Biomass partitioning in a miniature-scale loblolly pine spacing trial

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Abstract: Stand conditions influence the partitioning of biomass to stem, needle, branch, and root components. Using data from 4- to 6-year-old loblolly pine (*Pinus taeda* L.) trees grown in a miniature-scale spacing trial, this study determined the effect of initial spacing on the biomass partitioning of loblolly pine. Multivariate analysis of variance procedures concluded that row and column spacing did not have a significant effect on the relative amount of biomass among tree components. Root/shoot and height/diameter ratios, however, differed across densities, indicating that allometric-based partitioning trade-offs occurred. Results from the miniature-scale trees showed trends similar to those observed with mature-sized trees at operational spatial scales. Stem and woody roots were 70% and 14% of total mass, respectively. Since these trees were physiologically young at the time of harvest, the allocation of mass to needle continued to be a priority, accounting for 10% of the total mass. Initial planting spacing did not directly affect partitioning patterns; however, allometric ratios offered some evidence that partitioning may have changed between above- and below-ground tree components. This analysis offers insight into using principles from similarity analysis to analytically relate biomass partitioning from miniature to operational spatial scales.

Résumé : La situation dans un peuplement influence la répartition de la biomasse entre la tige, les aiguilles, les branches et les racines. À l'aide de données provenant de tiges de pin à encens (*Pinus taeda* L.) âgées de 4 à 6 ans et croissant dans un test d'espacement à échelle réduite, cette étude a déterminé les effets de l'espacement initial sur la répartition de la biomasse chez le pin à encens. L'analyse de variance multivariée a permis de conclure que l'espacement des rangées et des colonnes n'a pas eu d'effet significatif sur la quantité relative de biomasse parmi les composantes de l'arbre. Cependant, les rapports racines/tige et hauteur/diamètre différaient selon la densité, indiquant que la répartition de la biomasse a fait l'objet de compromis basés sur l'allométrie. Les résultats provenant du test à échelle réduite ont montré des tendances similaires à celles qui ont été observées chez les arbres matures à une échelle spatiale opérationnelle. La tige et les racines ligneuses représentaient respectivement 70 % et 14 % de la masse totale. Étant sonné que ces arbres étaient physiologiquement jeunes au moment de la récolte, l'allocation de biomasse vers les aiguilles, qui représentait 10 % de la masse totale, continuait à être prioritaire. L'espacement initial n'a pas directement affecté les patrons de répartition. Cependant, les rapports allométriques fournissaient quelques indices que la répartition entre les composantes aérienne et souterraine pouvait avoir changé. Cette analyse fournit un aperçu de l'utilisation des principes de l'analyse de similarité pour relier de façon analytique la répartition de la biomasse en passant d'une échelle spatiale réduite à une échelle spatiale opérationnelle.

[Traduit par la Rédaction]

Introduction

Biomass partitioning in forests is controlled by tree growth patterns and environmental conditions. One environmental condition that is under direct control of loblolly pine (*Pinus taeda* L.) plantation managers is initial spacing. Economic returns, management goals, growth relationships, and desired end products are all considered prior to selecting the appropriate initial spacing for a given site. At the stand level, high densities encourage greater production per unit area while low densities promote larger tree diameters and earlier sawtimber production. Intraspecific competition increases as stand density increases, which can alter partitioning priorities (Burkes et al. 2003). When considering belowground stocks, initial planting density can play a valuable role in determining the distribution of biomass in loblolly pine plantations.

Loblolly pine trees allocate more mass to stem in double- and quadruple-row configurations in comparison to single-row trees grown in a silvopasture (Ares and Brauer 2005). This would suggest that high density stands allocate a greater proportion of their resources to stem production, which is supported by data from Scots pine (*Pinus sylvestris* L.) (Nilsson and Albrektson 1993) and eastern cottonwood (*Populus deltoides* Bartram ex Marsh) (Puri et al. 1994). Similarly, partitioning to stem increases as density increases at the expense of needle and fine root components (Burkes et al. 2003). Increasing stand density increases the fixed proportion of biomass belowground (Litton et al. 2003), indicating that root/shoot ratios increase as stand density increases.

One experimental tool that may help to investigate density-partitioning relationships is microcosm experiments. Miniature-scale plantations, an example of a microcosm study, contain trees growing at very close spacings to accelerate stand development. These small-scale plantations provide a condensed

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experimentation time. To draw links between these small-scale studies and their more traditionally scaled counterparts, applications from similarity theory need to be employed. Similarity is achieved when corresponding variables from two systems are proportional at corresponding locations and times (Skoglund 1967). If two systems use the same equation forms and if numerical values for nondimensional variables are equivalent for both systems, then the foundations for similarity are established (Sharma et al. 2003). One major aspect of the scaling problem is that within-tree growth relationships among biomass components, i.e., allometry, are size dependent (Amateis et al. 2003a). However, by selecting the appropriate scaling functions or parameters, inferences from small- to large-scale studies can be quantitatively linked.

Many studies have used miniature-scale experiments to investigate forest stand dynamics. Red alder (*Alnus rubra* Bong.) grown at spacings ranging from 2 cm × 2 cm to 8 cm × 8 cm exhibited the –3/2 power rule of self-thinning (Smith and Hann 1984). Miniature-scale loblolly pine plantations have been used to relate height and diameter (Amateis et al. 2003b; Strub and Amateis 2008) and height and diameter mean annual increment (Sharma et al. 2003) to values for trees grown at conventional scales. In the future, miniature-scale experiments could be used to rapidly test changing environments and evaluate the performance of clonal stock with specific ideotypes.

As loblolly pine plantations become ever more intensively managed, our knowledge of the influence of initial planting spacing on biomass partitioning needs to be expanded. The objectives of this research were to (1) determine the effects of spacing on the biomass partitioning of loblolly pine grown in a miniature-scale plantation and (2) qualitatively relate the results from the closely spaced trees to trees grown at operational spatial scales.

