Branch and Stem Growth as Affected by Loss of Leaf Area on Selected Branches in Loblolly Pine

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BRANCH AND STEM GROWTH AS AFFECTED BY LOSS OF LEAF AREA ON SELECTED BRANCHES IN LOBLOLLY PINE

A Dissertation

Submitted to the Graduate Faculty of the Louisiana State University and Agricultural and Mechanical College in partial fulfillment of the requirements for the degree of Doctor of Philosophy

in

The School of Renewable Natural Resources

by

Shannon Dumo Kidombo
B.S. Moi University, Kenya, 2005
M.S. Southern University and A&M, 2013
August 2017
To mom

Jescah M. Anogole
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ABSTRACT

Leaf area and crown dynamics control how trees grow through their supply of carbohydrates and growth regulators, and their influence on tree mechanical stability. The influence of leaf area and crown dynamics to tree growth was investigated by testing the interdependence between leaf area, branch, and stem growth on young loblolly pine trees. The objectives were to (1) determine the influence of current and previous year’s leaf area on elongation of branches; (2) describe and test a unique way of quantitatively measuring the effect of neighbor branches on net growth of a target branch; (3) quantify the growth impact of reduced leaf area on selected branch whorls on stem diameter growth; and (4) describe the changes in the stem profile of young loblolly pine trees in response to different combinations of artificial defoliation and shade stress treatments. A series of shade and defoliation treatments were applied on branches on the fourth (target) whorl from the top of selected trees, considering the positional effect of branches in the crown. Ten trees were randomly assigned one of nine treatments designed to effect the carbohydrate production and growth factors on branch growth. Three levels of treatments unaltered control, foliage removed, or foliage shaded, were applied on the target branches or its upper and lower neighbors. Treatments were replicated twice in each of the five blocks in the field. Growth responses were measured from elongation of terminal leaders, diameter of branches on the target whorl, and the diameter of internodes adjacent to treated branches. Results show that elongation of terminal buds and growth of new leaves were affected by removal or shading of leaf area and the initial base diameter of the branch. The number of new fascicles, representing stem units carried on a bud, could be predicted with the length of the fully elongated bud using the power law. Growth in tree diameter was sensitive to minor changes in the leaf area of the tree crown. Stem profiles varied with reduction in leaf area of selected branches, and the
effect of treatments was localized to internodes immediately above or below the branch whorls that were treated.

Key words: Branch autonomy, Branch growth, Crown dynamics, Defoliation, Leaf area, Shade
CHAPTER 1 INTRODUCTION

Background

Extension growth in trees occurs when shoot and root apical meristems extend. Shoot apical meristems give rise to leaves and branches while root apical meristems give rise to roots. Basal area is by action of the cambium which divides to form xylem to the inside and phloem to the outside. The balance in growth of foliage and stem or branch components gives trees their distinct crown shapes and plays a role in determining their growth rates (Ford, 1985). Growth of branches to specific crown shapes is partly endogenously controlled by action of growth hormones (Wilson, 2000). Irrespective of the form, growth of the crown maximizes leaf display for light interception (Fisher and Honda, 1979; Monsi and Saeki, 2005).

Several mechanisms of stem formation have been proposed, among them are the crown centered mechanisms based on the pipe model (Rennolls, 1994; Shinozaki et al., 1964a) and the mechanical models that emphasize the distribution of bending stress on the stem (Dean and Long, 1986a; Metzger, 1893). However, no general mechanism has been agreed upon, but some authors have suggested that multiple factors, including mechanical bending and crown morphology are likely to be simultaneously involved in the development of stem form in trees (Osawa, 1993).

The functional link between leaf area and stem transport was first quantified by (Huber 1928), and was later expanded by Shinozaki and other workers (1964) to describe the pipe model theory. Per the pipe model, a unit mass of leaf area is serviced by a constant cross-sectional area of conducting sapwood. There is also the established principle that the cross-sectional area of the stem at a given height in the crown is linearly related to the total leaf area above that point
times the distance to the center of the leaf area raised to 1/3 power (Dean and Long, 1986a; Shinozaki et al., 1964a; Shinozaki et al., 1964b). The pipe model theory forms the basis for many established relationships between tree sapwood cross-sectional area and leaf mass (Grier and Waring, 1974) or leaf area (Dean and Long, 1986b; Dean et al., 1988; Kaufmann and Troendle, 1981).

