# MODELING THE BIOMASS PARTITIONING OF LOBLOLLY PINE GROWN IN A MINIATURE-SCALE PLANTATION

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## ABSTRACT

Stand conditions influence the partitioning of biomass to stem, foliage, 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 planting density on the biomass partitioning of loblolly pine. An analysis of covariance concluded that density did not have a significant effect ($\alpha = 0.05$) on the relative amount of biomass in aboveground components. Some measures of partitioning tradeoffs (such as root: shoot ratio) showed a significant positive slope when regressed against trees ha$^{-1}$. Systems of linear equations were developed based on tree measurements and age, and additivity was specified. By taking into account contemporaneous correlations among tree components, seemingly unrelated regression (SUR) methodologies led to efficient parameter estimates. When compared to studies with mature trees at operational scales, results from the miniature-scale trees showed similar trends. Stem and woody roots were 70 and 14% of total mass, respectively. Since these miniature-scale trees were physiologically young at time of harvest, allocation of mass to foliage continued to be a priority, occupying 10% of total mass.

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CHAPTER 1

JUSTIFICATION AND OBJECTIVES

**1.1 Justification**

Loblolly pine (*Pinus taeda* L.) is an important commercial tree species in the southeast United States and is highly responsive to silvicultural treatments. One silvicultural treatment that is under the control of loblolly pine plantation managers is initial planting density. Planting density influences stand development and subsequent silvicultural decisions. Quantifying the role that planting density has on the growth and yield response of loblolly pine is important because it will give plantation managers a clearer understanding concerning carbon sequestration and the products obtained from trees.

Biomass partitioning, the proportion of biomass allocated to stem, needle, branch, and root components, is important because it reveals how trees distribute resources to grow. Studying partitioning is vital in our understanding of ecosystem productivity and energy flow processes. Biomass partitioning patterns may change depending on stand conditions.

Miniature-scale studies are cost-effective experiments that enable researchers to obtain results more quickly than traditional studies. Treatments can be easily applied to small-scale experiments and extraneous variables can be easily controlled. The ability to quantitatively link small-scale studies to their large-scale counterparts makes miniature-scale plantations appealing to researchers investigating issues affecting loblolly pine plantations.

Determining the effects that initial planting density has on the biomass partitioning of loblolly pine at a small scale is of great practical value. Results from this investigation will give

plantation managers a clearer understanding concerning the role of planting density on biomass distribution in loblolly pine plantations. This research will also be beneficial to those seeking to quantify biomass levels for above and belowground components in some of the most productive and intensively managed forests in the world.

**1.2 Objectives**

The main objective of this research was to quantify the effects of initial planting density on the biomass partitioning of closely-spaced, young loblolly pine. Specific objectives were to:

(1) Determine the impact of initial planting density on the biomass partitioning of 4 to 6-year old loblolly pine grown in a miniature-scale plantation.

(2) Create systems of equations which predict loblolly pine component and total tree mass in terms of dry weight.

(3) Relate results from the closely-spaced trees to more conventionally-spaced trees.

CHAPTER 2

LITERATURE REVIEW

**2.1 Biomass partitioning patterns of loblolly pine**

The biomass production potential of a forest stand is correlated with the capacity of the stand to intercept light (Albaugh *et al.*, 1998). Biomass allocation is the distribution of biomass to each individual plant component and allocation patterns are a function of source-sink interactions. Generally, biomass allocation is controlled by plant factors (i.e. growth patterns) and environmental conditions (Friend *et al.*, 1994). In a given environment, a tree will partition its resources to the various structures and processes so that the result is maximum carbon gain. Waring and Schlesinger (1985) and Oliver and Larson (1990) affirm that trees undergo a hierarchy of allocation, where new foliage has priority followed by new roots and stem growth. Differences exist in the carbon partitioning of seedlings and mature trees, and partitioning patterns change as trees age (Gower *et al.*, 1995). Individual-tree root biomass increases as tree diameter increases in order to uphold a balance between above and belowground components (Waring and Schlesinger, 1985; Van Lear and Kapeluck, 1995).

The relative amount of biomass in the different components of loblolly pine changes throughout stand development (Naidu *et al.*, 1998; Albaugh *et al.*, 2004; Johnsen *et al.*, 2004; Albaugh *et al.*, 2006). At the start of stand development, a disproportionate amount of a tree's carbohydrate reserve is spent on producing foliage, while later in the stand's life, the proportion of biomass in stem increases at the expense of foliage and branch components (Waring and Schlesinger, 1985). Upon planting, the quantity of foliage biomass increases until it reaches a semi plateau. After the sapling stage, foliage biomass will occupy approximately 10% of total

stand biomass (Johnsen *et al.*, 2004). However, given that foliage is an ephemeral component and loblolly pine trees retain their needles for two growing seasons, the yearly relative allocation to foliage can be much higher than the estimated 10% in a closed-canopy forest. Leaf biomass, which is associated with leaf area, is a valuable component to quantify because it is highly correlated with stand productivity.

Belowground partitioning may also change throughout the development of a stand, as the coarse root biomass: aboveground biomass ratio typically declines with age (Johnsen *et al.*, 2004). Similar to foliage, fine roots comprise a small percentage of stand biomass yet the yearly photosynthate allocated to this component can be high. Some estimate that for pine forests in general, 50% of net carbon assimilated may be allocated to fine roots (Knight *et al.*, 1994).

Although needles and new roots have priority for healthy trees, deviations from this pattern of biomass allocation are indicative of tree stress (Waring and Pitman, 1985). The allocation of carbon to stem wood production is a priority for loblolly pine trees under stress (Naidu *et al.*, 1998). As loblolly pine is a shade intolerant species, when it is overtopped by neighboring trees it will alter its partitioning priorities by allocating more toward height growth in order to escape competition. In one study comparing dominant and suppressed loblolly pine of the same size (Naidu *et al.*, 1998), dominant loblolly pines allocated 63.4, 11.3, 13.2, and 12.0% of their total biomass to stem, needle, branch, and root components, respectively. Suppressed trees allocated 75.6, 5.6, 6.7, and 11.7% to those same components. This change in allocation between suppressed and dominant trees is supported by others with loblolly pine (Van Lear *et al.*, 1984) and Scots pine (*Pinus sylvestris* L.) (Nilsson and Albrektson, 1993). Suppressed trees also show a greater proportion of heterotrophic (stem, branch, and root) to autotrophic (foliage) tissue, which may increase the respiratory load of trees (Naidu *et al.*, 1998). Belowground, the

root mass in mature loblolly pine increases exponentially as crown class progresses from intermediate to dominant (Van Lear and Kapeluck, 1995).

The root: shoot ratio in loblolly pine was found to be 0.43 for age 5 trees (Retzlaff *et al.*, 2001), which suggests 30% of biomass in roots and 70% in aboveground components. Others have estimated loblolly pine root mass to comprise 20-25% of total biomass in mature trees (Johnsen *et al.*, 2004). Roots occupied 32% of total stand biomass in a 4-year-old loblolly pine plantation (Adegbidi *et al.*, 2002), 22-25% in a 6-year-old plantation (Samuelson *et al.*, 2004), and 20% in a 48-year-old plantation (Van Lear and Kapeluck, 1995). Similarly, root mass is approximately 50% of stem mass (Albaugh *et al.*, 2006).

Loblolly pine plantations have become more intensively managed in recent years. Increasing management intensity can accelerate stand development, which means that two plantations at the same age may not show similar biomass partitioning patterns. Therefore, the effects that multiple silvicultural treatments have had on partitioning of biomass have been investigated. These patterns were not affected by genetics, provenance, and nutrient level (Retzlaff *et al.*, 2001) for age 5 loblolly pine. Different combinations of treatments that included weed control, irrigation, fertilization, and pest control (Samuelson *et al.*, 2004) also did not affect the biomass partitioning of loblolly pine from ages three to six. In contrast, Albaugh *et al.* (1998) found that fertilization increased aboveground production at the expense of belowground components in 8-year-old trees. At that same study site, those trends were consistent at age 16 (Albaugh *et al.*, 2004), and more biomass was allocated to stem in fertilized and irrigated plots. Shifts in allocation aboveground in fertilized plots were small relative to above and belowground trade-offs (Albaugh *et al.*, 1998), illustrating that roots are a crucial component when considering biomass partitioning.

## 2.2 Density effects on biomass partitioning

Plantation managers control initial planting density. Economic returns, management goals, growth relationships, and desired end products are all considered prior to selecting the appropriate initial spacing for a given site. Close spacings support maximum total yield on a per unit area basis, whereas wide spacings encourage larger tree diameters and earlier sawtimber production. At the individual tree level, above and belowground intraspecific competition increases as stand density increases, which could alter biomass partitioning patterns.

As stand density increases, stem biomass on the stand level increases, coupled with a decrease in individual-tree stem biomass. Burkes *et al.* (2003) showed that growth efficiency (stem growth per unit leaf area) of 4-year-old loblolly pine increased successively as density increased from 740 to 2220, 3700, and 4400 stems ha$^{-1}$. The increase from 3700 to 4400 stems ha$^{-1}$ had little effect on stem biomass, indicating that stem growth was limited at higher densities. In another study in a silvopasture that quantified only aboveground partitioning, (Ares and Brauer, 2005), loblolly pine trees allocated more mass to stem in double and quadruple-row configurations when compared to single-row trees.

Stands at lower densities exhibit more mass belowground when compared to stands with greater densities. In a low-density stand (1115 stems ha$^{-1}$), greater root mass was recorded on a stand level when compared to stands with slightly greater densities (1359 and 1556 stems ha$^{-1}$) (Albaugh *et al.*, 2006), which is in agreement with the findings of Shelton *et al.* (1984).

At different planting densities, researchers have investigated the proportion of biomass allocated to tree components. These studies have found that as stand density increases the relative amount of biomass partitioned to root increases (Pearson *et al.*, 1984; Litton *et al.*, 2003), indicating that root: shoot ratios increase as stand density increases. In two 13-year-old

lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) stands, root biomass occupied 19% and 31% of total stand biomass in low and high-density stands, respectively (Litton *et al.*, 2003). Burkes *et al.* (2003) concluded that partitioning to stem increased as density increased at the expense of foliage and fine root components.

Similar results have been found by those who have quantified only the aboveground partitioning of trees. Ares and Brauer (2005) found that loblolly pine growing in a single-row configuration (308 stems ha$^{-1}$) allocated 52% of their total aboveground biomass to stems compared to the 63% allocated to trees growing in a quadruple-row configuration (932 stems ha$^{-1}$). The single-row trees in this study showed an increase in relative allocation to foliage. This suggests that trees in high density stands receive increased partitioning to stems, which is supported by data from Scots pine (Nilsson and Albrektson, 1993) and eastern cottonwood (*Populus deltoides* Bartr. ex Marsh) (Puri *et al.*, 1994).

Generally, when quantifying both above and belowground components, increasing the number of stems per unit area leads to increased allocation belowground. When only examining aboveground partitioning, increasing stand density generally leads to increased allocation to stem. Coupled with other site characteristics and tree size, stand density is an important variable for controlling the biomass distribution in forest stands.

**2.3 Microcosm studies**

A microcosm experiment is a small-scale, controllable study which seeks to emulate a larger process. Previously seldom used, the number of microcosm studies in ecology doubled in the 1990's (Fraser and Keddy, 1997) and these types of studies have also been used in forest

research. For example, Smith and Hann (1984) showed that closely-spaced red alder (*Alnus rubra* Bong.) growing in a greenhouse exhibited the -3/2 power rule of self-thinning. Similarly, loblolly pine and sweetgum (*Liquidambar styraciflua* L.) seedlings were grown in controlled-environment chambers to determine the photosynthetic response from differing levels of carbon dioxide, water stress, and nitrogen (Groninger *et al.*, 1996).

Miniature-scale plantations, one example of a microcosm study, contain trees growing at very close spacings in order to accelerate stand development. These small-scale plantations reach maturity faster than operationally-spaced plantations, which allows for a more condensed experimentation time. Small-scale plantations are cost-effective experiments because variables can be easily controlled and the land area needed for these studies is small compared to operationally-spaced plantations. Data collection can be accomplished more rapidly and the probability of a catastrophic event ruining experimental plots is reduced. These reasons make miniature-scale plantations appealing to forest growth and yield modelers for studying forest stand dynamics.

Miniature-scale loblolly pine plantations have been used to relate height and diameter (Amateis *et al.*, 2003; Strub and Amateis, 2008) and height and diameter mean annual increment (Sharma *et al.*, 2003) to values for trees growing at conventional scales. Taper relationships have been scaled from trees grown in closely-spaced plots to trees in operationally-spaced plots (Sharma *et al.*, 2007). The ability to quantitatively link seedlings to mature trees makes small-scale experimental plots appealing to address future issues in loblolly pine plantation management.

**2.4 Modeling tree component biomass**

The allometric model, the idea that the growth of one part of an organism can be related to another part, has been used extensively in estimating tree biomass. Since volume can be found by the cross-sectional area of a tree multiplied by its length, and volume is directly related to mass, the variable $D^2H$ is often an excellent predictor for stem weights. Measurements such as live crown length and crown ratio are often useful in estimating weights of canopy components. In predicting root mass, tree groundline diameter is often used as opposed to the conventional *DBH* measurement because groundline diameter is closer to where roots exist.

Site variables, such as stand age or site index, are sometimes used in estimating tree biomass. One site characteristic that has been included directly in estimating biomass is stand density. Brown  (1978) and Alemdag and Stiell (1982) used stand density as an independent variable in predicting biomass, noting improvements in terms of reduced variability. Others have not found an effect of density on tree allometry (António *et al.*, 2007).

In estimating tree biomass, it is often desirable that the sum of predictions for each tree component equal total tree biomass. If one creates component equations independently of one another, then their predicted values will not necessarily sum to total tree mass, and inconsistencies may result. Kozak (1970) first presented the methods for forcing the additivity of component biomass equations to sum to total tree mass. Reed and Green (1985) expanded these methods to apply to nonlinear equations. Consider *c* biomass components measured from *n* trees—their technique involved a simultaneous estimation method to minimize the loss function

$$L = \sum_{j=1}^{c} \left[ \sum_{i=1}^{n} \frac{\left(y_{ij} - \hat{y}_{ij}\right)^2}{\hat{\sigma}_j^2} \right]$$

[2.1]

where $y_{ij}$ is the $i$th observation of the $j$th component ($i = 1, 2, \ldots, n$; $j = 1, 2, \ldots, c$), $\hat{y}_{ij}$ is the

predicted value of that observation, and $\hat{\sigma}_j^2$ is an estimate of the conditional variance associated

with equation $j$. This simultaneous estimation method sacrifices some precision in estimating

individual components in order to insure additivity.

