall slopes of loblolly and slash pine were similar. Therefore, one slope was used to describe the relationship for both species and all sites (Figure 4a). However, there was variabil-
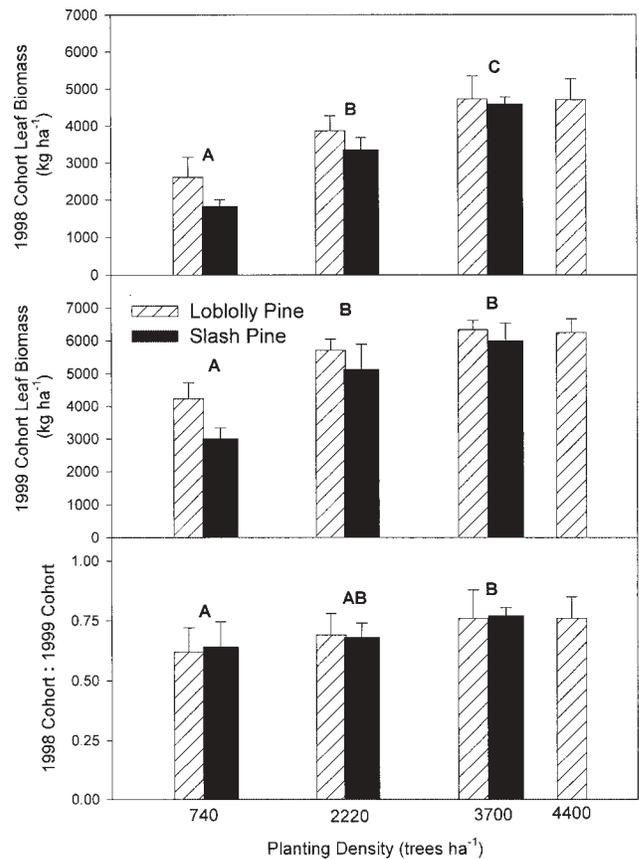

Figure 2. Leaf biomass of the 1998 foliage cohort, leaf biomass of the 1999 foliage cohort, and the ratio between leaf biomass from the 1998 and 1999 cohorts for intensively managed loblolly and slash pine stands planted at different densities. Vertical bars represent one standard error. Different letters indicate a significant difference between planting densities ($P < 0.05$). A significant difference between loblolly and slash pine is noted on the graph when it occurred. Statistical significance was determined from a two-way ANOVA with site serving as the blocking variable.

ity for loblolly pine between sites in the intercept of the relationship between 1999 stem biomass growth and 1998 cohort leaf biomass (the No Spodic, Argillic site had a more negative intercept). The relationship between 1999 stem biomass growth and 1999 cohort leaf biomass was significant, but had a lower r^2 than the relationship between stem biomass growth and the 1998 foliage cohort (Figure 4b). The relationship between 1999 stem biomass growth and 1998 + 1999 cohort leaf biomass also was significant and slightly greater in predictive capacity than the relationship between the 1998 cohort foliage biomass and stem biomass growth (Figure 4c).