The tree crown grows as a unit, but leaf area on individual branches in the crown has a controlling effect on how branches grow. The top young shoots initially depend on reserves and imported carbohydrates for growth due to undeveloped leaf area, but quickly adapt to self-sufficiency as leaves expand to maturity (Zimmerman and Brown, 1971). Branches in the middle crown are generally self-sufficient in carbohydrate supply due to fully developed leaf area and are able to export to neighboring shoots. Mature lower branches are considered autonomous in carbon demands (Sprugel et al., 1991) and therefore may have minimal contribution to carbohydrate requirements of other shoots or the stem (Roberts, 1994). Other studies have shown a more dynamic crown in which branches within the crown are interdependent in carbon supply in that carbohydrates are imported and exported depending on the need (Sprugel, 2002; Zimmerman and Brown, 1971). Growing tips and reproductive structures are documented to draw carbohydrates from far distances within the tree to satisfy their nutrient requirements (Wardlaw, 1990). Despite slowed growth, lower branches still respond to apical control exerted by terminal shoots, a phenomenon that demonstrates a more coordinated growth.

Trees are considered an assemblage of self-similar, repetitive modules (White, 1979) arranged in a hierarchical model giving rise to a fractal structure (West et al., 1999). The question of autonomy of units such as branches has been a subject of many studies but remains unresolved (Sprugel, 2002; Sprugel et al., 1991; Watson and Casper, 1984). While absolute branch
autonomy would be considered unrealistic, this question can be resolved by examining acquisition, recycling, and assimilation of resources of interest. Physiological and anatomical patterns observed in trees provide evidence that tree branches maintain unique local control of resources such as water and carbohydrates (McCutchan and Shackel, 1992). Branches rely on stem structure for anchorage and water supply and therefore cannot be considered autonomous regarding water and mineral element acquisition. Branches can however be autonomous in carbon requirements due to the photosynthetic ability of local foliage. Young terminal shoots rely on other branches for carbohydrate supply until they are able to satisfy local respiration needs (Pallardy, 2010). The threshold at which a branch becomes self-reliant on carbon is still unknown, though it is thought to be a gradual transition. Resolving the question of branch autonomy will be useful in explaining how trees respond to inter-crown competition, differential shading and defoliation.

Photosynthesis takes place primarily in foliage but wood constitute the bulk of biomass stock in trees. Complex mechanisms control allocation patterns of manufactured carbohydrate between foliage, growth, and wood. Studies show that allocation patterns are controlled by many factors including tree specific internal factors, source-sink relations (Kozlowski, 1992), environmental conditions (Dewar et al., 1994), hormones, and developmental stage (Wardlaw, 1990).

Growth patterns in trees vary widely between species. In the genus *Pinus*, some species such as *P. resinosa*, *P. contorta* and *P. sylvestris* exhibit determinate growth within a season, while others such as *P. radiata*, *P. elliottii* and *P. taeda* have indeterminate growth. Loblolly pine (*P. taeda* L) demonstrates free growth (Dougherty et al., 1994) and therefore has multiple flushes of shoot growth per growth season (Tang et al., 1999). The first flush grows from preformed buds while subsequent flushes develop from neoformed buds. The leaf primodia for the first flush is
laid in the previous growing season and therefore though elongation of the bud and foliage
occurs in the spring, the number of foliage was fixed in the previous fall. Development of shoot
and foliage primodia for the subsequent flushes occurs concurrently in the current growing
season (Dougherty et al., 1994). The extent and number of flushes per shoot is determined by
crown position (Tang et al., 1999), hormones, environment, and substrate availability. Variation
in number of flushes with crown depth is an indication of the role of stage of development of
individual branches and light availability within the crown.

There is coordinated growth between leaf area, main stem and branches based on the established
functional relationships that allow movement of substrates, water and growth regulators within
the tree. Various authors have studied the functional relationship between leaf area, leaf mass
and stem sapwood (Huber, 1928; Shinozaki et al., 1964a) (Grier and Waring, 1974) (Dean et al.,
1988; Kaufmann and Troendle, 1981). The mechanism on how leaf area contributes to form and
taper of stem could be attributed to carbon relations (Långström et al., 1990), physiological
responses (Larson, 1963), or distribution of mechanical stress (Dean and Long, 1986a). Studies
show that stem growth responds to changes in crown leaf area. In a pruning study, Stein (1955)
observed that diameter growth was significantly reduced when over 40% of the live crown was
pruned. When studying loss of leaf area on selected branches, it is anticipated that the effect of
treatments on branches would be reflected in growth of the tree stem.