Parresol (1999) discusses three methods for forcing additivity of linear biomass

equations. The first method involves fitting the best individual regressions for each component

independently and making the total tree biomass equation equal to the sum of the predicted

values for each component. The functions

$$\begin{aligned}
\hat{y}_1 &= f_1(x_1) \\
\hat{y}_2 &= f_2(x_2) \\
&\vdots \\
\hat{y}_c &= f_c(x_c) \\
\hat{y}_{total} &= \hat{y}_1 + \hat{y}_2 + \ldots + \hat{y}_c
\end{aligned}$$

[2.2]

comprise the system of equations. With this method, the variance for the total tree equation is

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$$\text{Var}(\hat{y}_{total}) = \sum_{i=1}^{c} \text{Var}(\hat{y}_i) + 2\sum_{i<j} \text{Cov}(\hat{y}_i, \hat{y}_j)$$

[2.3]

Method 2 involves using the same independent variables in each component equation. By forcing the regression coefficients in the total tree equation to equal the sum of the coefficients from all component equations, additivity is ensured. If $\mathbf{b}_i$ is a vector of parameter estimates for equation $i$, then this system is

$$\hat{y}_1 = x\mathbf{b}_1$$
$$\hat{y}_2 = x\mathbf{b}_2$$
$$\vdots$$
$$\hat{y}_c = x\mathbf{b}_c$$
$$\hat{y}_{total} = x(\mathbf{b}_1 + \mathbf{b}_2 + ... + \mathbf{b}_c)$$

[2.4]

Method 2 results in a lower variance for the total tree equation, as the covariance term in Eq. [2.3] drops out. Method 1 is often not preferred because the variance for the total tree equation is relatively large. With method 2, issues of multicolliniarity and significance of predictors arise because of the presence of the same independent variables across equations.

The third method to ensure additive biomass equations as suggested by Parresol (1999) uses the concepts of seemingly unrelated regression (SUR). If one assumes contemporaneous

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correlations among component equations, then SUR is an appropriate method for estimating

parameters. The structure for a system of equations fitted with SUR is

$$\mathbf{y}_1 = \mathbf{f}_1\left(\mathbf{X}_1, \boldsymbol{\beta}_1\right) + \boldsymbol{\varepsilon}_1$$
$$\mathbf{y}_2 = \mathbf{f}_2\left(\mathbf{X}_2, \boldsymbol{\beta}_2\right) + \boldsymbol{\varepsilon}_2$$
$$\vdots \qquad\qquad\qquad [2.5]$$
$$\mathbf{y}_c = \mathbf{f}_c\left(\mathbf{X}_c, \boldsymbol{\beta}_c\right) + \boldsymbol{\varepsilon}_c$$

$$\mathbf{y}_{total} = \mathbf{f}_{total}\left(\mathbf{X}_1, \mathbf{X}_2, \ldots, \mathbf{X}_c, \boldsymbol{\beta}_1, \boldsymbol{\beta}_2, \ldots, \boldsymbol{\beta}_c\right) + \boldsymbol{\varepsilon}_{total}$$

where for equation $i$, $\mathbf{y}_i$ is a vector for component mass, $\mathbf{X}_i$ is a matrix containing the

independent variables, $\boldsymbol{\beta}_i$ is a parameter vector, and $\boldsymbol{\varepsilon}_i$ is a random error vector. Additivity in

SUR can be accomplished by setting cross-equation constraints on the parameter estimates, i.e.

forcing predictions from component equations to sum in the total tree equation. SUR takes into

account the existing correlations among biomass components and results in a lower variance.

This method is similar to the loss function specified by Reed and Green (1985) in Eq. [2.1]. The

largest gain in using SUR methodologies is that confidence and prediction intervals for biomass

estimates are reduced (Parresol, 2001; Carvalho and Parresol, 2003).

CHAPTER 3

MODELING THE BIOMASS PARTITIONING OF LOBLOLLY PINE GROWN IN A

MINIATURE-SCALE PLANTATION

**3.1 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 plantation

managers is initial planting density. 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. At the individual-tree

level, within-tree competition increases as stand density increases, which can change partitioning

priorities (Burkes *et al.*, 2003). Initial planting density can play a valuable role in determining the

distribution of biomass in loblolly pine plantations.

Loblolly pine trees allocated more mass to stem in double and quadruple-row

configurations when compared to single-row trees grown in a silvopasture (Ares and Brauer,

2005). This would suggest that high density stands receive increased partitioning to stem, which

is supported by data from Scots pine (Nilsson and Albrektson, 1993) and eastern cottonwood

(*Populus deltoides* Bartr. ex Marsh) (Puri *et al.*, 1994). Similarly, partitioning to stem increased

as density increased at the expense of foliage and fine root components (Burkes *et al.*, 2003).

More root mass is found in stands with lower densities (Shelton *et al.*, 1984; Albaugh *et al.*,

2006). Increasing stand density increases the fixed proportion of biomass belowground (Pearson

*et al.*, 1984; Litton *et al.*, 2003), indicating that root: shoot ratios increase as stand density increases.

Common tree measurements such as tree diameter, total height, age, and occasionally live crown length or crown ratio are useful in predicting component and total tree biomass. In terms of loblolly pine allometry, diameter growth is more influenced by stand density than is height growth (Sharma *et al.*, 2002a). Brown (1978) and Alemdag and Stiell (1982) used stand density as an independent variable in predicting trees biomass, noting improvements in terms of reduced variability. The principle of additivity, the idea that the predicted values from components equations will sum to the predicted value in a total tree equation, has long been recognized (Kozak, 1970). By taking advantage of the contemporaneous correlations among different components from the same tree, seemingly unrelated regression (SUR) methodologies can be applied (Parresol, 2001).

Miniature-scale experiments are appealing to researchers studying forest stand dynamics because treatments can be easily controlled and data collection can be accomplished more rapidly. Red alder (*Alnus rubra* Bong.) grown at spacings ranging from $2 \times 2$ to $8 \times 8$ 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.*, 2003; 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, small-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 stand density on biomass partitioning needs to be expanded. The objectives of this research were to (1) determine the effects of initial planting density on the biomass partitioning of loblolly pine grown in a miniature-scale plantation, (2) create systems of equations which predict loblolly pine component and total tree mass, and (3) relate the results from the closely-spaced trees to more mature trees at operational scales.

## 3.2 Methods

### 3.2.1 Data

A small-scale spacing study planted with loblolly pine half-sib (Virginia Department of Forestry Piedmont Loblolly Clone 20-508) 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 $F = 7.6$ cm (3 in.). Four levels of this factor (7.6 cm, 11.4 cm, 15.2 cm and 22.9 cm) were used in row and column spacings, resulting in 16 treatment plots ranging in size from $2.845 \times 10^{-5}$ to $2.561 \times 10^{-4}$ ha with the most extreme spacing rectangularities of 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 approximate two-week intervals, a 237 ppm water soluble nitrogen solution was applied to the study area, which approximately covered $3.716 \times 10^{-3}$ ha. This fertilization occurred during the first growing season and ceased in mid-July. Total amount applied during season was approximately 138 L. Fertilization procedures

followed similarly for the second replication, which was planted on 4 May 1998. The same family was planted in both replications.

Biomass data from 108 sample trees were collected across the 16 plots from both 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. Mortality was high at the very high densities; hence, more sample trees were harvested at lower densities. 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 which had all four component parts (stem, needle, branch, and root) and 96 trees which had all aboveground parts (stem, needle, and branch).

In summary, all age 4 trees (aboveground components only) were harvested from the first replicate and all age 5 and 6 trees (above and belowground) 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. Mass measurements for needles included one cohort of foliage. Roots were excavated with a hand shovel and defined from the groundline down, including taproot and all woody roots greater than 5mm in diameter. All components were oven-dried to constant weight prior to weighing.

To determine the effect that initial planting density had on the relative amount of biomass partitioned to each component, an analysis of covariance was performed. When compared to a square spacing, spacing rectangularities of 3:1 did not show a significant effect on the development of height, diameter, and volume per hectare in a 16-year-old loblolly pine spacing trial (Sharma *et al.*, 2002b); hence, initial planting density was used as the treatment effect with age as the covariate. The component proportions were transformed with the arcsine transformation prior to this analysis.

*3.2.2 Model Fitting*

Seemingly unrelated regression (SUR), also called joint generalized least squares, is a generalization of ordinary least squares for systems of equations. SUR methodologies are useful in estimating tree biomass because cross-equation constraints ensure that predictions for tree components will sum to total tree mass. The independent variables chosen to predict the component masses are used to predict total tree mass, hence, a model for total tree mass does not necessarily need to be fitted to the data, assuming that one establishes the cross-equation constraints. Given that the residuals $\varepsilon_i$ of tree component equations are likely correlated, SUR takes advantage of these contemporaneous correlations among component equations to improve parameter estimates, which leads to narrower confidence and prediction intervals. Procedures for fitting biomass equations using SUR are well documented in Parresol (1999, 2001) and Carvalho and Parresol (2003).

If there are $c$ tree components measured, then the structure for a system of equations fitted with SUR is

$$\begin{aligned}
\mathbf{y}_1 &= \mathbf{f}_1\left(\mathbf{X}_1, \boldsymbol{\beta}_1\right) + \boldsymbol{\varepsilon}_1 \\
\mathbf{y}_2 &= \mathbf{f}_2\left(\mathbf{X}_2, \boldsymbol{\beta}_2\right) + \boldsymbol{\varepsilon}_2 \\
&\vdots \\
\mathbf{y}_c &= \mathbf{f}_c\left(\mathbf{X}_c, \boldsymbol{\beta}_c\right) + \boldsymbol{\varepsilon}_c
\end{aligned}$$

[3.1]

$$\mathbf{y}_{total} = \mathbf{f}_{total}\left(\mathbf{X}_1, \mathbf{X}_2, \ldots, \mathbf{X}_c, \boldsymbol{\beta}_1, \boldsymbol{\beta}_2, \ldots, \boldsymbol{\beta}_c\right) + \boldsymbol{\varepsilon}_{total}$$

where for equation $i$, $\mathbf{y}_i$ is a vector for the component mass, $\mathbf{X}_i$ is a matrix containing the independent variables, $\boldsymbol{\beta}_i$ is a parameter vector, and $\boldsymbol{\varepsilon}_i$ is a random error vector.

To select the proper independent variables for predicting component mass, linear equations were first fitted using ordinary least-squares. A stepwise regression procedure was carried out which examined the contribution of common measurements such as tree ground line diameter ($D$), total height ($H$), live crown length ($LCL$), age ($A$), combined forms of these variables (e.g. $D^2H$, $D^2LCL$), and initial planting density ($N$). Variance inflation factors (VIFs) were computed and residual plots were examined for candidate models. The final model chosen to estimate component mass was one that included significant independent variables, produced satisfactory residual plots, showed low values for VIF (maximum VIF $< 5.0$), and provided sufficient fit statistics.

If there are $c$ component equations within a system then there are $c + 1 = M$ equations in the system when total tree mass is included. Eq. [3.1] can be rewritten as

$$\mathbf{y} = \mathbf{f}(\mathbf{X}, \boldsymbol{\beta}) + \boldsymbol{\varepsilon} \qquad\qquad [3.2]$$

where

$$\mathbf{y} = \begin{bmatrix} \mathbf{y}_1 \\ \mathbf{y}_2 \\ \vdots \\ \mathbf{y}_M \end{bmatrix}, \quad \mathbf{f} = \begin{bmatrix} \mathbf{f}_1 \\ \mathbf{f}_2 \\ \vdots \\ \mathbf{f}_M \end{bmatrix}, \text{ and } \boldsymbol{\varepsilon} = \begin{bmatrix} \boldsymbol{\varepsilon}_1 \\ \boldsymbol{\varepsilon}_2 \\ \vdots \\ \boldsymbol{\varepsilon}_M \end{bmatrix} \qquad\qquad [3.3]$$

Concerning the random error vector $\boldsymbol{\varepsilon}_i$, the assumption is that $E(\boldsymbol{\varepsilon}_i) = 0$ and $E(\boldsymbol{\varepsilon}\boldsymbol{\varepsilon}') = \Sigma \otimes \mathbf{I}_T$,

where $\Sigma$ is an ($M$ x $M$) variance-covariance matrix, $\otimes$ is the Kronecker product, and $\mathbf{I}_T$ is an

identity matrix of order T, the number of observations per equation. The values in the variance-

covariance matrix $\Sigma$ need to be estimated so that

$$\hat{\Sigma} = \begin{bmatrix} \hat{\sigma}_{11} & \hat{\sigma}_{12} & \cdots & \hat{\sigma}_{1M} \\ \hat{\sigma}_{21} & \hat{\sigma}_{22} & \cdots & \hat{\sigma}_{2M} \\ \vdots & \vdots & \ddots & \vdots \\ \hat{\sigma}_{M1} & \hat{\sigma}_{M2} & \cdots & \hat{\sigma}_{MM} \end{bmatrix} \qquad\qquad [3.4]$$

where $\hat{\sigma}_{ij}$ is an estimate of the covariance between equations $i$ and $j$ and can be computed as

$$\hat{\sigma}_{ij} = \frac{1}{(T-K_i)^{0.5} (T-K_j)^{0.5}} \, \mathbf{e}_i' \, \mathbf{e}_j$$

[3.5]

where $K_i$ and $K_j$ are the number of coefficients estimated in equations $i$ and $j$, respectively. The random error vectors $\mathbf{e}_i$ and $\mathbf{e}_j$ are the residuals obtained from the OLS equations. The denominator in the first term in Eq. [3.5] accounts for the possibility that the degrees-of-freedom in equations $i$ and $j$ may differ.

If $\mathbf{b}$ is the SUR estimate for the parameter vector $\boldsymbol{\beta}$, then the proper values of $\mathbf{b}$ will be chosen to minimize the error sums of squares

$$R(\mathbf{b}) = \mathbf{e}' \left( \hat{\Sigma}^{-1} \otimes \mathbf{I}_T \right) \mathbf{e}$$

[3.6]

where

$$\mathbf{b} = \left[ \mathbf{X}' \left( \hat{\Sigma} \otimes \mathbf{I}_T \right) \mathbf{X} \right]^{-1} \mathbf{X}' \left( \hat{\Sigma} \otimes \mathbf{I}_T \right) \mathbf{y}$$

[3.7]

The parameter estimates for Eq. [3.7] were estimated using the SYSLIN procedure (SAS, 1995). Sample code and output can be found in Appendix I.