The 1999 stem biomass growth:fine root biomass ratios for loblolly and slash pine were not significantly different. Stem biomass growth: fine root biomass increased with increasing stand density (Table 2), with the ratio of the 740 trees ha^{-1} stands smaller than the ratios for the 2,220 and 3,700 trees ha^{-1} stands (Figure 5). The ratios for the loblolly pine stands planted at 3,700 and 4,400 trees ha^{-1} were 6.1 and 5.9 respectively. When the relationship between stem biomass growth and fine root biomass was examined (Figure 6), slopes for loblolly and slash pine were similar. There were significant differences among the slopes for the different
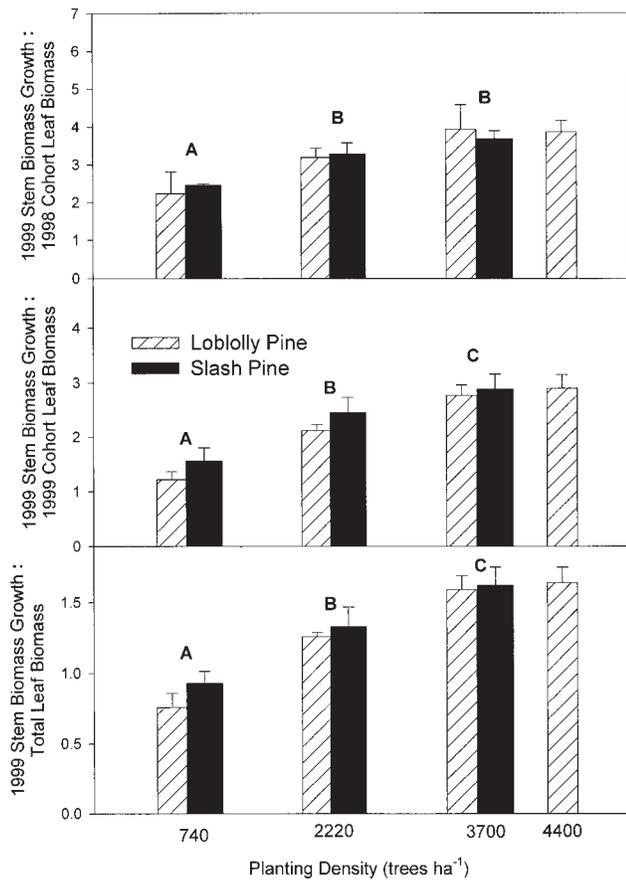
Figure 3. Growth efficiency calculated as stem biomass growth during 1999: leaf biomass of the 1998 foliage cohort, stem biomass growth during 1999: leaf biomass of the 1999 foliage cohort, and stem biomass growth during 1999: leaf biomass of the 1998 + 1999 foliage cohorts (total leaf biomass) for intensively managed, 4-yr-old loblolly and slash pine stands planted at different densities. Vertical bars represent one standard error. Different letters indicate a significant difference between planting densities ($P < 0.05$). Statistical significance was determined from a two-way ANOVA with site serving as the blocking variable.
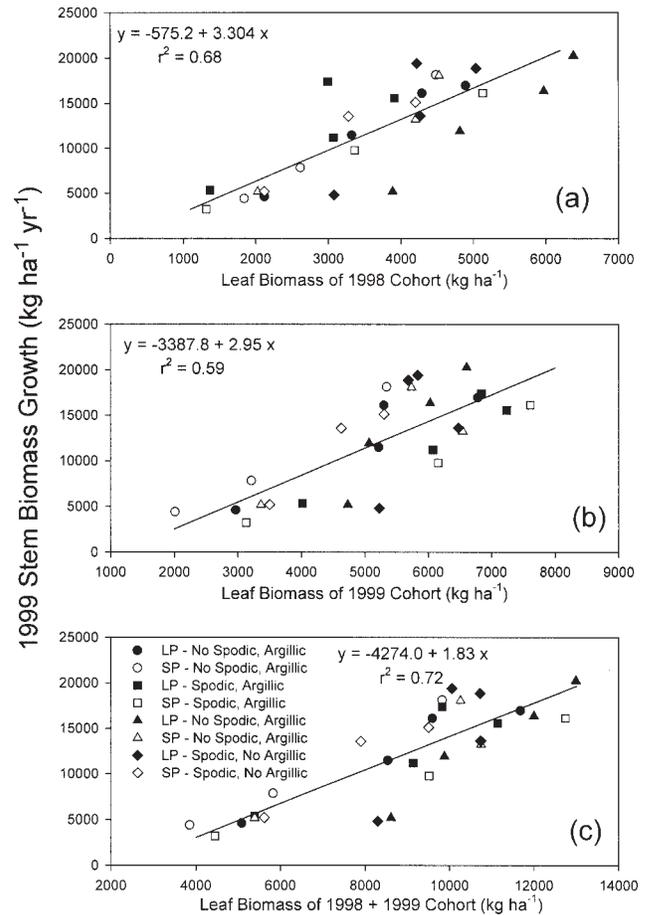