This study investigates the triggers of balance and interdependence between leaf area, branches
in the crown, and the mechanisms of how crown dynamics contributes to growth of stem wood. I
will attempt to quantify branch interactions in the crown using a series of defoliation and shading
treatments that are designed to effect carbohydrate and growth factors on branch whorls and
stem. The contribution of branch whorls to stem growth, and the distribution of growth along the stem is also examined in an attempt to describe the mechanisms behind stem formation.

**Research Objectives**

The overall objective of this study was to describe the how the crown centered models of stem formation are integrated into the knowledge of the functional crown in accounting for stem growth. The specific objectives include the following:

1. to describe and test a unique way of quantitatively measuring the effect of neighbor branches on net growth of a target branch (interdependence of branches);
2. to describe the changes in the stem profile of young loblolly pine trees in response to different combinations of artificial defoliation and shade stress treatments;
3. to quantify the growth impact of reduced leaf area on selected branch whorls on diameter growth; and
4. to determine the influence of current and previous year’s leaf area on elongation of branches.

**General Methods**

This study was conducted at Lee Memorial Forest, southeastern Louisiana (Fig 1-1). Trees used for this study were planted in 2012 in five isolated field blocks measuring 27 m x 27 m. Three blocks were planted at spacing of 3 m x 3 m while two blocks were planted at spacing of 1.59 m x 1.59 m. Second generation containerized loblolly pine (*Pinus taeda* L.) seedlings were sourced from the Plum Creek nursery in Hazlehurst, Mississippi. The seedlings were planted the same time using the same protocol. In 2015, 18 trees of good form were selected from each block
along the outer boundary of the blocks. Each of the nine treatment combinations were assigned on individual trees, and replicated in each block.

Figure 1-1 Location of Lee Memorial Forest of Louisiana State University, in southeastern Louisiana. Inset shows location of Louisiana, US
Synopsis of the chapters

This study reconciles the concepts of functional crown and the crown driven models of stem formation in an attempt to describe the mechanisms behind that control stem formation. Chapter 2 presents a unique method of quantifying the interaction of branches in the crown. The novel method helps to isolate the effect of neighbor branches on net growth of a target branch. The influence of neighbor branches is successfully quantified. Chapter 3 analyzes the effect of reduced leaf area and treatments on the upper stem. The effects of treatments are analyzed by comparing stem profiles of treated trees with that of the untreated control. Linear mixed effects model is used to describe the stem profiles. Chapter 4 describes the observed growth responses from reduced leaf area in the crown. Radial growth is determined from the width of growth rings and the cross-sectional area of growth rings along the stem profile for two growth seasons. The effect on stem form is also related to stem profile and it reveals predictable patterns of tree response to the proportion of leaf area removed from the tree. Chapter 5 examines how leaf area and shoot elongation interact. Elongation of terminal buds and growth of new leaves are affected by last year’s leaf area and size of the branch. The number of new fascicles, representing stem units carried on a bud, can be predicted from the length of the fully elongated bud.

References


CHAPTER 2 ELONGATION OF BRANCHES AND GROWTH OF NEW LEAVES AS INFLUENCED BY LOSS OF LEAF AREA

Introduction

Shoots grow from action of apical meristems, which are also responsible for production of leaves and branches. The balance of foliage and stem or branch components gives trees their distinct crown shapes (Ford, 1985) and plays a role in determining their growth rates. Shoots grow while putting on new leaves that are displayed to maximize light interception (Fisher and Honda, 1979). Branches are critical in supporting leaves just as leaves are critical in supplying carbohydrates for maintenance and growth. Growth of leaf area and shoots are therefore interdependent, but the distribution of growth between leaf area and shoot elongation varies.