### 3.2.3 System variance and reliability estimates

To compute an overall SUR system variance, which will be needed later in order to establish confidence and prediction bounds for individual observations, a matrix of partial derivatives of the random error with respect to the parameters needs to be taken. The partial derivatives matrix $\mathbf{P(\beta)}'$ is a ($K$ x $MT$) matrix found by

$$\mathbf{P(\beta)}' = \frac{\partial \mathbf{e}'}{\partial \boldsymbol{\beta}} = \left[ \frac{\partial \mathbf{f}_1'}{\partial \boldsymbol{\beta}}, \frac{\partial \mathbf{f}_2'}{\partial \boldsymbol{\beta}}, \dots, \frac{\partial \mathbf{f}_M'}{\partial \boldsymbol{\beta}} \right] \qquad [3.8]$$

If $\mathbf{P(b)}'$ is the estimate of the partial derivatives matrix $\mathbf{P(\beta)}'$, then the variance-covariance matrix of the parameter estimates can be estimated by

$$\hat{\Sigma}_{\mathbf{b}} = \left[ \mathbf{P(b)}' \, (\hat{\Sigma} \otimes \mathbf{I}_T) \, \mathbf{P(b)} \right]^{-1} \qquad [3.9]$$

Using the error sums of squares $R(\mathbf{b})$, the SUR system variance is found by

$$\hat{\sigma}_{SUR}^2 = \frac{R(\mathbf{b})}{MT - K} \qquad [3.10]$$

where $MT - K$ is the degrees-of-freedom for the system. If $\mathbf{p}_i(\mathbf{b})'$ is a row vector for the $i$th equation in the estimated partial derivatives matrix $\mathbf{P(b)}$, then the estimated variance for the $t$th observation from the $i$th equation is

$$S^2_{\hat{y}_{it}} = \mathbf{p}_i(\mathbf{b})' \, (\hat{\Sigma}_\mathbf{b}) \, \mathbf{p}_i(\mathbf{b})$$

[3.11]

Matrix and vector calculations were made with PROC IML in SAS, and sample code and output can be found in Appendix II.

For a given tree $t$ of certain dimensions, one can estimate component (or total tree) biomass from equation $i$ by

$$\hat{y}_{it} = f_i(\mathbf{x}, \mathbf{b})$$

[3.12]

and place upper and lower prediction bounds with $100\,(1-\alpha)\%$ probability around that estimate by using

$$\hat{y}_{it} \pm t_{(\alpha/2)} \sqrt{S^2_{\hat{y}_{it}}} \quad \text{and} \quad \hat{y}_{it} \pm t_{(\alpha/2)} \sqrt{S^2_{\hat{y}_{it}} + \hat{\sigma}^2_{SUR}\hat{\sigma}_{ii}}$$

[3.13]

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which denotes the mean confidence and prediction interval, respectively. The $\hat{\sigma}_{ii}$ term in the

prediction interval equation is the variance of equation $i$ in the $\hat{\Sigma}$ variance-covariance matrix.

An example in applying SUR methodologies to a given system of equations and creating

mean confidence and prediction limits can be found in Appendix III.

### 3.3 Results

*3.3.1 Effects of initial planting density on biomass partitioning*

Mean tree height and ground line diameter for each initial planting density at ages 4 and 5 are shown in Table 3.1. 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 x 22.9, 15.2 x 15.2, 11.4 x 11.4, and 7.6 x 7.6 cm, respectively.

Averaged across both replications, mortality at age 4 was 33, 68, 70, and 89% for square spacings of 22.9 x 22.9, 15.2 x 15.2, 11.4 x 11.4, and 7.6 x 7.6 cm, respectively. Mean live crown ratios at age 5 for the second replicate were 0.33, 0.34, 0.30, and 0.25 for those same spacings (Figure 3.1).

**Table 3.1** Mean plot ground line diameter (gld) and height (ht) at the end of the fourth and fifth growing season[a] for loblolly pine trees grown in a miniature-scale plantation at different initial planting densities (trees ha$^{-1}$). Standard errors in parentheses.

| Initial Planting Density (100,000 trees ha$^{-1}$) | Age 4 gld (mm) | Age 5 gld (mm) | Age 4 ht (cm) | Age 5 ht (cm) |
|---|---|---|---|---|
| 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) |

[a] Means for age 4 include observations from both replicates; means for age 5 include observations from second replicate, only.
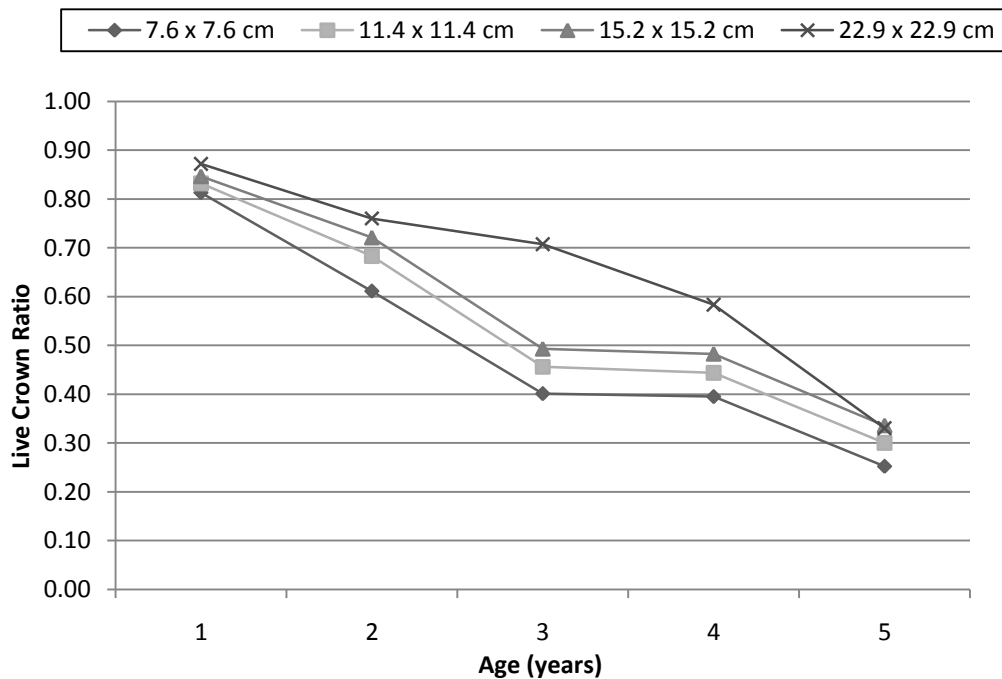
**Figure 3.1** Mean live crown ratios of a miniature-scale loblolly pine plantation at the end of each growing season for initial square spacings of 7.6 x 7.6 cm (♦), 11.4 x 11.4 cm (■), 15.2 x 15.2 cm (▲), and 22.9 x 22.9 cm (×). (Means for age 5 include observations from second replicate, only).

The analysis of covariance concluded that tree age (as a covariate) had a significant effect $(\alpha = 0.05)$ on all proportions except for the branch and root components when considering above and belowground components. Initial planting density did not have a significant effect on the relative amount of biomass partitioned to aboveground tree components (Table 3.2). When the mean component proportions are plotted against initial planting density, no discernable trend is seen (Figure 3.2).

Averaged across all densities, the relative proportion of biomass within each component changed at the different ages in the study (Figure 3.3). When considering above and belowground mass, the stem component occupied 68 and 72% of total mass, while foliage

accounted for 13 and 9% at ages 5 and 6, respectively. The stem occupied 68, 79, and 83% and

foliage accounted for 22, 15, and 10% of aboveground mass ages 4, 5, and 6, respectively.

**Table 3.2** Analysis of covariance results (*p*-values) for testing the effect of planting density on the relative amount[a] of biomass partitioned to loblolly pine tree components in a miniature-scale plantation.

| Effect | | Relative biomass partitioned to | | | |
|---|---|---|---|---|---|
| | | Stem | Needle | Branch | Root |
| *Age (covariate)* | Total tree | 0.0119 | <0.0001 | 0.0807 | 0.9005 |
| | Aboveground | <0.0001 | <0.0001 | <0.0001 | |
| *Planting density* | Total tree | 0.8318 | 0.4472 | 0.2070 | 0.0624 |
| | Aboveground | 0.5365 | 0.7424 | 0.5334 | |

[a] Proportions transformed with the arcsine transformation.
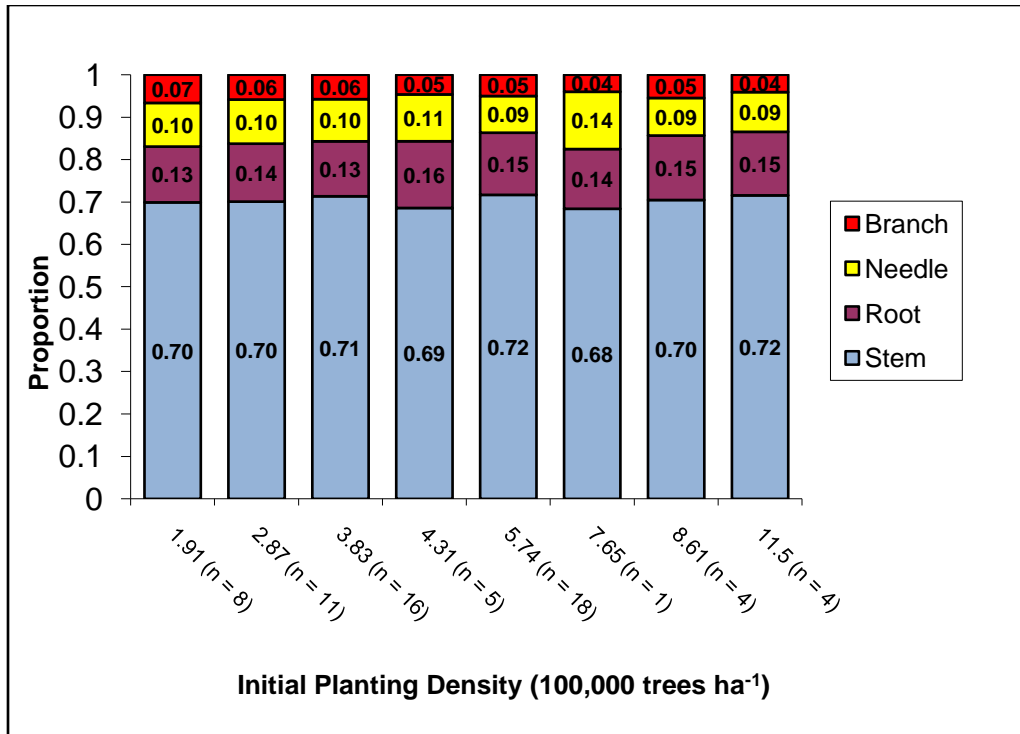
**(a)**
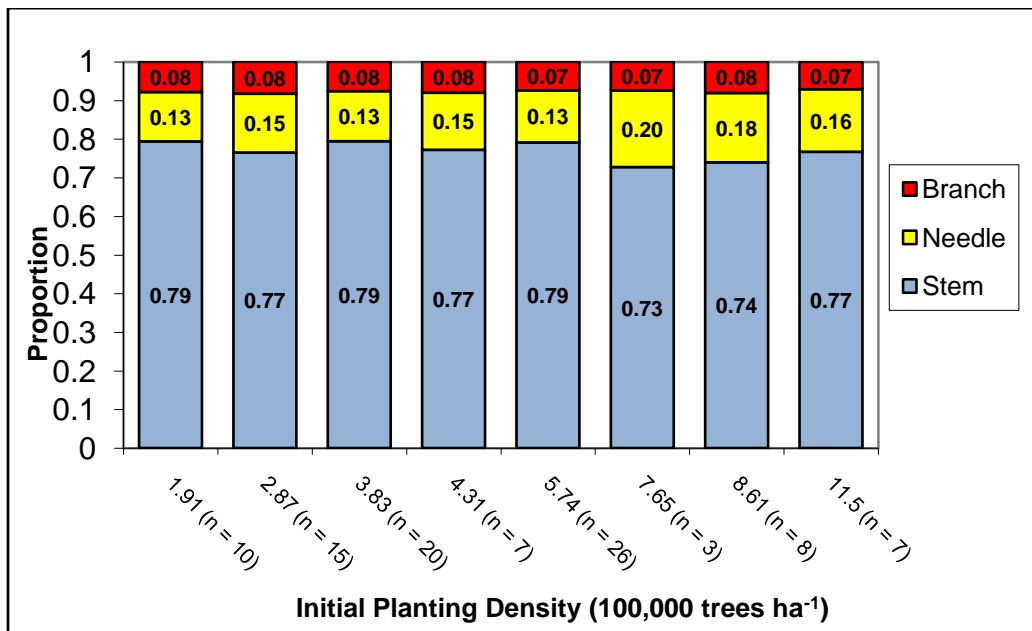