Figure 4. The relationship between stem biomass growth during the fourth growing season (1999) and leaf biomass of the 1998 foliage cohort (a), the 1999 foliage cohort (b), and the 1998 and 1999 foliage cohorts combined (c) for intensively managed loblolly and slash pine stands planted at different densities. Different symbols represent different sites and species (LP—loblolly pine, SP—slash pine). Each point represents a different plot.

sites, indicating that some sites had more fine root biomass per unit of stem biomass growth than others. In particular, the site with a spodic horizon, and no argillic horizon, had the most fine root biomass per stem biomass growth (Figure 6).

Total leaf biomass (1998 + 1999 cohort) best represents the quantity of leaf biomass in the canopies when fine root biomass was sampled in midsummer 1999. The ratios of fine root biomass:total leaf biomass were similar and not significantly different between stand densities (Table 2) (Figure 5). Also, the ratios were not significantly different between loblolly and slash pine stands. Although this ratio was fairly constant across planting densities and species, site had a large effect. The site with a spodic and no argillic horizon had more fine root biomass per leaf biomass than the other sites (Figure 6).

Discussion

Stem biomass growth was restricted by some factor(s) as stand density increased because stem biomass growth increased proportionally less than planting density for both loblolly and slash pine stands and appeared to reach a plateau for loblolly pine between 3,700 and 4,400 trees ha^{-1}. Fine root biomass and leaf biomass during the fourth growing season also increased proportionately less than planting density for loblolly and slash pine stands. In addition, when loblolly pine stands planted at 3,700 and 4,400 trees ha^{-1} were compared, site occupancy had apparently reached a maximum, as leaf biomass and fine root biomass were almost identical.

The growth rate of these stands at age 4 was exceptionally fast. The average stem biomass growth rates exceeded the greatest periodic stemwood biomass increments measured in loblolly and slash pine stands that received both fertilizer and interspecific competition control at a flatwoods site near Gainesville, Florida (Jokela and Martin 2000), 15 Mg ha^{-1} in that study vs. an average of 17.8 and 16.9 Mg ha^{-1}, respectively, for the highest density stands of loblolly and slash pine in this study. In addition, the stem biomass growth rates of the highest density stands in this study were similar to the maximum current annual increments measured for loblolly pine stands near Waycross, Georgia, receiving annual fertilization and complete interspecfic competition control (approximately 16.7 Mg ha^{-1}) that are generally considered to be some of the fastest growing stands in the southeastern United
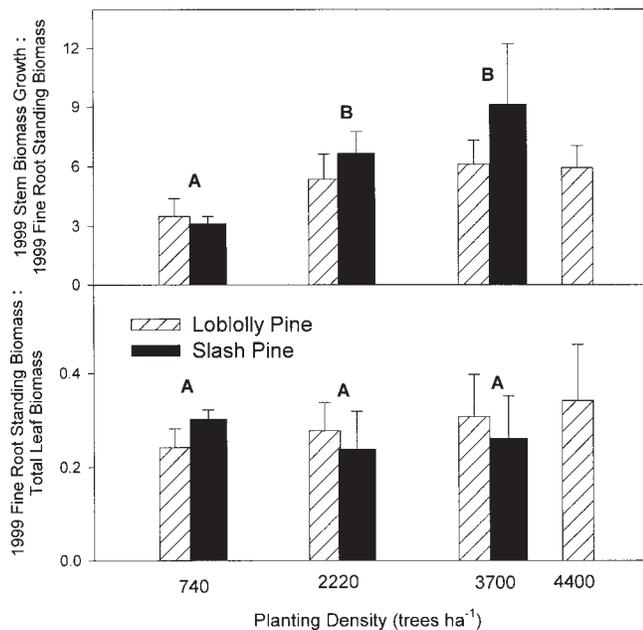
Figure 5. Ratio between stem biomass growth during the fourth growing season (1999) and fine root biomass during 1999, and fine root biomass and total leaf biomass (1998 and 1999 cohorts) during 1999 for intensively managed, 4-yr-old loblolly and slash pine stands planted at different densities. Vertical bars represent one standard error. Different letters indicate a significant difference between planting densities ($P < 0.05$). Statistical significance was determined from a two-way ANOVA with site serving as the blocking variable.
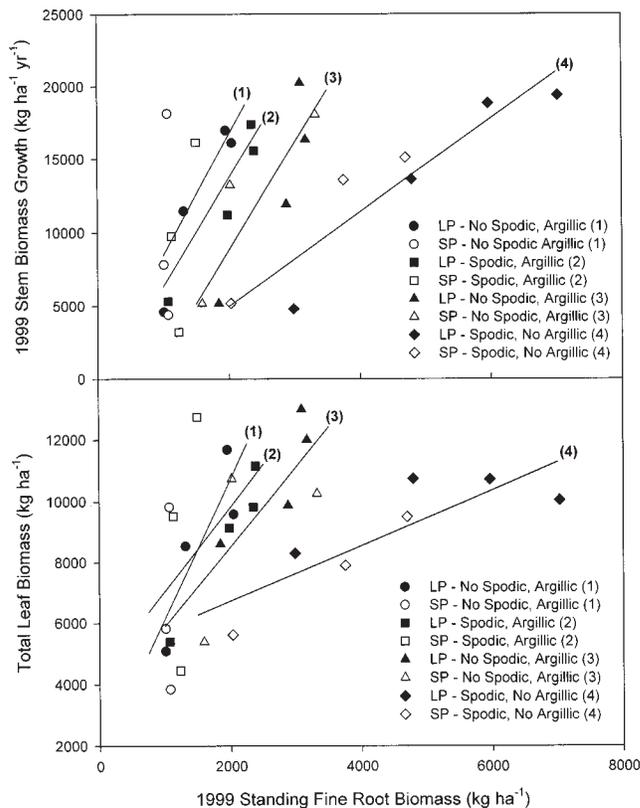