Methods

Data

A miniature-scale spacing trial planted with loblolly pine half-sib (Virginia Department of Forestry) was established adjacent to the Virginia Tech campus in Blacksburg, Virginia. Using the Lin and Morse (1975) split-block design, this miniature-scale plantation used a spacing factor of $F = 7.6$ cm. Four levels of this factor (7.6, 11.4, 15.2, and 22.9 cm) were used in row and column spacings, resulting in 16 treatment plots ranging in size from 2.845×10^{-5} to 2.561×10^{-4} ha. The most extreme spacing rectangularities were 3:1 and 1:3. Each measurement plot contained 49 trees with three rows of buffer trees separating adjacent plots. A second replication was planted on the same site upon the termination of the first.

The first replicate was planted on 4 May 1989. At approximately 2-week intervals, a 237 ppm water soluble nitrogen solution was applied to the study area, which covered approximately 3.716×10^{-3} ha. Fertilization occurred during the first growing season and ceased in mid-July. The total amount applied during the season was approximately 138 L. Fertilization procedures followed similarly for the second replication, which was planted on 4 May 1998 on the same site. The same family was planted in both replications.

Biomass data from a total of 108 sample trees were collected across the 16 plots from the two replications. Twenty-nine trees were harvested from the first replicate at the conclusion of the fourth growing season. Seventy-nine trees were harvested from the second replicate; 18 of these were harvested at the end of the fifth growing season and 61 at the end of the sixth growing season. Sample trees were collected randomly across all spacings. More sample trees were harvested from plots planted at lower densities because mortality was considerable at the very close spacings. One treatment (7.6 cm × 7.6 cm) was excluded because few trees remained in the plot at age of biomass harvesting and no trees were sampled. This resulted in 15 treatments used in the analysis. An unequal number of samples for all components resulted, and root measurements were only taken from second replication trees. The number of samples for the stem, needle, branch, and root components was 106, 102, 99, and 79, respectively. There were 67 trees that had all four component parts (stem, needle, branch, and root) and 96 trees that had all aboveground parts (stem, needle, and branch) sampled.

In summary, all age 4 trees (aboveground components only) were harvested from the first replicate and all age 5 and 6 trees (above- and below-ground) were from the second replicate.

Sample trees were cut at groundline and separated into their components. The stem was defined from groundline to tip, and branches from the point they contacted the stem out to their tip. Given that loblolly pine carries needles for two growing seasons and that trees were sampled during the dormant season, mass measurements for needles included only the previous year's cohort of needle. Roots were excavated with a hand shovel and defined from the groundline down, including taproot and all woody roots greater than 5 mm in diameter. All components were oven-dried to a constant mass prior to weighing.

Analysis

To determine the effect that row and column spacing had on the relative amount of biomass partitioned to each component, a stepwise multivariate analysis of variance procedure was initiated according to the methods of Jolliffe and Hoddinott (1988). To stabilize the variance associated with ratio-type data, the arcsine transformation was placed on the biomass proportions prior to this analysis, as calculated by

$$[1] \qquad p' = \arcsin \sqrt{p}$$

where p and p' are the observed and transformed proportions, respectively. The transformed proportions from the individual components harvested were used as the response variables.

Relative spacing (RS), a measure of stand density and an index of competitive stress, was calculated at the end of each growing season (Beekhuis 1966). RS was calculated by

$$\mathrm{RS} = \frac{\sqrt{10\ 000/N}}{H}$$

where N is the number of trees per hectare and H is the average height (m) of the dominant canopy, defined as the mean height of all trees greater than the average stand diameter.

Table 1. Mean plot groundline diameter and height at the end of the fourth and fifth growing season for loblolly pine trees grown in a miniature-scale plantation at nine initial planting densities.

Initial planting density (100 000 trees·ha^{-1})	Groundline diameter (mm)		Height (cm)	
	Age 4	Age 5	Age 4	Age 5
1.91	31.2 (8.2)	38.9 (9.7)	256 (40)	360 (53)
2.87	27.7 (7.9)	35.3 (9.2)	243 (44)	369 (55)
3.83	25.5 (7.7)	32.6 (10.6)	234 (44)	345 (65)
4.31	25.0 (7.3)	32.1 (5.6)	232 (40)	357 (33)
5.74	21.7 (6.2)	26.1 (10.0)	214 (43)	313 (68)
7.65	18.3 (6.6)	34.3 (15.4)	188 (34)	329 (27)
8.61	20.6 (6.5)	26.9 (12.1)	207 (34)	293 (57)
11.5	17.8 (5.1)	24.6 (8.4)	199 (38)	300 (49)
17.2	19.3 (7.1)	26.0 (9.4)	227 (50)	342 (67)

Note: Means for age 4 include observations from both replicates; means for age 5 include observations from second replicate, only. Standard errors are provided in parentheses.