**(b)**

**Figure 3.2** Mean proportions of mass within each tree component at each initial planting density for above and belowground mass (a; ages 5 and 6) and aboveground mass (b; ages 4, 5, and 6) for loblolly pine grown in a miniature-scale plantation.
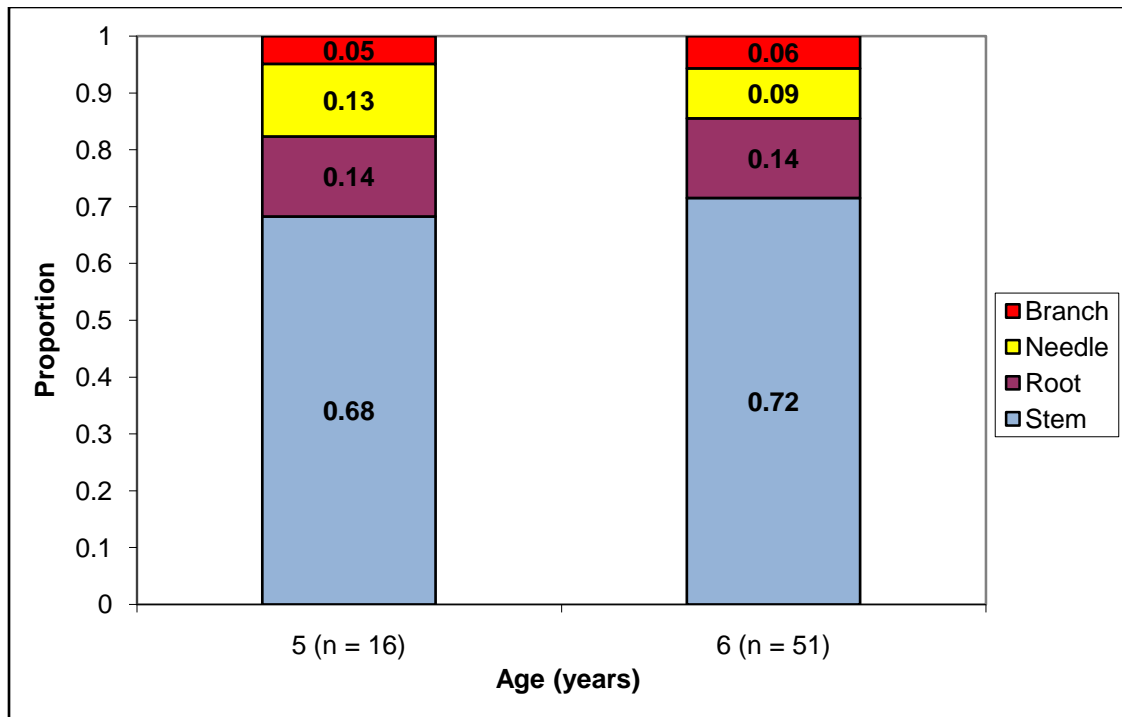
**(a)**
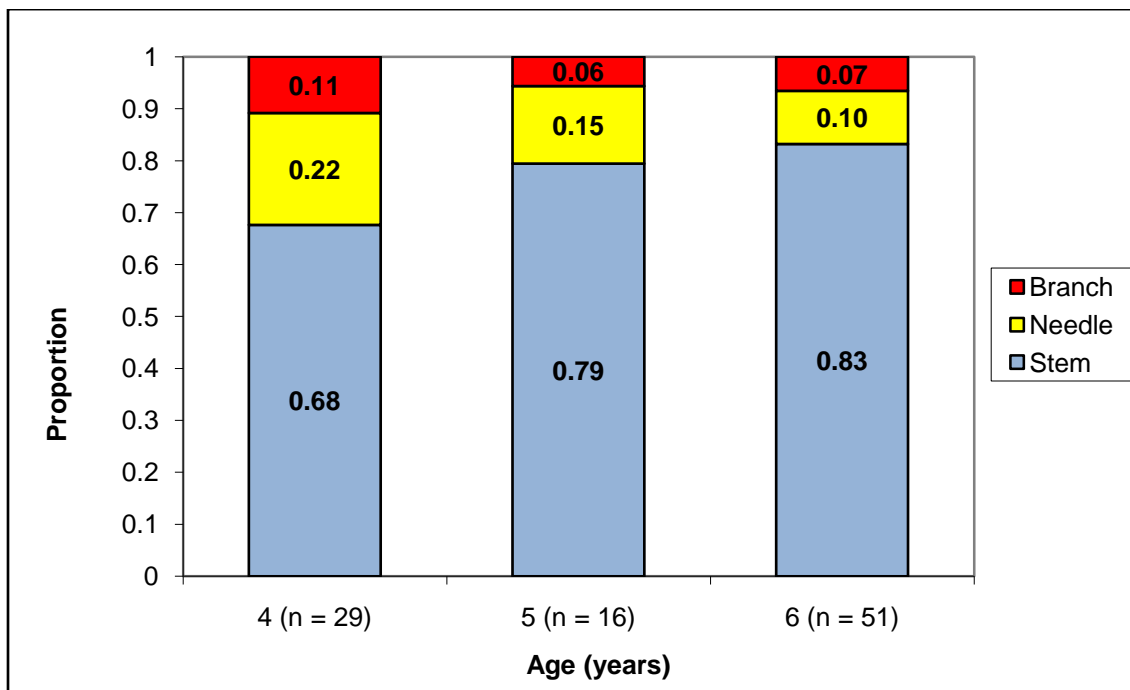


**(b)**

**Figure 3.3** Mean proportions of mass within each tree component at different ages for above and belowground mass (a) and aboveground mass (b) for loblolly pine grown in a miniature-scale plantation across eight initial planting densities.

To determine where allocation tradeoffs were occurring in the dataset, the equation

$\hat{R} = b_0 + b_1(N)$, where $\hat{R}$ is an estimated component: component weight ratio (such as root: stem

ratio) and $N$ is initial planting density (trees ha$^{-1}$), was fitted to the data. Every ratio that included

the root component was determined to have a significant slope for $N$ (Table 3.3). Weight 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 those ratios shifted

each year in the study window of 4 to 6 years (Figure 3.4). Mean needle: stem and needle: shoot

ratios were 0.32, 0.19, 0.13 and 0.22, 0.15, 0.10 for trees ages 4, 5, and 6, respectively.

**Table 3.3** *P*-values for the slope estimate associated with the regression equation
$\hat{R} = b_0 + b_1(N)$ where $\hat{R}$ is the estimated weight ratio and $N$ is initial planting density for 4 to 6-year-old loblolly pine grown in a miniature-scale plantation. $\pm$ indicates direction of slope.

|  | Ages 4, 5, and 6 | Age 4 | Age 5 | Age 6 |
| --- | --- | --- | --- | --- |
| Root: shoot | 0.0197 (+) | | | |
| Root: stem | 0.0171 (+) | | | |
| Needle: root | 0.0177 (-) | | | |
| Branch: root | 0.0003 (-) | | | |
| Branch: stem | 0.8702 | | | |
| Branch: needle | 0.4877 | | | |
| Branch: shoot | 0.5798 | | | |
| Stem: shoot | 0.2892 | | | |
| Needle: stem | | 0.1296 | 0.8949 | 0.0056 (-) |
| Needle: shoot | | 0.0994 | 0.9928 | 0.0137 (-) |

NOTE: Slope coefficients were not significantly different ($\alpha = 0.05$) among the three ages for all weight ratios except for needle: stem and needle: shoot.
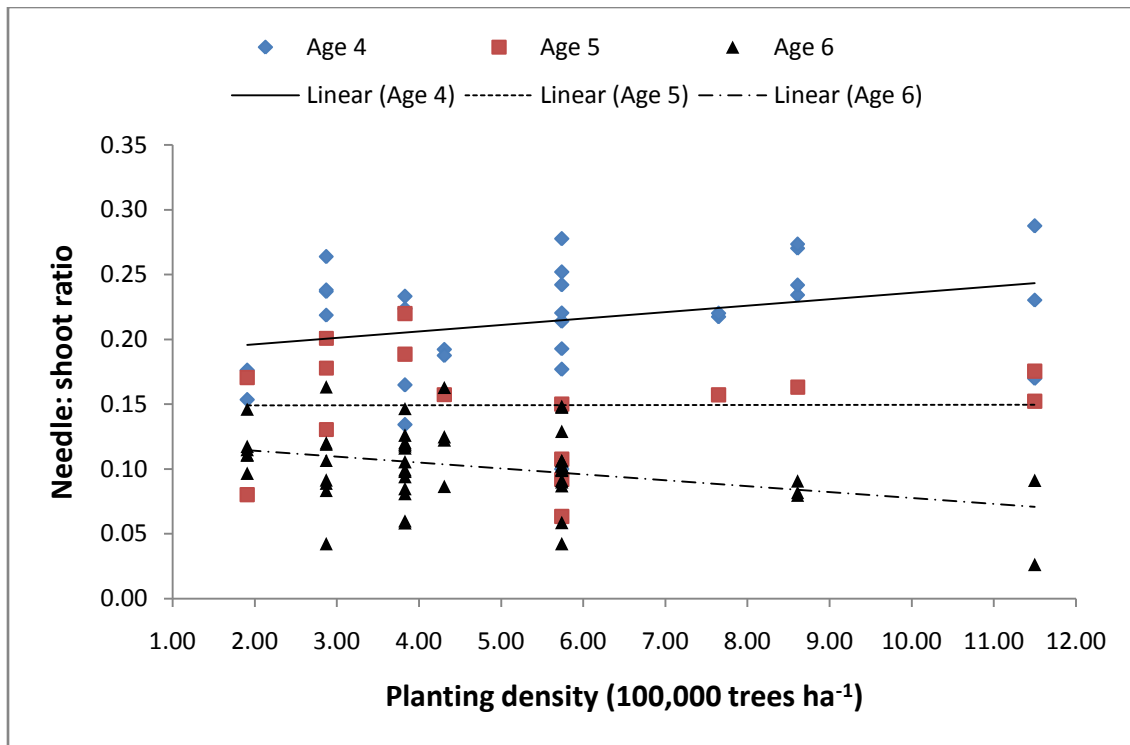
**(a)**
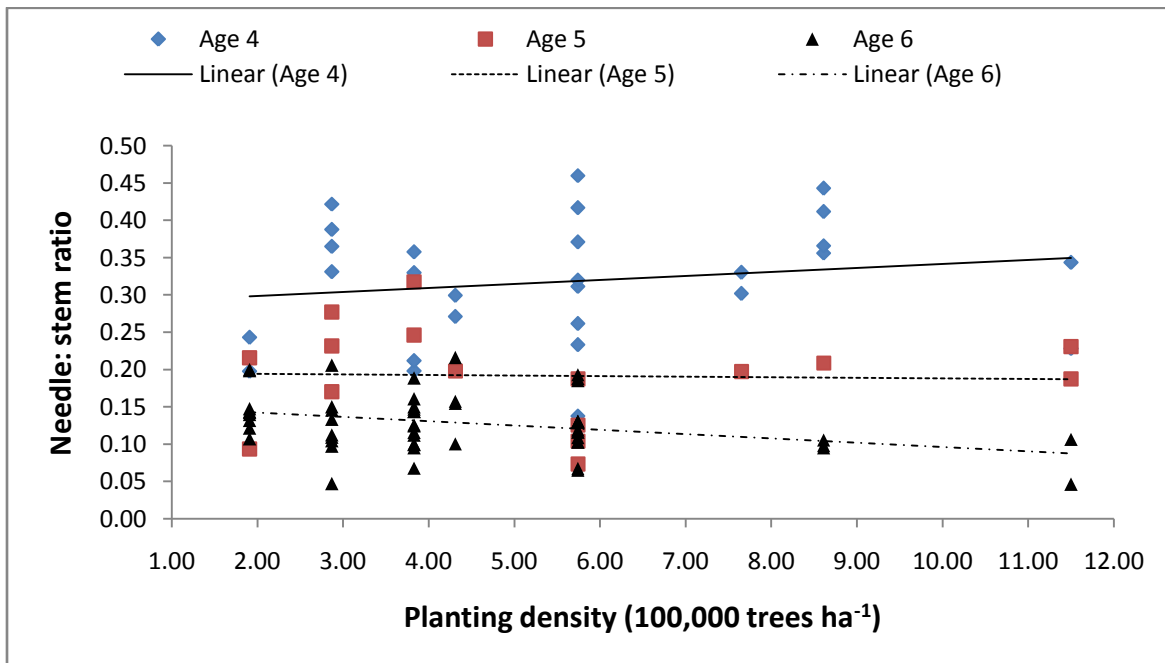


**(b)**

**Figure 3.4** Needle: shoot (a) and needle: stem ratios (b) for loblolly pine ages 4 (♦), 5 (■), and 6 (▲) at eight planting densities in a miniature-scale plantation.

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The mean root: shoot ratio for trees ages 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 ($p = 0.0196$; Figure 3.5).
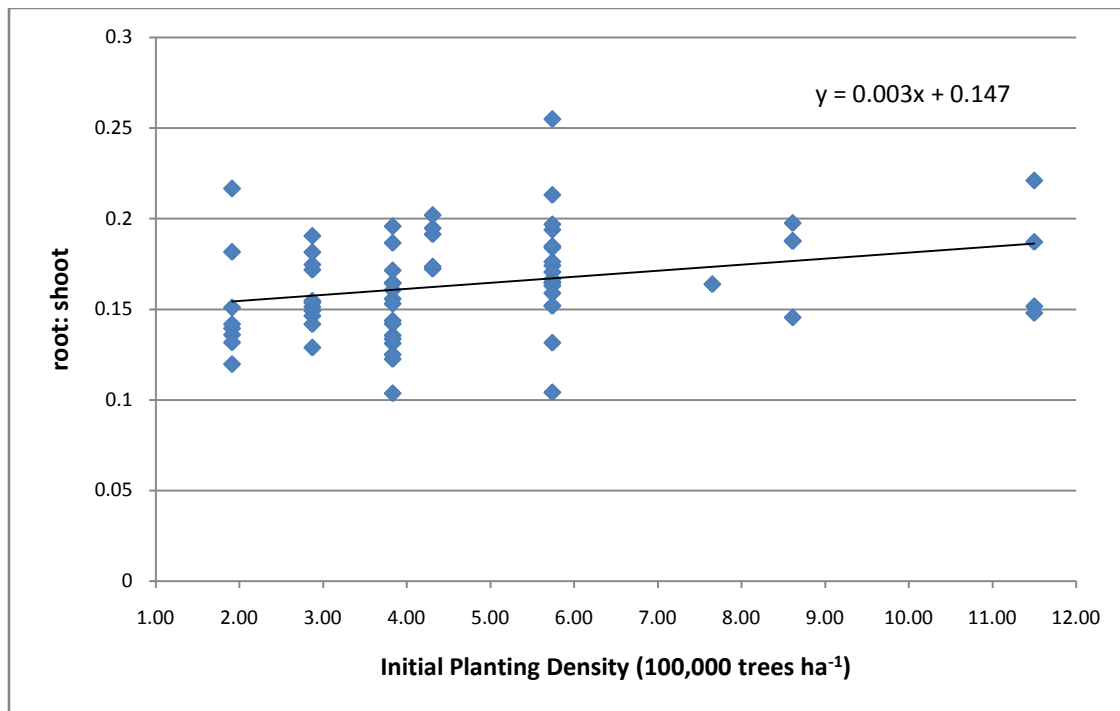


**Figure 3.5** Root: shoot ratios for 5 and 6-year-old loblolly pine grown at eight planting densities in a miniature-scale plantation.