Though photosynthesis takes place primarily in foliage, supporting structures such as branches and stem constitute the bulk of biomass stock in trees. This could be attributable to a tree’s growth to achieve mechanical stability, and the short lifespan of leaves. The mechanisms that control allocation patterns of manufactured carbohydrate between foliage, growth, and structures are influenced by many factors including tree specific internal factors, source-sink relations (Kozlowski, 1992) environmental conditions (Dewar et al., 1994), hormones, and developmental stage (Wardlaw, 1990). Studies show that carbohydrate allocation is driven by source-sink relations (Kozlowski, 1992; Wardlaw, 1990) and that strong carbohydrate sinks such as elongating buds and reproductive organs are able to draw assimilates from long distances in the plant. However, Weinstein and others (1991) observed that reduced carbon is acquired on a first-come first-served basis, based on proximity to the source. In this case, foliage carbon sinks are met first, then petiole, stem, branch, trunk and finally root sinks while water and nutrients are supplied to root sinks then trunk, branch, petiole and foliage.
Elongation of terminal buds has been shown to be endogenously controlled. In their study of shoot elongation in ponderosa pine (*Pinus ponderosa* var. *scopulorum* E.), Lanner and Connor (1988) surgically removed terminal meristems and needle fascicles from elongating buds. They observed that shoots whose apical meristems were removed elongated normally compared to controls but shoots whose fascicles were removed had reduced growth. They concluded that the elongation of terminal buds was therefore endogenously controlled by substances from within the elongating needle fascicles on the bud.

Though elongating needles supply growth regulators, they are not fully developed to synthesize adequate amounts of carbohydrates for growth of the bud. Initial growth of elongating buds is sustained by imported carbohydrates from leaf area proximal to the bud (Zimmerman and Brown, 1971). Studies have shown that elongating buds are strong carbohydrate sinks, and are capable of drawing substrates from neighboring leaves, or long distance sources to support initial growth (Kozlowski, 1992; Kozlowski and Pallardy, 1997).

Foliage forms the primary photosynthetic organs for plants and therefore influences availability of carbohydrates needed for growth. Limits to tree growth due to various stress factors at the site are often first observed in crown health in terms of leaf abscission, leaf coloration, die back or reduced crown size expansion as a response to competition when neighboring trees compete for space. Leaf contribution to growth can be assessed by observing net growth when the plant has limited access to light, is pruned, or is defoliated.

Most studies on leaf area and the effects of its loss to plant growth have been done by simulating the effects of insect and herbivore defoliation to plants. Artificial defoliation experiments have been used to simulate both intensity and timing of defoliation (Reich et al., 1993; Vanderklein
and Reich, 1999). In most studies, plants respond differentially to loss of foliage (Kulman, 1971). These variations occur due to differences in the intensity of defoliation, the timing of defoliation (Ericsson et al., 1980), nutritional status of the plant at the time of defoliation (Mattson Jr, 1980), and recovery time being considered in the studies (Oesterheld and McNaughton, 1988). Loss of leaf area generally affects photosynthesis in residual foliage, carbon partitioning, and allocation of biomass in the plant (McNaughton, 1983; Vanderklein and Reich, 1999).

Despite extensive literature on plant growth responses to defoliation, few researchers have examined the role of current foliage in establishment and growth of new shoots and leaf area. In a study to examine the contribution of early and late leaves to shoot elongation, Kozlowski and Clausen (1966) covered early leaves, late leaves, and early and late leaves of *Betula papyrifera* M. They observed that the contribution of early and late leaves to shoot elongation differed markedly. Covering of early leaves before mid-June inhibited shoot growth, the presence of normally growing early leaves was essential for normal shoot development and survival (Kozlowski and Clausen, 1966).

In trees with preformed buds such as *Pinus taeda*, the bud that elongates in the spring is formed in the previous year. Therefore, the shoot and leaf area are determined in the previous year, being influenced by the prevailing environmental conditions. It follows suite that the previous year’s foliage should be instrumental in establishing the preformed bud and could play a role in its elongation in the next growing season. The new elongating bud could depend on previous years foliage for supply of carbohydrates until new foliage is developed to supply requirements for growth.
The current study examines how leaf area and shoot elongation interact. It is hypothesized that shoot elongation is predictably related to preformed leaf area. Growth of shoots was examined under controlled carbohydrate supply by applying a series of defoliation and shade treatments on last year’s leaf area. The treatments reduced the effective leaf area on the branch and thus presumed to trigger an imbalance between carbohydrate source and sinks. Defoliation was anticipated to reduce plant leaf area load and elicit plant responses to defoliation and injury (Trumble et al., 1993). Shading reduces photosynthesis rates of the branch while initially retaining the respiration demand of foliage and maintaining hormonal balance. The terminal leaders of the branches were expected to grow despite defoliation and shading because of their ability to import photosynthates from long distances and the supply from reserves (Ericsson et al., 1980; Kozlowski and Winget, 1964).