Fig. 1. Mean live crown ratios of a miniature-scale loblolly pine plantation at the end of each growing season for initial square spacings of 7.6 cm × 7.6 cm (◆), 11.4 cm × 11.4 cm (■), 15.2 cm × 15.2 cm (▲), and 22.9 cm × 22.9 cm (×). The means for age 5 include observations from second replicate, only.
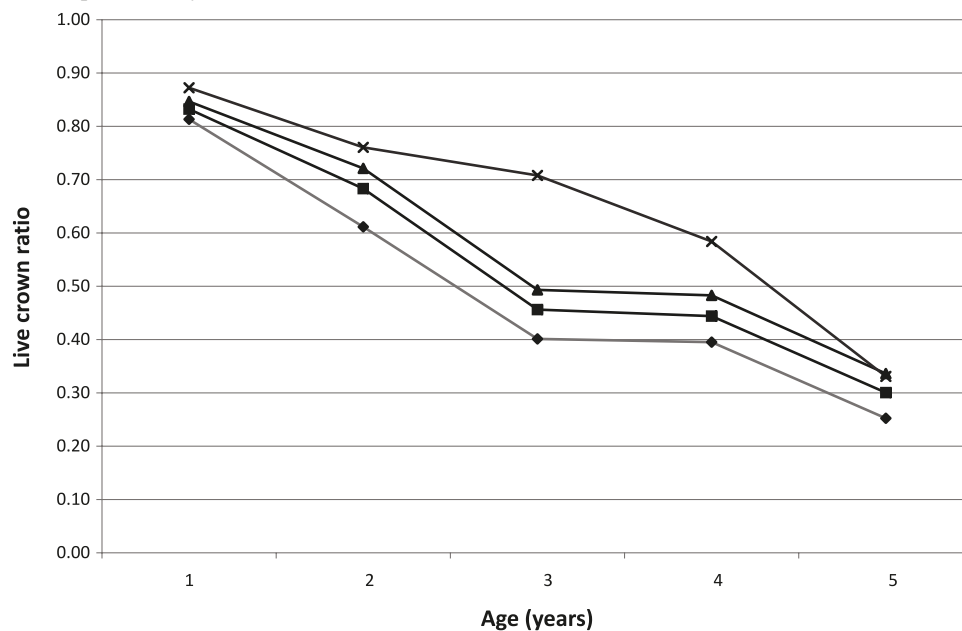
To examine the variability in terms of predicting component biomass for the miniature-scale trees, a system of linear equations fitted with seemingly unrelated regression (SUR) was developed (Parresol 2001) and additivity was specified (Kozak 1970). A system that adequately predicted the component masses was

$$
\begin{aligned}
y_{\text{stem}} &= b_{10} + b_{11}D^2H + b_{12}A + \varepsilon \\
y_{\text{needle}} &= b_{20} + b_{21}D^2\text{LCL} + \varepsilon \\
[2] \quad y_{\text{branch}} &= b_{30} + b_{31}D^2H + \varepsilon \\
y_{\text{root}} &= b_{40} + b_{41}D^2H + \varepsilon \\
y_{\text{tree}} &= b_{50} + b_{51}D^2H + b_{52}D^2\text{LCL} + b_{53}A + \varepsilon
\end{aligned}
$$

where y_c is the observed component (or total tree) mass (g), D is the groundline diameter (mm), H is the total tree height (cm), A is the tree age (years), LCL is the live crown length (cm), ε is the random error (assumed normally distributed with constant variance), and b_{ij} are the coefficients to be estimated for the jth parameter in the ith equation. The fit index (FI) was computed to evaluate the performance of eq. 2,

$$
\text{FI} = 1 - \left[\frac{\sum (y_c - \widehat{y}_c)^2}{\sum (y_c - \overline{y}_c)^2} \right]
$$

where $\widehat{y}_c$ is the predicted component (or total tree) mass (g) and $\overline{y}_c$ is the mean observed component (or total tree) mass (g). The b_{ij} coefficients in eq. 2 were estimated using the SYSLIN procedure (SAS 1995).

Fig. 2. Relative spacing development for replication 1 (*a*) and 2 (*b*) for four square spacings of 7.6 × 7.6 cm (◆), 11.4 × 11.4 cm (■), 15.2 × 15.2 cm (▲), and 22.9 × 22.9 cm (×) in a miniature-scale loblolly pine plantation.
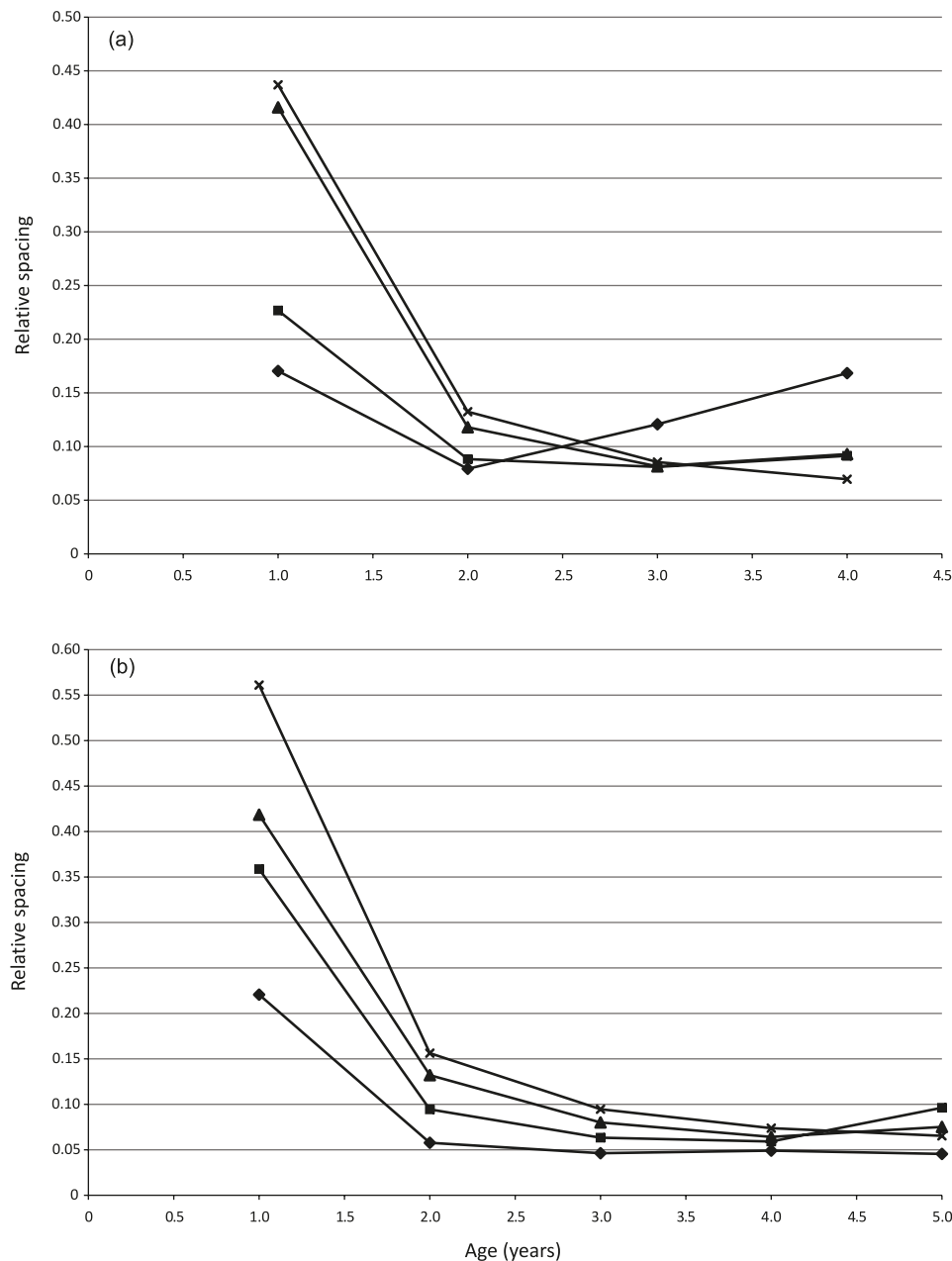
Results