Live crown ratios from 96 harvested trees at ages 4, 5, and 6 ranged from 0.16 to 0.79 with a mean of 0.45. Trees with small crown ratios allocated more to stem and less to canopy components, and vice versa (Figure 3.6). Live crown ratio was a significant variable in predicting the relative proportion of mass in each component, except for roots (Table 3.4).
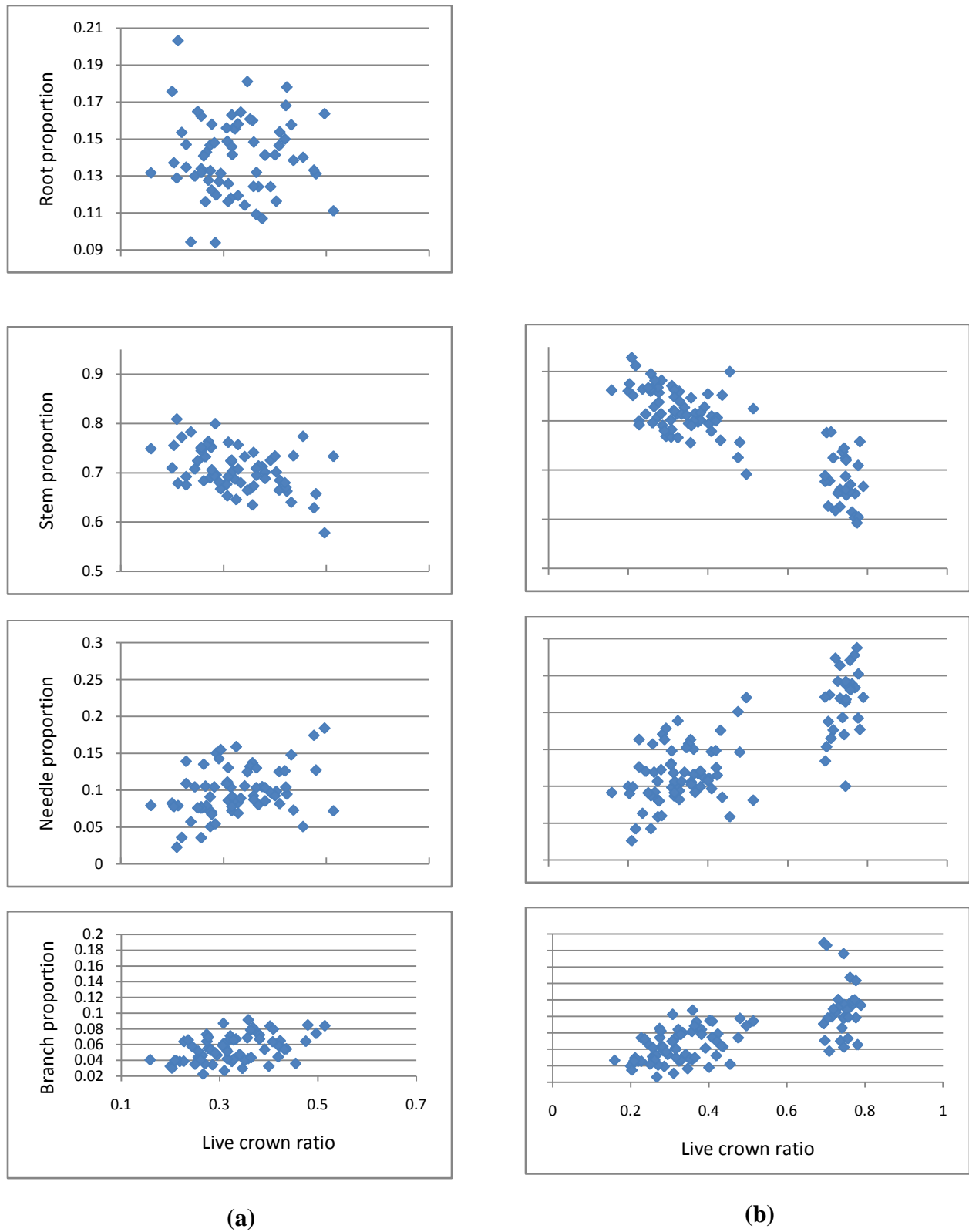
**Figure 3.6** Live crown ratios and relative proportions of mass in tree components for 5 and 6 (a) and 4, 5, and 6-year old loblolly pine (b) grown in a miniature-scale loblolly pine plantation.

**Table 3.4** Parameter estimates and *p*-values associated with the regression equation $\hat{P} = b_0 + b_1(LCR)$ where $\hat{P}$ is the estimated proportion and *LCR* is live crown ratio 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 Belowground:* | | | | |
| Stem | 0.79 | <0.0001 | -0.25 | 0.0002 |
| Needle | 0.05 | 0.0035 | 0.15 | 0.0028 |
| Branch | 0.02 | 0.0053 | 0.10 | 0.0001 |
| Root | 0.14 | <0.0001 | -0.001 | 0.9646 |
| | | | | |
| *Aboveground:* | | | | |
| Stem | 0.94 | <0.0001 | -0.35 | <0.0001 |
| Needle | 0.04 | 0.0003 | 0.24 | <0.0001 |
| Branch | 0.03 | <0.0001 | 0.11 | <0.0001 |

*3.3.2 Systems of equations for predicting loblolly pine mass*

In order to meet the needs of different potential users, eight systems of equations were developed depending on different tree variables measured and whether one chooses to estimate above and belowground mass, or aboveground mass solely (Table 3.5). The equation structures are found in Eqs. 3.14.1 to 3.14.8 and parameter estimates in Tables 3.6 and 3.7.

**Table 3.5** Tree measurements[a] required for system of equations for predicting loblolly pine component and total mass for trees grown at miniature scale.

| System Number | | Measurements |
|---|---|---|
| *Total Tree* | *Aboveground* | |
| I | V | *D, H* |
| II | VI | *D, H, LCL* |
| III | VII | *D, H, A* |
| IV | VIII | *D, H, A, LCL* |

[a]  *D* is diameter at ground line, *H* is total height, *LCL* is live crown length, and *A* is tree age.

System I

$$\hat{W}_{stem} = b_{10} + b_{11} D^2 H$$
$$\hat{W}_{foliage} = b_{20} + b_{21} D^2 H$$
$$\hat{W}_{branch} = b_{30} + b_{31} D^2 H$$
$$\hat{W}_{root} = b_{40} + b_{41} D^2$$
$$\hat{W}_{tree} = b_{50} + b_{51} D^2 H + b_{52} D^2$$

[3.14.1]

System II

$$\hat{W}_{stem} = b_{10} + b_{11} D^2 H$$
$$\hat{W}_{foliage} = b_{20} + b_{21} D^2 LCL$$
$$\hat{W}_{branch} = b_{30} + b_{31} D^2 H$$
$$\hat{W}_{root} = b_{40} + b_{41} D^2 H$$
$$\hat{W}_{tree} = b_{50} + b_{51} D^2 H + b_{52} D^2 LCL$$

[3.14.2]

System III

$$\hat{W}_{stem} = b_{10} + b_{11} D^2 H + b_{12} A$$
$$\hat{W}_{foliage} = b_{20} + b_{21} D^2 H$$
$$\hat{W}_{branch} = b_{30} + b_{31} D^2 H$$
$$\hat{W}_{root} = b_{40} + b_{41} D^2 H$$
$$\hat{W}_{tree} = b_{50} + b_{51} D^2 H + b_{52} A$$

[3.14.3]

System IV

$$\hat{W}_{stem} = b_{10} + b_{11} D^2 H + b_{12} A$$
$$\hat{W}_{foliage} = b_{20} + b_{21} D^2 LCL$$
$$\hat{W}_{branch} = b_{30} + b_{31} D^2 H$$
$$\hat{W}_{root} = b_{40} + b_{41} D^2 H$$
$$\hat{W}_{tree} = b_{50} + b_{51} D^2 H + b_{52} D^2 LCL + b_{53} A \qquad [3.14.4]$$

System V

$$\hat{W}_{stem} = b_{10} + b_{11} D^2 H$$
$$\hat{W}_{foliage} = b_{20} + b_{21} D^2$$
$$\hat{W}_{branch} = b_{30} + b_{31} D^2 H$$
$$\hat{W}_{tree} = b_{40} + b_{41} D^2 H + b_{42} D^2 \qquad [3.14.5]$$

System VI

$$\hat{W}_{stem} = b_{10} + b_{11} D^2 H$$
$$\hat{W}_{foliage} = b_{20} + b_{21} D^2 LCL + b_{22} H$$
$$\hat{W}_{branch} = b_{30} + b_{31} D^2 LCL + b_{22} H$$
$$\hat{W}_{tree} = b_{40} + b_{41} D^2 H + b_{42} D^2 LCL + b_{43} H \qquad [3.14.6]$$

System VII

$$\hat{W}_{stem} = b_{10} + b_{11} D^2 H + b_{12} A$$
$$\hat{W}_{foliage} = b_{20} + b_{21} D^2$$
$$\hat{W}_{branch} = b_{30} + b_{31} D^2 H$$
$$\hat{W}_{tree} = b_{40} + b_{41} D^2 H + b_{42} A + b_{43} D^2 \qquad [3.14.7]$$

System VIII

$$\hat{W}_{stem} = b_{10} + b_{11} D^2 H + b_{12} A$$
$$\hat{W}_{foliage} = b_{20} + b_{21} D^2 LCL + b_{22} H$$
$$\hat{W}_{branch} = b_{30} + b_{31} D^2 LCL + b_{22} A$$
$$\hat{W}_{tree} = b_{40} + b_{41} D^2 H + b_{42} D^2 LCL + b_{43} H + b_{44} A \qquad [3.14.8]$$

**Table 3.6** Parameter estimates (standard errors in parentheses) for above and belowground equations fitted with SUR for predicting loblolly pine component and total mass for trees grown at miniature scale.

| | System | | | |
|---|---|---|---|---|
| | I | II | III | IV |
| $b_{10}$ | 10.088 (14.5) | 11.518 (17.0) | -465.45 (108) | -493.82 (99.9) |
| $b_{11}$ | 0.0010353 ($2.29 \times 10^{-5}$) | 0.0010325 ($2.68 \times 10^{-5}$) | 0.0010282 ($2.49 \times 10^{-5}$) | 0.0010170 ($2.45 \times 10^{-5}$) |
| $b_{12}$ | | | 83.172 (18.7) | 89.088 (17.3) |
| $b_{20}$ | -15.912 (5.76) | 0.16932 (4.66) | -16.455 (5.54) | 0.78512 (4.56) |
| $b_{21}$ | 0.00019303 ($9.09 \times 10^{-6}$) | 0.00046346 ($1.95 \times 10^{-5}$) | 0.00019409 ($8.76 \times 10^{-6}$) | 0.00046000 ($1.90 \times 10^{-5}$) |
| $b_{30}$ | -12.562 (3.04) | -12.515 (2.89) | -12.737 (3.07) | -12.343 (2.76) |
| $b_{31}$ | 0.00011729 ($4.81 \times 10^{-6}$) | .00011720 ($4.57 \times 10^{-6}$) | 0.00011763 ($4.85 \times 10^{-6}$) | 0.00011686 ($4.36 \times 10^{-6}$) |
| $b_{40}$ | -30.860 (4.67) | -2.6147 (3.97) | -3.4988 (3.92) | -2.2567 (3.94) |
| $b_{41}$ | 0.11032 (0.00319) | 0.00021753 ($6.26 \times 10^{-6}$) | 0.00021926 ($6.17 \times 10^{-6}$) | 0.00021682 ($6.20 \times 10^{-6}$) |
| $b_{50}$ | -49.247 (20.2) | -3.4411 (22.2) | -498.14 (109) | -507.63 (101) |
| $b_{51}$ | 0.0013456 ($2.83 \times 10^{-5}$) | 0.0013672 ($3.18 \times 10^{-5}$) | 0.0015591 ($3.48 \times 10^{-5}$) | 0.0013507 ($2.88 \times 10^{-5}$) |
| $b_{52}$ | 0.11032 (0.00319) | 0.00046346 ($1.95 \times 10^{-5}$) | 83.172 (18.7) | 0.00046000 ($1.90 \times 10^{-5}$) |
| $b_{53}$ | | | | 89.088 (17.3) |

**Table 3.7** Parameter estimates (standard errors in parentheses) for aboveground equations fitted with SUR for predicting loblolly pine component and total mass for trees grown at miniature scale.

| | System | | | |
| --- | --- | --- | --- | --- |
| | V | VI | VII | VIII |
| $b_{10}$ | -14.632 (9.43) | -10.392 (10.8) | -265.96 (35.1) | -237.77 (41.2) |
| $b_{11}$ | 0.0010606 ($1.75 \times 10^{-5}$) | 0.0010501 ($2.00 \times 10^{-5}$) | 0.0010007 ($1.92 \times 10^{-5}$) | 0.00098928 ($2.09 \times 10^{-5}$) |
| $b_{12}$ | | | 52.688 (7.10) | 48.164 (8.33) |
| $b_{20}$ | -28.496 (5.31) | -19.614 (10.1) | -28.874 (4.79) | -28.821 (9.66) |
| $b_{21}$ | 0.091594 (0.00412) | 0.00044835 ($2.15 \times 10^{-5}$) | 0.091942 (0.00372) | 0.00042340 ($2.06 \times 10^{-5}$) |
| $b_{22}$ | | 0.057501 (0.0349) | | 0.097505 (0.0335) |
| $b_{30}$ | -4.2004 (2.27) | -15.898 (5.58) | -4.2641 (2.26) | -37.822 (7.61) |
| $b_{31}$ | 0.00010831 ($4.21 \times 10^{-6}$) | 0.00026529 ($1.19 \times 10^{-5}$) | 0.00010847 ($4.19 \times 10^{-6}$) | 0.00026432 ($9.19 \times 10^{-6}$) |
| $b_{32}$ | | 0.039732 (0.0190) | | 6.7284 (1.46) |
| $b_{40}$ | -47.329 (12.9) | -45.901 (18.2) | -299.10 (36.2) | -304.31 (49.4) |
| $b_{41}$ | 0.0011689 ($1.95 \times 10^{-5}$) | 0.0010501 ($2.00 \times 10^{-5}$) | 0.0011092 ($2.11 \times 10^{-6}$) | 0.00098928 ($2.09 \times 10^{-5}$) |
| $b_{42}$ | 0.091594 (0.00412) | 0.00071364 ($2.63 \times 10^{-5}$) | 52.688 (7.10) | 0.00068772 ($2.40 \times 10^{-6}$) |
| $b_{43}$ | | 0.097233 (0.042) | 0.091941 (0.00372) | 0.097505 (0.0335) |
| $b_{44}$ | | | | 54.893 (9.16) |

Fit statistics for each system are found in Table 3.8. Fit indices ranged from 0.934 to 0.949 for the root component. For systems that incorporate belowground mass, fit indices for the total tree ranged from 0.965 to 0.970, while for systems that incorporate aboveground mass solely, fit indices ranged from 0.964 to 0.969. In terms of root mean square error, System III (which included *D, H,* and *A*) showed the lowest variance for a system that included belowground components. System VIII (which included *D, H, A,* and *LCL*) showed the lowest variance for a system that included only aboveground components.