Materials and methods

Study area

This study was conducted at the Louisiana State University’s Lee Memorial Forest in southeastern Louisiana, USA (30°52’52.5” N 89°58’ 43.4” W) (Fig 2-1). The general site conditions have been described by Dicus and Dean (2008). Lee Forest has subtropical climate with average daily temperature range of 12.5°C to 25°C and mean annual rainfall of 1600 mm. The average monthly temperature and rainfall during the study period were recorded by a weather station at the site. The soil at the study site is well drained, fine loamy, siliceous, thermic typic Paleudult (Ruston series) with a high level of exchangeable aluminum. There is North-South soil fertility gradient at the site (Dicus and Dean, 2008).
Figure 2-1 Location of Lee Memorial Forest in Louisiana, USA

**Study methods and design**

The trees used in this study were planted in 2012 at Lee Memorial forest in five isolated field plots measuring 27 m x 27 m. The field plots constitute experimental blocks for this study. Trees were planted at the spacing of 3 m x 3 m in three of the blocks and at 1.59 m x 1.59 m in two blocks. The trees were considered open grown in all the blocks at the start of the study. Trees of good form, vigorous, without injuries, and free of disease or insect damage were selected for treatment. Each block in the field received 9 treatment combinations applied separately on individual trees and replicated within the block. The treatments composed of removing foliage from the branches, covering foliage with shade cloth, and untreated control. The treatments were applied on the fourth branch whorl from the top (referred to as the target branches), and the
immediate upper and lower neighbors to the target branches, (referred to as neighbors) (Table 2-1). For trees receiving defoliation treatments, current foliage was carefully removed such that the branch remained with terminal bud only. For trees receiving shading treatment, current foliage was carefully pulled back from growing buds and secured using a tape. The leaves were then covered with shade cloth to prevent light penetration.

Table 2-1 Treatment combinations and theoretical expectation of the source of carbohydrates for elongation of terminal leaders

<table>
<thead>
<tr>
<th>Target branch whorl treatment</th>
<th>Neighbor treatment</th>
<th>label</th>
<th>Treatment combinations and effect</th>
<th>Source of Substrate</th>
</tr>
</thead>
<tbody>
<tr>
<td>Defoliation</td>
<td>Defoliation</td>
<td>DD</td>
<td>Defoliated target branch whorl and defoliated neighbors</td>
<td>Reserves + new foliage</td>
</tr>
<tr>
<td>Shade cloth</td>
<td>DS</td>
<td></td>
<td>Defoliated target branch whorl and shaded neighbors</td>
<td>Reserves + new foliage</td>
</tr>
<tr>
<td>No treatment</td>
<td>DC</td>
<td></td>
<td>Defoliated target branch whorl and untreated neighbors</td>
<td>Reserves + new foliage + import</td>
</tr>
<tr>
<td>Shade cloth</td>
<td>Defoliation</td>
<td>SD</td>
<td>Shaded target branch whorl and defoliated neighbors</td>
<td>Reserves + new foliage</td>
</tr>
<tr>
<td>Shade cloth</td>
<td>SS</td>
<td></td>
<td>Shaded branch whorl and shaded neighbors</td>
<td>Reserves + new foliage</td>
</tr>
<tr>
<td>No treatment</td>
<td>SC</td>
<td></td>
<td>Shaded target branch whorl and untreated neighbors</td>
<td>Reserves + new foliage + import</td>
</tr>
<tr>
<td>No treatment</td>
<td>Defoliation</td>
<td>CD</td>
<td>Untreated target and defoliated neighbors</td>
<td>Current foliage + new foliage – export</td>
</tr>
<tr>
<td>Shade cloth</td>
<td>CS</td>
<td></td>
<td>Untreated target and shaded neighbors</td>
<td>Current foliage + new foliage - (export)</td>
</tr>
<tr>
<td>No treatment</td>
<td>CC</td>
<td></td>
<td>Untreated target and neighbors</td>
<td>Current foliage + new foliage</td>
</tr>
</tbody>
</table>

- New foliage – accounts for carbohydrates from developing foliage on the new buds
- Export – accounts for substrate supplied to neighbor from target branch whorl
- Import – accounts for substrate acquired by target branch from neighbor branch whorls