Mean tree height and groundline diameter for each initial planting density at ages 4 and 5 are shown in Table 1. Tree groundline diameter and height were both found to be significantly negatively correlated with initial planting density ($P <$ 0.001). Averaged across both replications, height/diameter ratios (m/mm) at age 4 were 0.0826, 0.0928, 0.1044, and 0.1195 for square spacings of 22.9 cm × 22.9 cm, 15.2 cm × 15.2 cm, 11.4 cm × 11.4 cm, and 7.6 cm × 7.6 cm, respectively. Mean live crown ratios (LCRs) at age 5 for the second replicate trees were 0.33, 0.34, 0.30, and 0.25 for those same spacings (Fig. 1). Relative spacing for square spacings converged to a lower asymptote in both replications (Fig. 2).

Homogeneity of variance for the ANOVA was assumed from the arcsine transformation placed on the proportions prior to the analysis (eq. 1). ANOVA procedures concluded that for most row and column spacings, biomass proportions were largely not affected by initial spacing (α = 0.05; Table 2); however, root partitioning was affected by row and column spacing at age 6. When considering all tree components taken together, P values for Wilks' λ and Pillai's trace, two MANOVA test statistics that arise from the assumption of homogeneity of covariance matrices, confirmed that partitioning was not affected by spacing treatments (Table 3). Tests of block effects were not available with this experimental design. Overall, the stem occupied 68%, 79%, and 83% and needle accounted for 22%, 15%, and 10% of aboveground mass at ages 4, 5, and 6, respectively. When

Table 2. Analysis of variance results (*P* values) for testing the effect of row (R), column (C), and row × column (R×C) spacing on the relative amount of biomass partitioned to loblolly pine tree components in a miniature-scale plantation.

| Age | Effect | Relative biomass partitioned to: | | | |
		Stem	Needle	Branch	Root
4	R	0.147	0.323	0.492	—
	C	0.008	0.156	0.204	—
	R×C	0.443	0.286	0.700	—
5	R	0.333	0.721	0.910	0.338
	C	0.866	0.986	0.983	0.528
	R×C	0.061	0.246	0.558	0.538
6	R	0.289	0.078	0.295	0.009
	C	0.004	0.068	0.099	0.015
	R×C	0.185	0.438	0.333	0.166

Note: Proportions transformed with the arcsine transformation.

Table 3. Multivariate analysis of variance results (*P* values) for testing the effect of row (R), column (C), and row × column (R×C) spacing on the relative amount of biomass partitioned to all loblolly pine tree components in a miniature-scale plantation.

| Age | Effect | Test statistic | |
		Wilks' λ	Pillai's trace
4	R	0.212	0.203
	C	0.018	0.066
	R×C	0.701	0.737
5	R	0.950	0.903
	C	0.860	0.857
	R×C	0.664	0.692
6	R	0.389	0.377
	C	0.120	0.126
	R×C	0.249	0.231

Note: Proportions transformed with the arcsine transformation. An explanation of test statistics can be found in (Srivastava 2002).

Table 4. *P* values for the slope estimate associated with the regression equation $\hat{R} = b_0 + b_1(N)$ for 4- to 6-year-old loblolly pine grown in a miniature-scale plantation.

| | Age | | | |
	4, 5, and 6	4	5	6
Root/shoot	0.020 (+)			
Root/stem	0.017 (+)			
Needle/root	0.018 (–)			
Branch/root	<0.001 (–)			
Branch/stem	0.870			
Branch/needle	0.488			
Branch/shoot	0.580			
Stem/shoot	0.289			
Needle/stem		0.123	0.895	0.006 (–)
Needle/shoot		0.099	0.993	0.014 (–)

Note: Slope coefficients were not significantly different among the three ages for all mass ratios except for needle/stem and needle/shoot. + and – indicate direction of slope. In the equation, $\hat{R}$ is the estimated mass ratio and *N* is the initial planting density.

Table 5. Parameter estimates and *P* values associated with the regression equation $\hat{P} = b_0 + b_1(\text{LCR})$ for 4- to 6-year-old loblolly pine grown in a miniature-scale plantation.

Proportion	b_0	*P* value	b_1	*P* value
Above- and below-ground				
Stem	0.79	<0.001	–0.25	<0.001
Needle	0.05	0.004	0.15	0.003
Branch	0.02	0.005	0.10	<0.001
Root	0.14	<0.001	–0.001	0.965
Aboveground				
Stem	0.94	<0.001	–0.35	<0.001
Needle	0.04	<0.001	0.24	<0.001
Branch	0.03	<0.001	0.11	<0.001

Note: In the equation, $\hat{P}$ is the estimated proportion and LCR is live crown ratio.

the mean component proportions were plotted against initial planting density, no discernable trend was seen (Fig. 3).