**Table 3.8** Fit indices[a] and RMSE[b] (g; parentheses) associated with component and total tree equations fitted with SUR for 4 to 6-year-old loblolly pine grown at a miniature scale.

| | System | | | | | | | |
| | *Above and belowground* | | | | *Aboveground only* | | | |
| | I | II | III | IV | V | VI | VII | VIII |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| *Stem* | 0.958 | 0.958 | 0.965 | 0.965 | 0.964 | 0.964 | 0.970 | 0.970 |
| | (82.43) | (82.45) | (75.93) | (76.17) | (73.04) | (73.15) | (67.60) | (67.40) |
| *Foliage* | 0.872 | 0.889 | 0.872 | 0.889 | 0.838 | 0.889 | 0.838 | 0.890 |
| | (28.17) | (26.30) | (28.16) | (26.31) | (28.18) | (23.45) | (28.18) | (23.38) |
| *Branch* | 0.896 | 0.896 | 0.896 | 0.896 | 0.874 | 0.890 | 0.874 | 0.896 |
| | (15.20) | (15.20) | (15.20) | (15.20) | (14.77) | (13.89) | (14.77) | (13.54) |
| *Root* | 0.934 | 0.949 | 0.949 | 0.949 | | | | |
| | (21.88) | (19.29) | (19.29) | (19.31) | | | | |
| *Total Tree* | 0.965 | 0.967 | 0.969 | 0.970 | 0.966 | 0.965 | 0.964 | 0.969 |
| | (114.90) | (110.32) | (106.59) | (107.09) | (90.79) | (92.30) | (94.13) | (88.57) |

[a] $FI = 1 - \left[ \dfrac{\sum \left(y_i - \hat{y}_i\right)^2}{\sum \left(y_i - \bar{y}_i\right)^2} \right]$ 　　[b] $RMSE = \sqrt{\sum \left(y_i - \hat{y}_i\right)^2 / n - p}$

# CHAPTER 4

## SUMMARY, DISCUSSION, AND CONCLUSIONS

### 4.1 Summary

Height and diameter development differed across initial planting densities from 1.91 x $10^5$ to 17.2 x $10^5$ trees ha$^{-1}$ at ages 4 and 5. Initial planting density did not have a significant effect on the relative amount of biomass partitioned to aboveground tree components. Some tradeoffs between above and belowground components were noted, e.g. the slope for the root: shoot ratio showed significance when plotted against initial planting density. Trees with low crown ratios allocated more biomass to stem and less to canopy components in comparison to trees with high crown ratios, and vice versa. Partitioning patterns also changed between ages 4 and 6, indicating that trees were altering their partitioning priorities on a year-to-year basis.

Eight separate systems of equations were developed to predict component and total tree mass. These systems differ in terms of tree variables measured. The combined variable $D^2H$ predicted component mass well—$D^2LCL$ and $H$ predicted foliage mass better than $D^2H$ for some foliage and branch equations, and including age aided in the prediction of stem mass. Fit statistics showed that the systems of equations provided satisfactory estimates of component and total tree mass.

**4.2 Discussion**

*4.1 Effects of density on partitioning*

   Initial planting density did not have a significant effect on the relative amount of biomass

partitioned to aboveground tree components. This result parallels with Shelton (1984) who found

that stand density did not affect the aboveground biomass partitioning (stand-level) of loblolly

pine. Although eight different densities existed in this study, perhaps no effect of density on

partitioning was seen due small differences in terms of spacing. In terms of allocation of

photosynthate, can loblolly pine detect differences grown in row and column spacings between

7.6 and 22.9 cm? The mean proportion of biomass in the stem component ranged from 0.68 to

0.72 when considering above and belowground mass from densities of 1.91 x $10^5$ to 11.5 x $10^5$

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. There

was evidence, however, that the amount partitioned to roots changed across the range of densities

$(p = 0.0624)$.

   Age showed significance when used as a covariate in determining the effect of density,

showing that changes in partitioning occurred in these trees from age 4 to 6. Since stand

development was greatly accelerated in this miniature-scale plantation and mortality was high,

surviving trees were altering their partitioning patterns as they attempted to outcompete

neighboring trees. Trees increased partitioning to stem at the expense of canopy components as

they developed (from age 4 to 6), which supports the suggestions of others (Waring and

Schlesinger, 1985).

When considering components on a weight ratio approach, these results reflect what others have found. Root: shoot ratios were higher in dense stands of lodgepole pine (Pearson *et al.*, 1984; Litton *et al.*, 2003), and our results indicate similar trends.

Albaugh et al. (1998) concluded that shifts in allocation aboveground due to fertilization were small relative to above versus belowground tradeoffs. Our data supports this statement but with regard to density rather than fertilization. Weight ratios involving the root component in Table 3.3 show a significant slope when fitted against trees ha$^{-1}$. 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 be greater when considering above and belowground components, rather than studying aboveground components only.

When measured on a continuous scale, live crown ratio was a significant predictor for the proportion of mass in aboveground components (Table 3.4). The results from this small-scale study confirm those of Naidu et al. (1998) who found that more suppressed trees, i.e. those trees with smaller live crown ratios, have a greater proportion of heterotrophic to autotrophic tissue.

New foliage has priority for allocation, followed by new roots and stem growth (Waring and Schlesinger, 1985; Oliver and Larson, 1990). It is commonly thought that the root: shoot ratio decreases with increasing age (Litton *et al.*, 2003; Johnsen *et al.*, 2004). In this study, evidence existed of tradeoffs between stem and foliage components at ages 5 and 6 while the percent biomass fixed in the root component remained at 14%, supporting these beliefs. These results signify that changes in stand development occurred in this one-year window and trees may have re-prioritized their biomass allocation patterns. King et al. (2007) concluded that root:

shoot partitioning peaks early in stand development and then declines. Whether or not the trees in this study reached that peak prior to the ages in which they were harvested is unknown. To what extent partitioning changed before the ages studied here would be useful to determine at what ages partitioning patterns in the miniature-scale plantation might scale to operational plantations.

*4.2 Modeling biomass partitioning*

Some may note that for system I, the independent variable $D^2$ is used to predict root mass, while for the other equations, $D^2H$ shows a slightly higher FI and lower RMSE. This is because the SUR estimation method using the SYSLIN procedure will produce the same parameter estimates as OLS if all component equations use the same model form. Hence, the predictive power of the root equation in system I was sacrificed slightly in order to obtain SUR parameter estimates for the entire system.

The fit index (FI) values (comparable to $R^2$) in this study relate well with what others have recorded in biomass equations for loblolly pine. The proportion of variability explained typically exceeds 0.95 when predicting stem mass, which was found in this study (FI ranged from 0.958 to 0.970). Naidu et al. (1998) found $R^2$ values for needles of 0.92 and 0.85 for dominant and suppressed trees, respectively, which relates to FI values that we found (0.838 to 0.890). The FI values from 0.874 to 0.896 found in this study compare to the $R^2$ value recorded by Pehl et al. (1984) when predicting live branch mass (0.91). FI values for woody roots in this study (0.934 to 0.949) are high when compared to the tap root (0.59) and coarse root (0.55) $R^2$ values recorded by Samuelson et al. (2004) for age 6 trees, but reflect the $R^2$ value of 0.90

recorded for the taproot equation based on 25-year-old trees (Pehl *et al.*, 1984). The FI values for roots in this study may be high because equations predict root mass based on groundline diameter, in closer proximity to the component when compared to the conventional DBH measurement. Generally, it appears that the amount of variability that occurred in this miniature-scale plantation in terms of biomass prediction is comparable to what others have found for trees grown in conventional plantations.

It is interesting to note that when tree age is included as a regressor in the stem equation, it shows significance regardless of which system is being used. Including live crown length in a system leads to an increase in $R^2$ and lower RMSE values for the foliage component; however *LCL* only aids in the prediction of branch biomass for systems predicting aboveground mass. When predicting aboveground mass, System VIII (which includes measurements of *D*, *H*, *A*, and *LCL*) shows the highest predictive power and lowest variance. When predicting above and belowground mass, Systems III (*D*, *H*, and *A*) and IV (*D*, *H*, *A*, and *LCL*) perform best, with both systems nearly identical in terms of $R^2$ and RMSE.

Some may speculate why the equations presented here were not transformed in some way, perhaps by weighted SUR or logarithmic transformations. A weighted approach would lead to more emphasis on values with small mass; hence, weighting our data would not necessarily lead to increased accuracy in predictions of trees with larger masses. A log transformation could stabilize the variance; however, transforming our systems of equations in this way would lead to a total tree equation that is in a nonlinear form. This would arise due to the additivity restriction that was placed on the system, and obtaining parameter estimates for nonlinear equations could be problematical. The equations presented herein should provide reasonable estimates for those

who wish to estimate biomass for trees at similar ages and densities as the trees used in this dataset.

*4.3 Comparing results to operationally-spaced studies*

Comparing the results found in this miniature-scale study to other studies of biomass partitioning from stands with more mature trees at operational spacings is fundamental. This comparison will tell us whether or not the biomass partitioning patterns observed at small-scale also occur at a large scale. If trees partition biomass similarly at both scales, then using small-scale studies as a way to determine other silvicultural effects on partitioning is justified.

One issue that arises in this investigation is accounting for differences between scales. As an example, loblolly pine grown at miniature scales do not flower earlier, so no photosynthate was allocated to reproductive structures in these sample trees. For trees grown at operational scales, however, the percentage of biomass in cones on a stand level is likely to be small. Given these differences, evaluating general trends of biomass partitioning between small and large scales is possible.

Live crown ratio is a relative measure of tree development. At the start of stand development, a disproportionate amount of a tree's carbohydrate reserve is spent on producing foliage, while later in the stand's life, the proportion of biomass in stem increases (Waring and Schlesinger, 1985). Similarly, the coarse root: aboveground biomass ratio typically declines with age in loblolly pine plantations (Johnsen *et al.*, 2004). Using the results from this study, one hypothesis (although not statistically testable) is that biomass partitioning patterns are similar for two trees that have equal measures of crown ratio, regardless of what scale (miniature versus

operational) they are grown in. Crown ratios for age 5 trees in this study are roughly 0.30 (Figure 3.1), which is equivalent to what one would expect for loblolly pine plantations at or near rotation age. If two trees have the same crown ratio, but the amount of time and physiological processes differed in the way they reached that value, is the relative amount of biomass allocated to component parts similar for those two trees? It is recognized that other studies involving biomass partitioning are site-specific; however, the aim here is to evaluate the general trends of biomass partitioning observed at the small-scale to those with mature trees at operational scales. To make this comparison, studies with trees ages 15 to 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 to mature trees at operational scales can be seen in Table 4.1. Generally, it appeared that our trees were allocating a large proportion of biomass to the foliage component, which received 10% of above and belowground and 14% of aboveground allocation. This value is high when compared to other studies, although foliage mass did occupy 11% of total stand mass for dominant trees ages 10 to 41 years (Naidu *et al.*, 1998). Leaf biomass typically reaches a peak as canopies close, and then decreases with stand age (Ryan *et al.*, 1997; Burkes *et al.*, 2003). The relative amount of biomass allocated to foliage in this study decreased successively each year (Figure 3.3). Similarly, Samuelson et al. (2004) noted a change in the amount partitioned to foliage between ages 4 and 5 for trees under different management intensities. Burkes et al. (2003) also found that foliage 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, it appears that in terms of biomass allocated to foliage, the miniature-scale trees resembled trees at the

same age at larger scales. Therefore, decreased partitioning to foliage may be primarily a

function of tree age.

**Table 4.1** Comparisons of biomass partitioning in 4 to 6-year-old loblolly pine grown in miniature-scale to operational-scale plantations 15 to 25 years old.

| | | Percentages | | | | |
|---|---|---|---|---|---|---|
| *Study* | *Age* | *Stem* | *Foliage* | *Branch* | *Root* | *Notes* |
| *Above and belowground:* | | | | | | |
| Current study[a] | 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 |
| | 25 | 72 | 2 | 7 | 17 | taproot only |
| *Aboveground:* | | | | | | |
| Current study[b] | 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 | | Fert. x irr. |
| Metz and Wells (1965) | 21 | 82 | 5 | 13 | | Means for two 21-year-old trees |

[a] Percentages are means for trees measured with above and belowground components (n = 67).
[b] Percentages are means for trees measured with aboveground components (n = 96).

Mean individual tree branch biomass percentages (5 and 8% of above and belowground and aboveground mass, respectively) were low for these trees in comparison to mature trees at operational scales (Table 4.1). 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 indicates that needle mass tends to exceed branch mass in young stands, and vice versa for mature stands. It seems that by forcing trees through stand development at an earlier chronological age, as was accomplished with the miniature-scale plots, partitioning patterns in canopy components still resemble those of young trees.

The mean root: shoot ratio across all densities in this study was 0.16. This value is less than the 0.18 to 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 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 comprised primarily of woody roots. By not sampling the fine root component, root allocations would naturally be lower when compared to other studies that sampled roots to a smaller diameter. Fine roots in pine forests can occupy 3 to 7% of total stand biomass (Knight *et al.*, 1994), and one-third of total stand biomass in a high-density lodgepole pine forest (14,000 trees

ha$^{-1}$) was occupied by roots (Pearson *et al.*, 1984). Sampling roots to a smaller diameter would increase the belowground mass pool, increasing partitioning to root on a stand level, and increasing root: shoot ratios.

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 x 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 age 4 trees growing at densities ranging from 740 to 4400 trees ha$^{-1}$. The results from this study mirror those of Burkes et al. (2003) by showing an increase in height: diameter ratio as stand density increases. The larger values in this study are most likely due to the trees allocating a large amount of photosynthate to height growth due to being under high competitive stress. Given that loblolly pine is a shade-intolerant species, increasing height growth in order to outcompete neighboring trees for light is a priority. These results 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.

Biomass partitioning patterns seen at the miniature scale resemble those of trees at operational scales. Needle biomass decreased from 22, 15, and 10% of total aboveground mass for trees ages 4, 5, and 6, indicating that needle mass likely reached a peak. Stem biomass increased at those same ages from 68, 79, and 83%. Allocation of mass to stem is a priority for suppressed trees (Van Lear *et al.*, 1984; Naidu *et al.*, 1998), and it appears that stem is continuing to be a priority for the miniature-scale trees through age 6. Trees are attempting to outcompete neighboring trees by allocating biomass to height growth, given the large height: diameter ratios seen in this study.