Figure 6. The relationship between stem biomass growth during the fourth growing season (1999) and fine root biomass during 1999, and relationship between total leaf biomass (1998 + 1999 cohorts) and fine root biomass during 1999 for intensively managed loblolly and slash pine stands planted at different densities. Different symbols represent different sites and species (LP—loblolly pine, SP—slash pine). The slope for each site is labeled with a different number. Each point represents a different plot.

States (Borders and Bailey 2001) and greater than fourth year growth (12.8 Mg ha^{-1}) than 4-yr-old stands receiving fertilization, irrigation, and pest control growing in southwest Georgia planted at a density of 1,126 trees ha^{-1} (Samuelson et al. 2001).

We could not separate bark and wood production during the fourth growing season. However, bark is a relatively minor component of the stem at this age in these exceptionally fast growing stands, composing 11 or 13% of the total stem volume. Estimates of stem biomass were based on outside bark diameter measurements and did not take into account different specific gravities of bark and wood. However, a previous study found that bark specific gravity of southern pines generally increases with height, 0.35 at groundline to 0.74 at 12 m for 16 m tall trees (Stohr 1980). Given the probable overlap in wood and bark specific gravities and the small contribution that bark made to total stem growth, any errors calculating stem biomass growth were minor.

Although leaf biomass increased between the 1998 and 1999 foliage cohorts, the increase between years was smaller for the stands planted at higher densities. This slowing in canopy development of the higher density stands indicates they were probably approaching maximum leaf development. Canopy size (leaf biomass or leaf area) typically reaches a peak as canopies close and then decreases with stand age (see review by Ryan et al. 1997). Using a chronosequence approach, peak annual production of leaf biomass occurred at age 14 (3.3 Mg ha^{-1}) for low input slash pine plantations (Gholz and Fisher 1982) and at age 30 (4.1 Mg ha^{-1}) for naturally occurring loblolly pine stands on a

good site (Switzer et al. 1966). However, due to the intensive management of these stands, we expect peak foliage to occur early during stand development. For loblolly and slash pine stands receiving fertilization and complete control of interspecific vegetation, needle fall reached maximums of 6.0 Mg ha^{-1} by age 8 and 7.0 Mg ha^{-1} by age 10, respectively (Jokela and Martin 2000) which are similar to the leaf production in our study at age 4.