The FI values for a system of additive equations fitted with SUR were 0.965, 0.889, 0.896, 0.949, and 0.970 for the stem, needle, branch, root, and total trees mass equations, respectively.

Defining shoot as the sum of stem, needle, and branch masses, the mean root/shoot ratio for trees aged 5 and 6 across all densities was 0.16 with a standard deviation of 0.03. Root/shoot ratios ranged from 0.10 to 0.25. When regressed against planting density, the slope showed a significant positive slope (*P* = 0.020; Fig. 4).

To determine where the allocation tradeoffs were occurring in the dataset, the equation $\hat{R} = b_0 + b_1(N)$ was fitted to the data. $\hat{R}$ is an estimated component/component mass ratio (such as root/stem ratio) and *N* is the initial planting density (trees·ha^{-1}). Every ratio that included the root component was determined to have a significant slope for *N* (Table 4). Allometric ratios that included any two aboveground components were not found to be significant, with

the exception of the needle/stem and needle/shoot ratios at age 6 (the slope on these ratios shifted each year in trees ages 4, 5, and 6). For trees aged 4, 5, and 6, the mean needle/stem ratios were 0.32, 0.19, and 0.13 and the mean needle/shoot ratios were 0.22, 0.15, and 0.10, respectively.

LCRs from 96 harvested trees at ages 4, 5, and 6 ranged from 0.16 to 0.79 with a mean of 0.45. The equation $\hat{P} = b_0 + b_1(\text{LCR})$ was fitted to the data, where $\hat{P}$ is the estimated proportion. LCR was a significant variable in predicting the relative proportion of mass in each component, with the exception of roots (Table 5). Trees with smaller crown ratios allocated more to stem and less to canopy components (Fig. 5).

Discussion

Effects of spacing on partitioning

Row and column spacing did not have a significant effect ($\alpha = 0.05$) on the relative amount of biomass partitioned to tree components in this miniature-scale plantation. Given

Fig. 3. Mean biomass proportions within each tree component at each initial planting density for (*a*) above- and below-ground mass (ages 5 and 6) and (*b*) aboveground mass (ages 4, 5, and 6) for loblolly pine grown in a miniature-scale plantation.
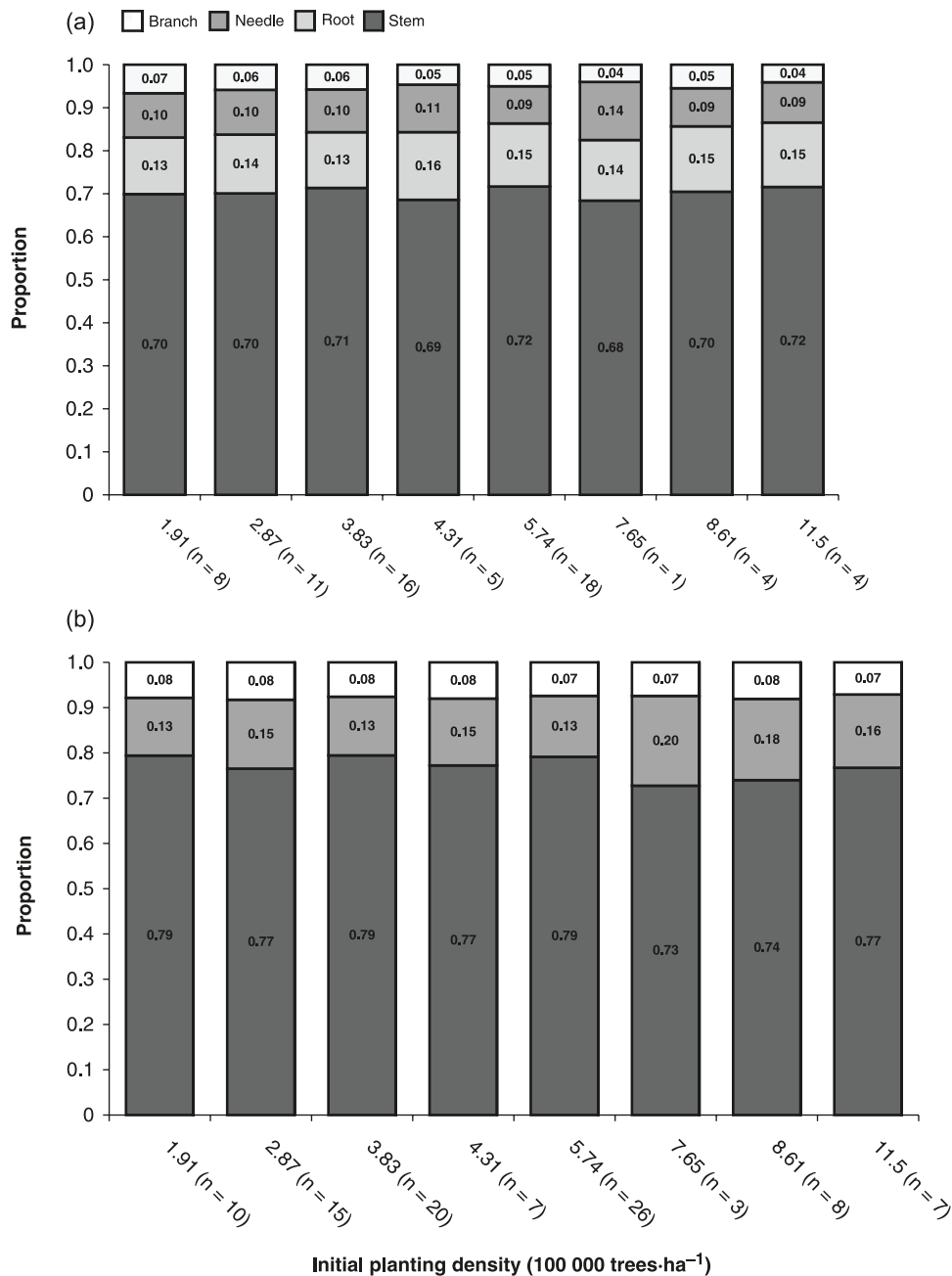
these results, a stepwise approach to analyze the multivariate nature of the biomass proportions, according to the methods of Jolliffe and Hoddinott (1988), is not warranted. These results parallel Shelton (1984) who found that stand density did not affect the aboveground biomass partitioning (stand level) of loblolly pine. The mean proportion of biomass in the stem component ranged from 0.68 to 0.72 when considering above- and below-ground mass from densities of 1.91×10^5 to 11.5×10^5 trees·ha^{-1}, and 0.73 to 0.79 when taking into account aboveground mass solely. No trend is observed when mean component proportions are plotted against initial planting density. Given that the relative spacing index for the miniature-scale trees planted at square spacings converged to an asymptote around 0.1 at age 4,