**4.3 Conclusions**

Initial planting density did not have a significant effect $(\alpha = 0.05)$ on the relative amount of biomass partitioned to aboveground components. This may have been due to the small differences in terms of spacings. All spacings in this study are extremely narrow, even when considering the most widely-spaced plot. Some tradeoffs between above and belowground components were found across densities. Aboveground tradeoffs alone due to density were not found, indicating that density effects on biomass partitioning may be greater when considering both above and belowground components. Since partitioning changed on a year-to-year basis in this study, it reiterates the statement that stand development plays a significant role in biomass dimensions in loblolly pine stands.

Seemingly unrelated regression methodologies lead to efficient parameter estimates by taking into account inherent correlations among masses of tree components. Specifying additivity ensured that predicted masses from component equations added to total tree mass. The fit index (FI) values in this study relate well with what others have recorded in biomass equations for loblolly pine, indicating that the variability in terms of estimating component and total tree mass in this small-scale study is comparable to mature trees at more traditional scales. The systems of equations presented herein will provide reasonable estimates for those who wish to estimate biomass for trees at similar ages and densities as used in this study.

One general hypothesis was that biomass partitioning patterns are similar for two trees that have equal measures of crown ratio, regardless of what scale they are grown in. In terms of biomass partitioning, the trends observed with these miniature-scale plots showed the same general trends when compared to operationally-spaced stands. Height growth, and hence stem growth, was a priority for more suppressed trees, and trees with smaller crown ratios allocated

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more to stem growth. Similarly, root: shoot ratios changed across the different initial planting densities. The results from this small-scale study indicate that density can be used by managers to influence above and belowground partitioning in loblolly pine plantations.

In terms of biomass partitioning, given that the trends seen at this small scale are similar to those of large scale stands, using miniature-scale experiments to model partitioning patterns at operational scales can be achieved. 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 mature trees.

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APPENDICES

## Appendix I.

## SAS Code and Output for SYSLIN Procedure

SAS Code

```
proc syslin data=above_mass sur simple;
stem: model dwstem = d2h age;
needle: model dwneed = d2 ;
branch: model dwbran = d2h ;
tree: model dwtotal = d2h age d2 ;
srestrict stem.intercept + needle.intercept + branch.intercept =
tree.intercept;
srestrict stem.d2h + branch.d2h = tree.d2h;
srestrict stem.age = tree.age;
srestrict needle.d2 = tree.d2;
run;
```

SAS Output

```
The SYSLIN Procedure
```

### Descriptive Statistics

| Variables | Sum | Mean | Uncorrected SS | Variance | Std Deviation |
|---|---|---|---|---|---|
| Intercept | 96.0000 | 1.0000 | 96.0000 | 0 | 0 |
| DWstem | 39770.5 | 414.3 | 30580368 | 148468 | 385.3 |
| DWneed | 6816.2 | 71.0024 | 945284 | 4856.0 | 69.6847 |
| DWbran | 3801.9 | 39.6032 | 314025 | 1720.6 | 41.4801 |
| dwtotal | 50388.6 | 524.9 | 49109175 | 238538 | 488.4 |
| d2h | 38824289 | 404420 | 2.777E13 | 1.271E11 | 356490 |
| age | 502.0 | 5.2292 | 2700.0 | 0.7890 | 0.8883 |
| d2 | 104285 | 1086.3 | 1.5906E8 | 481802 | 694.1 |

```
The SYSLIN Procedure
Ordinary Least Squares Estimation


Model                     STEM
Dependent Variable        DWstem
Label                     DWstem



                        Analysis of Variance

                          Sum of        Mean
Source              DF    Squares      Square    F Value    Pr > F

Model                2   13691360     6845680    1541.30    <.0001
Error               93   413059.3    4441.497
Corrected Total     95   14104420


Root MSE              66.64456    R-Square      0.97071
Dependent Mean      414.27583    Adj R-Sq      0.97008
Coeff Var            16.08700


                        Parameter Estimates

                  Parameter    Standard                      Variable
Variable      DF   Estimate      Error    t Value   Pr > |t|  Label

Intercept      1    -198.932   42.49689     -4.68    <.0001   Intercept
d2h            1    0.001018   0.000022     47.28    <.0001
age            1    38.54691   8.639903      4.46    <.0001   age




Model                     NEEDLE
Dependent Variable        DWneed
Label                     DWneed



                        Analysis of Variance

                          Sum of        Mean
Source              DF    Squares      Square    F Value    Pr > F

Model                1    386659.8    386659.8    486.85    <.0001
Error               94    74655.66    794.2092
Corrected Total     95    461315.5


Root MSE              28.18172    R-Square      0.83817
Dependent Mean       71.00240    Adj R-Sq      0.83645
Coeff Var            39.69122
```

```
                        Parameter Estimates

                    Parameter    Standard                        Variable
Variable        DF    Estimate      Error    t Value   Pr > |t|   Label

Intercept        1    -28.8406    5.361793      -5.38    <.0001    Intercept
d2               1     0.091911   0.004166      22.06    <.0001


Model                     BRANCH
Dependent Variable        DWbran
Label                     DWbran


                      Analysis of Variance

                              Sum of        Mean
Source              DF       Squares      Square    F Value    Pr > F

Model                1      142949.1    142949.1     655.22    <.0001
Error               94     20508.06    218.1708
Corrected Total     95      163457.2


Root MSE            14.77061    R-Square      0.87454
Dependent Mean      39.60323    Adj R-Sq      0.87320
Coeff Var           37.29647


                        Parameter Estimates

                    Parameter    Standard                        Variable
Variable        DF    Estimate      Error    t Value   Pr > |t|   Label

Intercept        1    -4.40303    2.286526      -1.93    0.0572    Intercept
d2h              1    0.000109    4.251E-6       25.60    <.0001


Model                    TREE
Dependent Variable    dwtotal
Label


                      Analysis of Variance

                              Sum of        Mean
Source              DF       Squares      Square    F Value    Pr > F

Model                3     22070344     7356781    1145.65    <.0001
Error               92     590779.2    6421.513
Corrected Total     95     22661123
```

```
Root MSE              80.13434     R-Square       0.97393
Dependent Mean       524.88146     Adj R-Sq       0.97308
Coeff Var             15.26713
```

```
                        Parameter Estimates

                    Parameter    Standard                        Variable
Variable      DF    Estimate      Error     t Value   Pr > |t|   Label

Intercept     1     114.4725     72.41592      1.58     0.1174    Intercept
d2h           1      0.002009     0.000176    11.38    <.0001     d2h
age           1     -6.41609     11.57135     -0.55     0.5806    age
d2            1     -0.33934      0.087703    -3.87     0.0002    d2
```

The SYSLIN Procedure
Seemingly Unrelated Regression Estimation

```
               Cross Model Covariance

           STEM         NEEDLE        BRANCH        TREE

STEM      4441.50       810.14       414.020      4446.58
NEEDLE     810.14       794.21       172.910      1227.22
BRANCH     414.02       172.91       218.171       702.75
TREE      4446.58      1227.22       702.747      6421.51
```

```
               Cross Model Correlation

           STEM         NEEDLE        BRANCH        TREE

STEM      1.00000      0.43135       0.42059       0.83261
NEEDLE    0.43135      1.00000       0.41539       0.54342
BRANCH    0.42059      0.41539       1.00000       0.59372
TREE      0.83261      0.54342       0.59372       1.00000
```

```
            Cross Model Inverse Correlation

           STEM         NEEDLE        BRANCH        TREE

STEM      3.35350      0.05115       0.37464      -3.04239
NEEDLE    0.05115      1.44710      -0.20146      -0.70937
BRANCH    0.37464     -0.20146       1.61594      -1.16186
TREE     -3.04239     -0.70937      -1.16186       4.60844
```

```
            Cross Model Inverse Covariance

           STEM         NEEDLE        BRANCH        TREE

STEM      0.000755     0.000027      0.000381     -.000570
NEEDLE    0.000027     0.001822     -.000484      -.000314
BRANCH    0.000381    -.000484       0.007407     -.000982
TREE     -.000570     -.000314      -.000982       0.000718
```

```
System Weighted MSE            0.8279
Degrees of freedom               377
System Weighted R-Square       0.9245



Model                   STEM
Dependent Variable      DWstem
Label                   DWstem


The SYSLIN Procedure
Seemingly Unrelated Regression Estimation


                        Parameter Estimates


                    Parameter    Standard                        Variable
Variable       DF    Estimate      Error    t Value   Pr > |t|   Label

Intercept       1    -265.959    35.12938     -7.57    <.0001    Intercept
d2h             1     0.001001    0.000019     52.13    <.0001
age             1     52.68766    7.101338      7.42    <.0001    age


Model                   NEEDLE
Dependent Variable      DWneed
Label                   DWneed


                        Parameter Estimates


                    Parameter    Standard                        Variable
Variable       DF    Estimate      Error    t Value   Pr > |t|   Label

Intercept       1     -28.8736    4.791349     -6.03    <.0001    Intercept
d2              1     0.091942    0.003720     24.72    <.0001


Model                   BRANCH
Dependent Variable      DWbran
Label                   DWbran


                        Parameter Estimates


                    Parameter    Standard                        Variable
Variable       DF    Estimate      Error    t Value   Pr > |t|   Label

Intercept       1     -4.26410    2.255052     -1.89    0.0617    Intercept
d2h             1     0.000108    4.189E-6     25.90    <.0001
```

```
Model                    TREE
Dependent Variable    dwtotal
Label
```

Parameter Estimates

| Variable | DF | Parameter Estimate | Standard Error | t Value | Pr > \|t\| | Variable Label |
|----------|----|--------------------|----------------|---------|-----------|----------------|
| Intercept | 1 | -299.097 | 36.18718 | -8.27 | <.0001 | Intercept |
| d2h | 1 | 0.001109 | 0.000021 | 52.66 | <.0001 | |
| age | 1 | 52.68766 | 7.101338 | 7.42 | <.0001 | age |
| d2 | 1 | 0.091942 | 0.003720 | 24.72 | <.0001 | |

Parameter Estimates

| Variable | DF | Parameter Estimate | Standard Error | t Value | Pr > \|t\| | Variable Label |
|----------|----|--------------------|----------------|---------|-----------|----------------|
| RESTRICT | -1 | -124E-17 | 0.223815 | -0.00 | 1.0000 | |
| RESTRICT | -1 | -8292.96 | 120562.3 | -0.07 | 0.9456 | |
| RESTRICT | -1 | 0.346597 | 1.190444 | 0.29 | 0.7727 | |
| RESTRICT | -1 | 35.48665 | 288.2705 | 0.12 | 0.9028 | |

**SAS Code and Output for SYSLIN Procedure**

SAS Code

```
data system7; set above_mass;
pred_stem = -265.96 + 0.0010007 * d2h + 52.688 *age;        *predicted values using SUR estimates*;
pred_need = -28.874 + 0.091942 * d2;
pred_bran = -4.2641 + 0.00010847 * d2h;
pred_total = -299.10 + 0.0011092 * d2h + 52.688 * age + 0.091941 * d2;

e1 = dwstem - pred_stem;                                    *random errors*;
e2 = dwneed - pred_need;
e3 = dwbran - pred_bran;
e4 = dwtotal - pred_total;

b10 = -265.96;                                             *SUR parameter estimates*;
b11 = 0.0010007;
b12 = 52.688;
b20 = -28.874;
b21 = 0.091942;
b30 = -4.2641;
b31 = 0.00010847;

*parameter estimate * independent variable follow*;

x10 = b10;  x11 = b11*d2h;   x12 = b12*age;   x13 = 0;   x14 = 0;       x15 = 0;   x16 = 0;
x20 = 0;    x21 = 0;         x22 = 0;         x23 = b20; x24 = b21*d2;  x25 = 0;   x26 = 0;
x30 = 0;    x31 = 0;         x32 = 0;         x33 = 0;   x34 = 0;       x35 = b30; x36 = b31*d2h;
x40 = b10;  x41 = b11*d2h;   x42 = b12*age;   x43 = b20; x44 = b21*d2;  x45 = b30; x46 = b31*d2h;

run;
```

```sas
data Smatrix_Sys7;                              *This is the sigma hat matrix obtained from PROC SYSLIN output*;
input component $ S1 S2 S3 S4;
datalines;

STEM            4441.50         810.14          414.020         4446.58
NEEDLE           810.14         794.21          172.910         1227.22
BRANCH           414.02         172.91          218.171          702.75
TREE            4446.58        1227.22          702.747         6421.51

; run;


options source;

proc iml;
reset noprint;
use system7;
read all var{dwstem dwneed dwbran dwtotal dia_mm ht_cm age
    x10 x11 x12 x13 x14 x15 x16
    x20 x21 x22 x23 x24 x25 x26
    x30 x31 x32 x33 x34 x35 x36
    x40 x41 x42 x43 x44 x45 x46
    e1 e2 e3 e4};

reset print;

    M = 4;              *number of equations in system*;
    T = 96;             *number of observations in each equation*;
    K = 7;              *number of parameters estimated in system*;

reset noprint;

    X1 = x10||x11||x12||x13||x14||x15||x16;    *partial derivatives matrix for stem (96x7)*;
    X2 = x20||x21||x22||x23||x24||x25||x26;    *partial derivatives matrix for needle (96x7)*;
    X3 = x30||x31||x32||x33||x34||x35||x36;    *partial derivatives matrix for branch (96x7)*;
    X4 = x40||x41||x42||x43||x44||x45||x46;    *partial derivatives matrix for total tree (96x7)*;

    X  = X1 // X2 // X3 // X4;                  *partial derivatives matrix for system (384x7)*;
    e  = e1 // e2 // e3 // e4;                  *random error vector matrix (384x1);
```

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```
          free x10 x11 x12 x13 x14 x15 x16 ;
          free x20 x21 x22 x23 x24 x25 x26 ;
          free x30 x31 x32 x33 x34 x35 x36 ;
          free x40 x41 x42 x43 x44 x45 x46 ;
          free e1 e2 e3 e4;




   use Smatrix_Sys7;
          read all var {S1 S2 S3 S4};

reset print;

          S = S1 || S2 || S3 || S4;          *Sigma hat matrix (4x4)*;
          S_inv = inv(S);
          covb = inv(X`*(S_inv@I(T))*X);   *this is the covariance matrix (7x7) of parameter
                                             estimates... @ denotes direct product, I(T) is
                                             an identity matrix of order T (number of observations)*;


          R_b = e`*(S_inv@I(T))*e;               *this is the residual sums of squares*;
          sys_df = M*T - K;                      *degrees of freedom for system*;
          var_sur = R_b / sys_df;                *SUR system variance*;