Regardless of how GE was calculated, GE increased with increasing stand density. Growth efficiency either increased between stands planted at 740 and 2,220 trees ha^{-1} stands (calculated using 1998 cohort), or increased with each increase in planting density (calculated using the 1999 cohort or total leaf biomass). Therefore, a decrease in GE did not limit stem biomass growth as stand density increased. These findings do not support our original hypothesis and differ from previous studies that found the amount of stem production per unit of foliage was greater, in part due to higher average irradiance per unit foliage, for stands planted at lower densities (Waring 1983, Shelton 1984) or for lower density stands resulting from thinning (Brix 1983, Binkley and Reid 1984, Sheriff 1996). Although we did not quantify the light environment of foliage in our study, average irradiance experienced by foliage probably decreased as planting

density and leaf biomass increased. Earlier measurements of light saturated net photosynthesis on foliage from the upper half of the canopy indicated no differences in photosynthetic capacity occurred due to planting density (Will et al. 2001). Although not measured, photosynthetic capacity in the lower canopy was probably lower in the higher density stands because lower light environment probably caused morphological and physiological changes related to the production of shade foliage. Therefore, increased GE in higher density stands was not due to greater carbon gain per unit of foliage, i.e., higher density stands had lower average radiation intercepted per unit of foliage as well as no measured difference (upper canopy) and potential decrease (lower canopy) in photosynthetic capacity. Rather, the increase in GE of higher density stands probably was a result of increased biomass partitioning to stem relative to other tree components.

A better relationship existed between stem growth and the 1998 cohort leaf biomass than for stem growth and the 1999 cohort indicating that year-old foliage is a better determinant of stem biomass growth than current-year foliage. More than two-thirds of stem growth for loblolly and slash pine occurs before mid-June in the southeastern United States (Harkin 1962, Bassett 1966), which is before first-flush, current-year foliage is 25% of its final size (Chung and Barnes 1980a, Ragodlou and Teskey 1997). In addition, an assessment of loblolly pine photosynthate allocation using CO_2 exchange, growth, and biochemical composition indicated that current-year foliage was a net sink of carbon during the year it developed and that the carbon exported from branches to stem and root was almost exclusively produced by 1-yr-old foliage (Chung and Barnes 1980b). These differences in the relationship between stem biomass growth and the different foliage cohorts may be critical when examining GE in stands with canopies that change in size from year to year. As total leaf biomass (1998 + 1999 cohort biomass) was the best predictor of stem biomass growth, a more detailed model that incorporates factors such as needle accretion and needle abscission may result in very accurate estimates of stem growth.

Within each comparison of the relationship between leaf biomass and stem biomass growth, one slope was adequate to describe the response of the different species and sites. However, in all cases, the intercepts were negative. Because the intercepts were negative, GE decreased with decreases in planting density. A negative intercept in the relationship between foliage biomass and stem biomass growth may represent respiratory carbon use or growth of stand components other than stem having a higher priority for photosynthate. Therefore, a certain amount of foliage, and its photosynthate production, may be necessary before carbohydrate is made available for stem growth. Site variability in the relationship between 1998 cohort foliage biomass and 1999 stem biomass growth for loblolly pine was particularly apparent for the No spodic, Argillic site which had a more negative intercept than the other sites. This site difference could be size-related (more woody tissue to support) or related to water or nutrient availability. Following the 1999 growing season, the No spodic, Argillic site had the largest

trees with an average height more than 0.5 m taller than trees at the next tallest site.