density-dependent mortality undoubtedly occurred. By age 4, trees planted at different initial spacings appear to be at similar competitive stress levels, possibly attributing to the result that spacing did not affect partitioning. Also, given that more trees were sampled from plots with lower initial planting densities (Fig. 3), the presence of spacing effects may have been underestimated. Sampling equally across all spacings would partition the variance differently among the different row and column combinations.

However, when considering components on an allometric ratio approach, there was some evidence of partitioning tradeoffs (Table 4). Higher root/shoot ratios have been observed in dense stands of lodgepole pine (Litton et al. 2003) and red pine (King et al. 2007), and the results in this study

Fig. 4. Root/shoot ratios for 5- and 6-year-old loblolly pine grown at eight planting densities in a miniature-scale plantation.
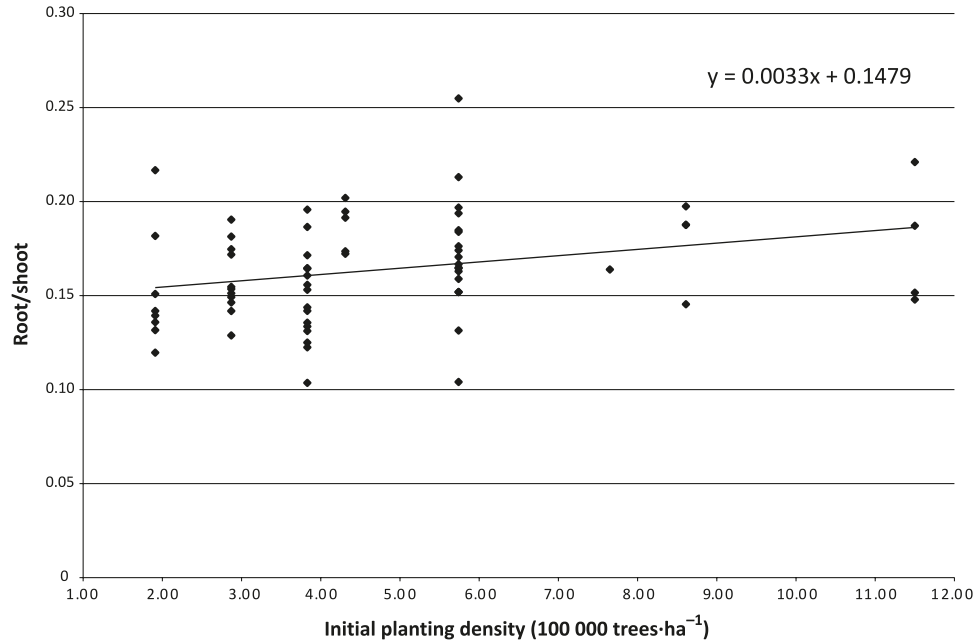
Fig. 5. Live crown ratios and relative proportions of mass in tree components for 5- and 6-year-old loblolly pine grown in a miniature-scale plantation at eight planting densities.
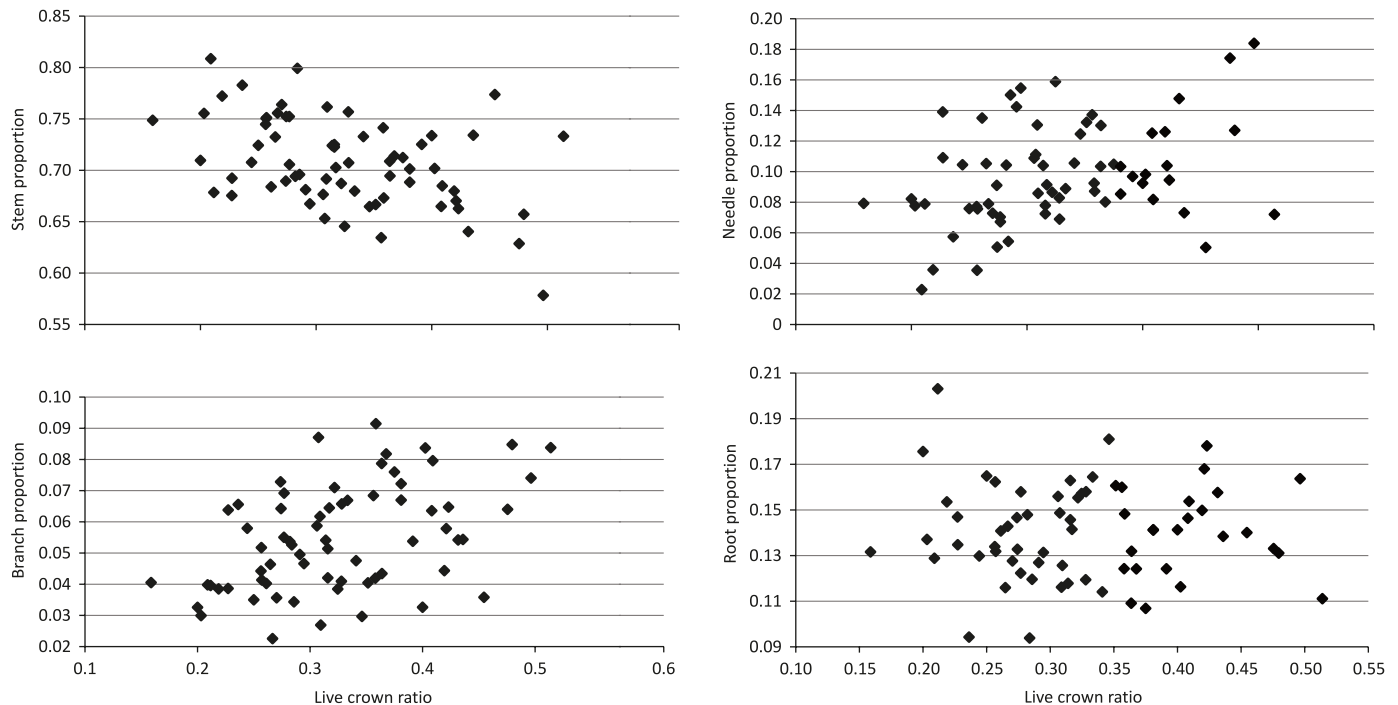
showed similar trends. The increase in height/diameter ratio for trees grown at greater stand densities provides additional indications that allometric ratios changed across different densities.