*Example: predict component and total tree weight with confidence and prediction intervals*;

reset noname noprint;
      use System7;
      read all var{b10 b11 b12 b20 b21 b30 b31};
reset print;
      print "Example with dia_mm = 30, ht_cm = 310, age = 5 yrs";
      dia_mm =30;
      ht_cm = 310;
      age = 5;
```

```
print "STEM equation";
f_STEM = {-265.96, 279.20, 263.44, 0, 0, 0, 0};        *row vector from X*;

yhat_STEM = -265.96 + (0.0010007 * dia_mm * dia_mm * ht_cm) + (52.688 * age);

s2y_cl_STEM =(f_STEM` * covb * f_STEM);                *variance for individual observation from stem
                                                        equation*;

cl_STEM = 2 * sqrt(s2y_cl_STEM);                       *approximate 95% confidence interval with
                                                        t(alpha/2)= 2*;

S1_1 = S[1,1];

s2y_pl_STEM = s2y_cl_STEM + (var_sur * S1_1);

pl_STEM = 2 * sqrt(s2y_pl_STEM);                       *approximate 95% prediction interval with
                                                        t(alpha/2)= 2*;




print "predicted stem weight is:" yhat_STEM "g";
print "95% confidence limit is:" cl_STEM "g";
print "system variance is:" var_sur;
print "variance of stem equation is:" S1_1;
print "variance of yhat(new) is:" s2y_pl_STEM;
print "95% prediction limit:" pl_STEM "g";
```

```
print "NEEDLE equation";

f_NEED = {0, 0, 0, -28.874, 82.748, 0, 0};
yhat_NEED = -28.874 + (0.091942 * dia_mm * dia_mm);
s2y_cl_NEED =(f_NEED` * covb * f_NEED);
cl_NEED = 2 * sqrt(s2y_cl_NEED);
S2_2 = S[2,2];
s2y_pl_NEED = s2y_cl_NEED + (var_sur * S2_2);
pl_NEED = 2 * sqrt(s2y_pl_NEED);


print "predicted needle weight is:" yhat_NEED "g";
print "95% confidence limit is:" cl_NEED "g";
print "system variance is:" var_sur;
print "variance of needle equation is:" S2_2;
print "variance of yhat(new) is:" s2y_pl_NEED;
print "95% prediction limit:" pl_NEED "g";




print "BRANCH equation";

f_BRAN = {0, 0, 0, 0, 0, -4.2641, 30.263};
yhat_BRAN = -4.2641 + (0.00010847 * dia_mm * dia_mm * ht_cm);
s2y_cl_BRAN =(f_BRAN` * covb * f_BRAN);
cl_BRAN = 2 * sqrt(s2y_cl_BRAN);
S3_3 = S[3,3];
s2y_pl_BRAN = s2y_cl_BRAN + (var_sur * S3_3);
pl_BRAN = 2 * sqrt(s2y_pl_BRAN);


print "predicted branch weight is:" yhat_BRAN "g";
print "95% confidence limit is:" cl_BRAN "g";
print "system variance is:" var_sur;
print "variance of branch equation is:" S3_3;
print "variance of yhat(new) is:" s2y_pl_BRAN;
print "95% prediction limit:" pl_BRAN "g";
```

```
print "TREE equation";

f_TREE = {-265.96, 279.20, 263.44, -28.874, 82.748, -4.2641, 30.263};
yhat_TREE = -299.10 + (0.001109 * dia_mm * dia_mm * ht_cm) + (52.688 * age) +
            (0.091942 * dia_mm * dia_mm);
s2y_cl_TREE =(f_TREE` * covb * f_TREE);
cl_TREE = 2 * sqrt(s2y_cl_TREE);
S4_4 = S[4,4];
s2y_pl_TREE = s2y_cl_TREE + (var_sur * S4_4);
pl_TREE = 2 * sqrt(s2y_pl_TREE);


print "predicted total tree weight is:" yhat_TREE "g";
print "95% confidence limit is:" cl_TREE "g";
print "system variance is:" var_sur;
print "variance of total tree equation is:" S4_4;
print "variance of yhat(new) is:" s2y_pl_TREE;
print "95% prediction limit:" pl_TREE "g";



quit;
run;
```

```
M       1 row       1 col      (numeric)


                              4



T       1 row       1 col      (numeric)


                              96



K       1 row       1 col      (numeric)


                              7



S      4 rows      4 cols     (numeric)


     4441.5      810.14      414.02     4446.58
     810.14      794.21      172.91     1227.22
     414.02      172.91     218.171      702.75
    4446.58     1227.22     702.747     6421.51



S_INV      4 rows       4 cols     (numeric)


  0.000755 0.0000272 0.0003806  -0.00057
 0.0000272 0.0018221 -0.000484 -0.000314
 0.0003806 -0.000484 0.0074068 -0.000982
  -0.00057 -0.000314 -0.000982 0.0007177
```

```
            COVB      7 rows      7 cols    (numeric)


0.0174465   -0.00057 0.0171581 0.0015003 0.0002532 0.0070914 0.0003778
 -0.00057   0.000368 -0.001091 0.0007385 0.0002135 0.0027324 0.0002656
0.0171581 -0.001091 0.0181659 -0.000239 -0.000069 -0.000262 -0.000025
0.0015003 0.0007385 -0.000239 0.0275361 0.0056621   0.033581 0.0020838
0.0002532 0.0002135 -0.000069 0.0056621 0.0016369 0.0061975 0.0006024
0.0070914 0.0027325 -0.000262 0.0335812 0.0061975 0.2796783 0.0153409
0.0003778 0.0002656 -0.000025 0.0020838 0.0006024 0.0153409 0.0014912



            R_B     1 row      1 col     (numeric)



                         312.1254



            SYS_DF     1 row      1 col     (numeric)



                           377



            VAR_SUR     1 row      1 col     (numeric)



                         0.8279188



     Example with dia_mm = 30, ht_cm = 310, age = 5 yrs


            DIA_MM     1 row      1 col     (numeric)


                           30


            HT_CM     1 row      1 col     (numeric)


                           310


            AGE     1 row      1 col     (numeric)



                            5
```

```
                          STEM equation


        F_STEM      7 rows      1 col      (numeric)

                            -265.96
                             279.2
                             263.44
                               0
                               0
                               0
                               0



        YHAT_STEM     1 row       1 col      (numeric)

                          276.6753

      S2Y_CL_STEM     1 row       1 col      (numeric)

                          43.32572

        CL_STEM     1 row       1 col      (numeric)

                          13.164455

         S1_1      1 row       1 col      (numeric)

                           4441.5

      S2Y_PL_STEM     1 row       1 col      (numeric)

                          3720.5272

        PL_STEM     1 row       1 col      (numeric)

                          121.99225


        predicted stem weight is:  276.6753 g


       95% confidence limit is: 13.164455 g


           system variance is: 0.8279188


        variance of stem equation is:    4441.5


        variance of yhat(new) is: 3720.5272


         95% prediction limit: 121.99225 g
```

```
                          NEEDLE equation


     F_NEED      7 rows       1 col      (numeric)

                              O
                              O
                              O
                          -28.874
                           82.748
                              O
                              O



    YHAT_NEED      1 row       1 col      (numeric)

                           53.8738

  S2Y_CL_NEED      1 row       1 col      (numeric)

                          7.1087962

    CL_NEED      1 row       1 col      (numeric)

                          5.3324652

     S2_2      1 row       1 col      (numeric)

                           794.21

  S2Y_PL_NEED      1 row       1 col      (numeric)

                          664.65021

    PL_NEED      1 row       1 col      (numeric)

                          51.561622


     predicted needle weight is:   53.8738 g


    95% confidence limit is: 5.3324652 g


        system variance is: 0.8279188


   variance of needle equation is:   794.21


      variance of yhat(new) is: 664.65021


      95% prediction limit: 51.561622 g
```

```
                         BRANCH equation


        F_BRAN        7 rows      1 col      (numeric)

                                    O
                                    O
                                    O
                                    O
                                    O
                               -4.2641
                                30.263



        YHAT_BRAN       1 row      1 col      (numeric)

                            25.99903

      S2Y_CL_BRAN       1 row      1 col      (numeric)

                            2.4916639

        CL_BRAN       1 row      1 col      (numeric)

                            3.1570011

          S3_3       1 row      1 col      (numeric)

                             218.171

      S2Y_PL_BRAN       1 row      1 col      (numeric)

                            183.11954

        PL_BRAN       1 row      1 col      (numeric)

                            27.064334



        predicted branch weight is:  25.99903 g


        95% confidence limit is: 3.1570011 g


            system variance is: 0.8279188


      variance of branch equation is:   218.171


        variance of yhat(new) is: 183.11954


        95% prediction limit: 27.064334 g
```

```
                          TREE equation


       F_TREE      7 rows      1 col      (numeric)

                           -265.96
                            279.2
                            263.44
                           -28.874
                            82.748
                           -4.2641
                            30.263



       YHAT_TREE     1 row      1 col      (numeric)

                           356.4988

      S2Y_CL_TREE      1 row      1 col      (numeric)

                           74.842692

       CL_TREE      1 row      1 col      (numeric)

                           17.302334

        S4_4      1 row      1 col      (numeric)

                           6421.51

      S2Y_PL_TREE      1 row      1 col      (numeric)

                           5391.3317

       PL_TREE      1 row      1 col      (numeric)

                           146.85138



     predicted total tree weight is:  356.4988 g


        95% confidence limit is: 17.302334 g


           system variance is: 0.8279188


    variance of total tree equation is:   6421.51


        variance of yhat(new) is: 5391.3317


        95% prediction limit: 146.85138 g
```

**Example Using SUR Equations**

The following calculations follow the SAS code and output given in Appendices I and II. Consider a tree with the following dimensions: $D = 30$ mm, $H = 310$ cm, $A = 5$ years. Assume we wish to estimate total tree and component mass (grams) using System VII (Eq. 3.14.7). The system is:

$$\hat{W}_{stem} = -265.96 + 0.0010007\, D^2 H + 52.688 A$$
$$\hat{W}_{foliage} = -28.874 + 0.091942\, D^2$$
$$\hat{W}_{branch} = -4.2641 + 0.00010847\, D^2 H$$
$$\hat{W}_{tree} = -299.10 + 0.0011092\, D^2 H + 52.688\, A + 0.091942\, D^2$$

The estimate of the variance-covariance matrix $\Sigma$ from Eq. 3.4 is:

$$\hat{\Sigma} = \begin{bmatrix} 4441.50 & 810.14 & 414.020 & 4446.58 \\ 810.14 & 794.21 & 172.910 & 1227.22 \\ 414.02 & 172.91 & 218.171 & 702.75 \\ 4446.58 & 1227.22 & 702.747 & 6421.51 \end{bmatrix}$$

The residual sums of squares $R(\mathbf{b})$ from Eq. 3.6 is 312.13. After estimating the partial derivatives matrix $\mathbf{P}(\boldsymbol{\beta})'$ from Eq. 3.8, the variance-covariance matrix of the parameters is a $(7 \times 7)$ matrix and is:

$$
\hat{\Sigma}_{\mathbf{b}} = \begin{bmatrix} 0.01745 & -0.00057 & \cdots & 0.0003778 \\ -0.00057 & 0.0003678 & \cdots & 0.0002656 \\ \vdots & \vdots & \ddots & \vdots \\ 0.0003794 & 0.0002667 & \cdots & 0.001491 \end{bmatrix}
$$

Using the residual sums of squares $R(\mathbf{b})$, the SUR system variance is found by

$$
\hat{\sigma}^2_{SUR} = \frac{R(\mathbf{b})}{MT - K} = \frac{312.13}{(4)(96) - (7)} = 0.8279
$$

The vector $\mathbf{p}_{tree}(\mathbf{b})$ contains the partial derivatives for the $\hat{W}_{tree}$ equation. The estimated variance for the tree equation for system VII is

$$
S^2_{\hat{y}_{tree}} = \mathbf{p}_{tree}(\mathbf{b})' \, (\hat{\Sigma}_{\mathbf{b}}) \, \mathbf{p}_{tree}(\mathbf{b}) = 74.84
$$

Using the given trees dimensions, one can solve for total tree and component mass to obtain estimates in grams:

$$
\hat{W}_{stem} = 276.7 \, \text{g}
$$
$$
\hat{W}_{foliage} = 53.87 \, \text{g}
$$
$$
\hat{W}_{branch} = 26.00 \, \text{g}
$$
$$
\hat{W}_{tree} = 356.6 \, \text{g}
$$

Using Eq. 3.13, an approximate 95% confidence interval for $\hat{W}_{tree}$, with $t = 2$ is

$$356.6 \pm 2\sqrt{74.84} = 356.6 \pm 17.30 = \{339.3; 373.9\}$$

Similarly, the 95% prediction interval, with $\hat{\sigma}_{tree,tree} = 6421.5$ (the variance for the tree equation from $\hat{\Sigma}$) is

$$356.6 \pm 2\sqrt{74.84 + (0.8279)(6421.5)} = 356.6 \pm 146.9 = \{209.7; 503.5\}$$

Approximate 95% confidence and prediction intervals follow similarly for component equations:

$\hat{W}_{stem}$

$$276.7 \pm 2\sqrt{43.33} = 276.7 \pm 13.2 = \{263.5; 289.9\}$$

$$276.7 \pm 2\sqrt{43.33 + (0.8279)(4441.5)} = 276.7 \pm 122.0 = \{154.7; 398.7\}$$

$\hat{W}_{foliage}$

$$53.87 \pm 2\sqrt{7.11} = 53.87 \pm 5.33 = \{48.54; 59.20\}$$

$$53.87 \pm 2\sqrt{7.11 + (0.8279)(794.21)} = 53.87 \pm 51.56 = \{2.31; 105.43\}$$

$\hat{W}_{branch}$

$$26.00 \pm 2\sqrt{2.49} = 26.00 \pm 3.16 = \left\{22.84\, ; 29.16\right\}$$

$$26.00 \pm 2\sqrt{2.49 + (0.8279)(218.27)} = 26.00 \pm 27.06 = \left\{-1.06\, ; 53.06\right\}$$

VITA

Matthew Brian Russell was born in 1983 in Sharon, Connecticut to parents Thomas R. and Katherine S. Russell. He graduated in 2002 from the Arlington Central School District, LaGrangeville, New York. In 2004 he obtained an A.A.S. in Pre-Professional Forestry and in 2006 a B.S. in Forestry-Forest Biology Concentration from Paul Smith's College, Paul Smiths, New York. After defending on 28 January 2008 he obtained a M.S. in Forest Biometrics from Virginia Polytechnic Institute and State University, Blacksburg, VA.