Growth efficiency calculated as the 1999 stem biomass growth:1999 cohort foliage biomass represents the partitioning of biomass to these two stand components during 1999. GE calculated this way more than doubled as planting density increased from 740 to 3,700 trees ha^{-1}, indicating that during 1999, relatively more biomass was partitioned to stem growth compared to foliage growth at the higher densities.

In our study, the GE of loblolly and slash pine was not significantly different. A previous study examining the GE of young loblolly and slash pine stands receiving fertilization and competition control found that slash pine had significantly greater GE compared to loblolly pine (Colbert et al. 1990) in large part because slash pine partitioned more biomass to stem whereas loblolly pine partitioned more biomass to branch and foliage. Colbert et al. expressed GE on a leaf area basis. If we were to express the data from this study on a leaf area basis, slash pine also would have greater GE because slash pine had significantly lower specific leaf area than loblolly pine by approximately 20% (Will et al. 2001). However, the differences in GE between loblolly and slash pine found by Colbert et al. were greater than ours converted to a leaf area basis. Reasons for this difference could be associated with genetic stock (one half-sib family of each species used), site differences, stand age, or stage of stand development.

Compared to dominant loblolly pine trees, suppressed loblolly pine trees partition more biomass to bole than leaf or branch (Van Lear et al. 1984, Naidu et al. 1998). Therefore, a shift in biomass partitioning from branch and foliage to stem probably contributed to the greater GE of the higher density stands that were undergoing greater intraspecific competition. Similarly, trees with wide crowns partition a larger proportion of biomass into branch support (i.e., branch diameter growth) because branches are longer, and more foliage is located further from the stem (Ford 1985). Therefore, the amount of branch biomass per unit of stem biomass is greater at lower stand densities than at higher stand densities (Shelton 1984, Smith and Long 1989, Nilsson and Albrektson 1993, Puri et al. 1993). Rough estimates of branch biomass from our study, based on branch diameter and total number of branches, indicate that branch production per unit of stem biomass was about twice as great in stands planted at 740 trees ha^{-1} compared to stands planted at 2,220 and 3,700 trees ha^{-1} stand (data not shown).

Opposite our original hypothesis, the amount of standing fine root biomass per unit of stem biomass growth was significantly lower at the higher stand densities compared to the stands planted at 740 trees ha^{-1}. Similarly, Puri et al. (1993) found that the proportion of biomass partitioned to fine roots decreased as stand density increased in 9-yr-old *Populus deltoides* Bartr. ex Marsh, and Shelton (1984) found greater total root production in loblolly pine stands planted at lower densities. In contrast, Nilsson and Albrektson (1993) found that Scots pine (*Pinus sylvestris* L.) growing under a low level of intraspecific competition produced more stem volume per unit of fine root production than did stands

growing under high intraspecific competition. Using photosynthate to produce fine roots and exploit soil volume at the expense of stem growth could increase resource acquisition and subsequent stand growth. A trade-off between fine root production and stem growth has been reported previously (Santantonio 1989, Beets and Whitehead 1996). As the case with branch production, greater partitioning of biomass to fine roots at the expense of stem growth probably contributed to the lower GE of the stands planted at 740 trees ha^{-1}.

Increasing stand density had no significant effects on the overall relationship between fine root biomass and leaf biomass. Although there were significant differences between sites, a certain amount of fine root biomass appeared necessary to support a given amount of foliage regardless of planting density. Newton and Cole (1991) found increasing stand competition had no effect on root:shoot ratios of Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco). This suggests that roots and foliage exist in a "functional balance" (Davidson 1969). Sanantonio (1989) also found a positive relationship between foliage and fine root biomass and that the relationship depended on site quality for different aged *Pinus* species. In contrast, Nilsson and Albrektson (1993) found less leaf biomass per unit of fine root biomass in a higher density Scots pine stand than in a lower density stand.