Albaugh et al. (1998) concluded that shifts in biomass allocation aboveground caused by fertilization are small relative to the above- versus below-ground tradeoffs; our data support this statement to some extent with regard to density rather than fertilization. Allometric ratios involving the root component in Table 4 show a significant slope when fitted

against trees per hectare. With the exception of the needle/shoot and needle/stem ratios at age 6, no ratio involving two aboveground components showed a significant slope. Combining these results with those of Shelton (1984), it appears that density effects on biomass partitioning may result when considering both above- and below-ground components rather than studying aboveground components only.

When measured on a continuous scale, LCR was a significant predictor for the proportion of mass in aboveground components. The signs for the slope estimates in Table 5 in-

Table 6. Comparison of loblolly pine biomass partitioning in a miniature-scale plantation to operational-scale plantations 15–25 years old.

Study	Age (years)	Percentage of mass partitioned to:				Notes
		Stem	Needle	Branch	Root	
Above- and below-ground						
Miniature-scale study ($n = 67$)	5 and 6	71	10	5	14	
Wells et al. 1975	16	65	4	12	19	Thinned once
Naidu et al. 1998	10–48	63	11	13	12	Dominant trees
		76	7	6	12	Suppressed trees
Pehl et al. 1984	16	65	4	12	19	Value for root is taproot only
	25	72	2	7	17	
Aboveground						
Miniature-scale study ($n = 96$)	4, 5, and 6	78	14	8	—	
Smith et al. 1963	23	78	8	14	—	
Albaugh et al. 2004	16	67	5	27	—	Control
		70	6	24	—	Irrigation
		71	4	24	—	Fertilizer
		75	5	20	—	Fertilizer × irrigation
Metz and Wells 1965	21	82	5	13	—	Means for two 21-year-old trees

dicate that trees with large crown ratios partition less mass to stem and more to canopy components. The results from this miniature-scale study confirm those of Van Lear et al. (1984) and Naidu et al. (1998) who found that more suppressed trees, i.e., those trees with smaller LCRs, have a greater proportion of heterotrophic than autotrophic tissue.

Comparing results with that of operationally spaced studies

One issue that arises in comparing the results found in this miniature-scale study with that of operational scales is accounting for the differences between scales. As an example, loblolly pine grown at miniature scales had not yet flowered, so no photosynthate was allocated to reproductive structures in these sample trees. For trees grown at operational scales, however, cone mass on a stand level is likely to be small. (Satoo (1982) estimates as little as 2 Mg·ha^{-1} of total stand mass is contributed by cones in *Pinus* trees.) Similarly, trees grown at small scales will show a different allometry than trees at traditional scales (Amateis et al. 2003*a*). Given these differences and considering the variability in sites across various studies, evaluating only the general trends of biomass partitioning between miniature and operational scales is possible.

As a relative measure of tree development, LCR could be used as a variable for modeling from miniature to operational scale. Using the results from this study, one hypothesis (although not statistically testable) is that biomass partitioning patterns are similar for two trees that have comparable crown ratios, regardless of the scale at which they are grown. Crown ratios for 5-year-old trees in this study are roughly 0.30 (Fig. 1), which is equivalent to what one would expect for loblolly pine plantations at or near rotation age. Similarity theory practitioners would consider this a 1:1 scaling function. If two trees have the same crown ratio, but the amount of time and physiological processes differ in the way they reach that value, is the relative amount of biomass allocated to component parts similar for those two trees?

The aim here is to qualitatively evaluate the general trends of biomass partitioning observed at the miniature scale to those with mature trees at operational scales. To make this comparison, studies with trees ages 15–25 were examined with the assumption that these trees displayed similar crown ratios to those in our study.

Comparisons of the results of this study with that of mature trees at operational scales can be seen in Table 6. Generally, it appeared that our trees were allocating a large proportion of biomass to the needle component, which received 10% of above- and below-ground allocation and 14% of aboveground allocation. Given that only one cohort of needle was sampled, needle mass would be approximately double if harvests occurred at some time during the growing season; however, most studies with loblolly pine biomass are sampled during the dormant season, allowing a fairly direct comparison across studies. Needle mass in this study is high when compared with that of other studies, although needle mass did occupy 11% of total stand mass for dominant trees ages 10–41 years (Naidu et al. 1998). Leaf biomass typically reaches a peak as canopies close, and then decreases with stand age (Burkes et al. 2003). A decrease in the amount of mass partitioned to needle from the ages of 4–6 was observed in this study. Samuelson et al. (2004) noted a decrease in the amount of mass partitioned to needle between ages 4 and 5 for trees under different management intensities. Burkes et al. (2003) also found that needle biomass was decreasing at higher densities by age 4, postulating that leaf development was soon approaching a maximum. Although this miniature-scale plantation went through accelerated stand development, in terms of partitioning mass to needle, these trees showed similar trends to trees of the same age grown at large scales. This suggests that decreased partitioning to needle may be primarily a function of tree age, and miniature spacings do not induce trees to allocate less biomass to needle at earlier ages.

Mean individual tree branch biomass percentages (5% of above- and below-ground and 8% of aboveground mass, re-

spectively) were low for these trees in comparison with mature trees at operational scales. Branch and needle biomass occupied around 28% and 38%, respectively, of aboveground stand biomass in 3-year-old trees (Samuelson et al. 2004). Similarly, branch mass exceeded needle mass in 5-year-old trees with different combinations of genetics and fertilization (Retzlaff et al. 2001). In contrast, in a 23-year-old stand, Smith et al. (1963) found 14% and 8% of aboveground mass allocated to branch and needle components, respectively, and these same components contained 19% and 3% of aboveground biomass in a 48-year-old stand (Van Lear and Kapeluck 1995). The results of this study, in combination with previous research, indicate that needle mass tends to exceed branch mass in young trees, and vice versa for mature trees. By forcing loblolly pine through stand development at an earlier chronological age, partitioning to canopy components resembled that of young trees grown at large scales. Nevertheless, given these disparities between scales, similarity analysis methodologies could be applied to account for these differences by selecting the appropriate scaling functions.

The mean root/shoot ratio across all densities in this study was 0.16. This value is less than the 0.18–0.35 range reported for pine and other conifers (Cairns et al. 1997). Similarly, root mass averaged 14% of total tree biomass in this study, which is slightly less than the value reported by Miller et al. (2006) for 23-year-old trees (19%–24%) but is in the range of 13%–25% given for various species of pine (Nemeth 1973). The low percentages for the root component in this study may be because only roots greater than 5 mm in diameter were sampled, which were composed primarily of woody roots. By not sampling the fine root component, root allocations would naturally be lower when compared with that of other studies that sampled roots to a smaller diameter. Fine roots can occupy 3%–7% of total stand biomass in pine forests in general (Knight et al. 1994), or 2% in mature loblolly pine stands (Van Lear and Kapeluck 1995). Sampling roots to a smaller diameter would increase the belowground mass pool, increasing partitioning to roots on a stand level and increasing root/shoot ratios. Also, new foliage tends to have priority over new root growth (Waring and Pitman 1985), which could be why this study showed a high proportion for needle mass and a low proportion for root mass.

Average height/diameter ratios of 0.0826, 0.0928, 0.1044, and 0.1195 for densities of 1.91, 4.31, 7.65, and 17.2×10^5 trees·ha^{-1} were observed at age 4. Burkes et al. (2003) found height/diameter ratios of 0.0551, 0.0663, 0.0731, and 0.0768 for 4-year-old trees growing at densities of 740, 2220, 3700, and 4400 trees·ha^{-1}, respectively. The results from this study mirror those of Burkes et al. (2003) by showing an increase in height:diameter ratio as stand density increases. Generally, it is thought that density effects have minimal affect on height growth, however, a significantly negative correlation ($P < 0.001$) existed between height and initial planting density in these trees. The larger height/diameter ratios seen in this study most likely occurred because trees allocated a considerable amount of photosynthate to height growth caused by being under high competitive stress. Given that loblolly pine is shade-intolerant, increasing height growth to outcompete neighboring trees for light is

a priority. These results, coupled with the finding that trees with low crown ratios allocated more to stem, confirm those of Van Lear et al. (1984) and Naidu et al. (1998) who found that height growth, and hence stem growth, is a priority for suppressed trees.

Amateis et al. (2003a) showed that height and diameter growth progress similarly at both miniature and operational scales. This analysis showed similar variability in terms of predicting tree biomass components at both scales. FI values for the stem and needle were 0.960 and 0.889, respectively. One prerequisite for similarity analysis is that the equation forms be identical for both scales (Sharma et al. 2003). Hence, the ability for miniature-scale studies to use equation forms (as seen in the combined variable D^2H in eq. 2) similar to that commonly used for trees growing at more traditional scales is practical. Similarity principles can be employed to address the growth and yield responses of trees with alternative silvicultural regimes or varying climatic conditions.

Conclusions

Initial spacing did not affect biomass partitioning in this miniature-scale plantation; however, allometric ratios showed some indications of allocation tradeoffs. Competitive stress levels need to be acknowledged when considering tree biomass data. In particular, allometric ratios offer some evidence that partitioning may change between above- and below-ground components.

In terms of biomass partitioning, the trends observed with these miniature-scale plots showed the same general trends when compared with operationally spaced stands. The amount of variability that occurred in this miniature-scale plantation in terms of biomass prediction was comparable with what others have found for trees grown in operationally spaced stands. Stem growth was a priority for suppressed trees, and trees with small crown ratios allocated more biomass to stem. Similarly, root/shoot ratios changed across the different initial planting densities. The results from this small-scale study indicate that spacings can affect the allometry of loblolly pine when considering above- and below-ground biomass components.

Given the similarities between miniature- and operational-scale studies, using miniature-scale experiments to model partitioning patterns at operational scales can be achieved using principles from similarity analysis. Assuming that one employs a large-scale tree biomass dataset and selects the appropriate scaling functions to model between the two scales, equations could be developed for estimating component biomass for trees grown at operational scales. Miniature-scale studies can also possibly be used in the future to quantify gains originating from silvicultural decisions, such as estimating the yield response of trees from the planting of clonal stock.

Acknowledgements

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