In our study, site characteristics had a large effect on the relationship between stem biomass growth and fine root biomass and on the relationship between fine root biomass and leaf biomass (Figure 6). In particular, the site with a spodic, but no argillic horizon required substantially more fine root biomass per unit of stem biomass growth or leaf biomass. The site specificity of these ratios was probably due to the amount of fine root biomass necessary to support a given amount of leaf biomass on the different sites. Perhaps the absence of an argillic horizon reduced nutrient retention and decreased site fertility. This decrease in nutrient availability may have necessitated greater fine root production to provide enough nutrients to produce a given amount of leaf biomass. Decreased site fertility has been shown to increase the partitioning to fine root in loblolly pine (Albaugh et al. 1998, King et al. 1999). Another possibility is that differences in proximity of the water table to the soil surface or differences in seasonal inundation between the sites resulted in variation in the amount of fine root biomass production and turnover. Increased seasonal inundation could increase nutrient volatilization or fine root mortality. Both of these results may alter fine root production and greatly affect standing fine root biomass.

Our estimates of fine root biomass were of mid-summer standing crop during the fourth growing season. Fine root turnover varies throughout the growing season and ranges from 3,175 to 9,979 kg ha^{-1}yr^{-1} in coniferous forests (Waring and Schlesinger 1985). Fine root turnover is an important component of stand carbon dynamics, representing up to 77% of NPP (Fogel 1983). Since we did not estimate fine root turnover, measurements of standing crop fine root biomass during the fourth growing season may underestimate carbon partitioned to fine roots. In addition, rates of fine root turnover may depend on stand density. Shelton (1984) found

more fine root turnover in 22-yr-old loblolly pine stands growing at higher densities than stands growing at lower densities. Similar findings were reported in Scots pine (Nilsson and Albrektson 1993). Therefore, higher density stands might partition more biomass to fine roots even though standing crop biomass is similar.

Results from Shelton (1984) and Nilsson and Albrektson (1993) were from stands older than those in our study. Evidence does show that fine root turnover increases with age (Grier et al. 1981, Nambiar 1990). As a result, the lack of fine root turnover data may not be as large a source of error in our estimation of fine root biomass partitioning conducted on young, fertilized stands. Importantly, Nilsson and Albrektson (1993) found that fine root production was proportional to standing crop fine root biomass. Therefore, the fine root data in our study should be indicative of total partitioning of biomass to fine roots during the fourth growing season.

Results of this study indicate that higher density stands partitioned more biomass to stem production. Stem production per unit of foliage, and stem production per unit of fine root biomass were greater in higher density stands. As stand density increased, partitioning of biomass to components not measured in our study (branch, coarse root, and tap root) probably decreased or remained constant relative to stem biomass production. Branch production per unit of stem production is lower for trees planted at higher densities (Shelton 1984, Smith and Long 1989, Nilsson and Albrektson 1993, Puri et al. 1993). For loblolly pine, tap root is a fairly constant fraction of biomass relative to stem (Van Lear and Kapeluck 1995) and biomass partitioning to coarse root decreases relative to stem production as stand density increases (Shelton 1984). Therefore, decreased partitioning to stem relative to other stand components does not appear to limit stem biomass growth on a per hectare basis as planting density increases.

Rather than a change in biomass partitioning, the limitation in stem biomass growth rate that occurred at the stand level was probably due to a limitation or decrease in net primary production (NPP). Measurements of light saturated net photosynthesis of these stands did not indicate a decrease in the photosynthetic capacity in the higher density stands that might decrease the ability of foliage to produce photosynthate (Will et al. 2001). Similarly, respiration rates of foliage and stem biomass were similar between different density stands (Will et al. 2001), indicating that the limitation in NPP was not due to proportionately greater respiratory carbon use in higher density stands. Net primary production could have been limited by light interception or the ability of stands to produce foliage due to excessive within canopy shading or nutritional limitations. The implication of these findings is that, if anything, increasing planting density increases the proportion of fixed carbon used in stem production. Therefore, planting and maintaining high stand densities increases total stem productivity by increasing site resource use and by increasing partitioning to stem. However, other important factors such as wood quality or differences between total volume and merchantable volume must also be considered when choosing a planting density.

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