For all the selected trees, initial tree height, basal diameter, branch diameter, and branch length were measured and recorded from each tree. After treatment application, the length of the terminal bud was measured weekly until growth ceased. Its final length was measured at the end of the growing season for the year.
Measurement of leaf area

The foliage removed from the branches was stored separately in labelled bags and transported to the lab on ice to prevent desiccation. From each labelled bag, a sample of 30 fascicles were randomly picked and labelled separately. Projected leaf area for each branch was determined from the 30 randomly selected fascicles by passing them through Licor LI-3100 leaf area meter. Each set of fascicles used in leaf area measurement was dried at 60°C to constant weight. Leaves in each labelled bags from the field was also dried to constant weight.

The dry weight and measured leaf area of the samples were used to calculate specific leaf area as cm²/g of dry weight. Leaf area removed from the branch was then calculated based on the specific leaf area. An allometric relationship was developed from branch leaf area and the cross-sectional area at the base of the branch.

The data showed a linear relationship between the cross-sectional area at the base of the branch and the leaf area carried on the branch. A simple linear model of the form \( y = a + bx \) was sufficient to generalize the branch-leaf area relationship. The linear model (Equation 2.1) explained 78% of the data and was used to calculate the initial leaf area on the target branches for all the trees before treatment application (Fig 2-2). The fitted model is

\[
\hat{y} = 1305.7A_b - 248.21; \quad (2.1)
\]

where \( \hat{y} \) is the previous year’s branch leaf area (cm²); and

\( A_b \) is initial cross-sectional area at the base of the branch.
Figure 2-2 Relationship between initial cross-sectional area at the base of the branch (A_b) and the initial leaf area on the branch (LA)

**Number of new leaves**

In the summer of 2016, the number of fascicles on the first flush of growth on each target branch were counted and recorded. This was to keep track of the new leaf area developed in the second year of the study as in relation to the elongating bud. Preformed buds in loblolly pine are formed in the previous growth season and are therefore influenced by the prevailing condition of the tree when they are produced (Dougherty et al., 1994). The number of fascicles could be affected by the reduced leaf area on the tree when the bud was set.

**Data analysis**

The effect of treatments on newly formed leaf area was determined from the number of new fascicles in the first flush of the next growing season. The average measured values for number of fascicles in the second growing season was analyzed by analysis of variance. The general mean model for fascicle data analysis is given in equation 2.2:
\[ y_i = \mu + \tau_i + \beta_j + \gamma_{ij} + \varepsilon_{ijk} \]  \hspace{1cm} (2.2)

where \( \mu \) is the overall mean,
\( \beta_j \) is the \( j \)th block effect,
\( \tau_i \) is the \( i \)th treatment effect,
\( \gamma_{ij} \) is the interaction effect from the \( i \)th treatment and \( j \)th block, and
\( \varepsilon_{ijk} \) is the experimental error assumed to be normally distributed with uniform variance.

In determining the relationship between shoot length and newly formed leaf area, the number of new fascicles on the fully elongated bud was predicted using a simple power model (equation 2.3):
\[ y = ax^b; \]  \hspace{1cm} (2.3)

where \( y \) is the number of fascicles on a fully elongated terminal bud;
\( x \) is the length of fully elongated terminal bud;
\( a \) is the scaling factor; and
\( b \) is the exponent.

The effect of leaf area, branch length, branch diameter and treatments in predicting the growth of the terminal bud were examined. Initial values of cross-sectional area at the base of the branch, length of the branch, and leaf area were used as the predictors for the length of terminal leader in a linear model (equation 2.4):
\[ y_i = a + A_b + LA + BL + \varepsilon_i; \]  \hspace{1cm} (2.4)

where \( y_i \) is the length of a fully elongated branch terminal bud;
\( A_b \) is the initial cross-sectional area of the branch;
\( BL \) is the initial branch length;
LA is the initial leaf area on the branch, representing previous year’s foliage;

$\varepsilon_i$ is the error.

The effect of reducing leaf area on branches was accounted for by treatments, which were added to the model to simulate the decreased leaf area over the growing period. The predictive model for the magnitude of growth of the branch terminal leader had initial cross-sectional area at the base of the branch, branch length, treatment class variable and interactions between treatment and branch size as the predictors.

$$y_i = A_b + BL + I_\tau + A_b \cdot I_\tau + BL \cdot I_\tau + \varepsilon_i ;$$

where $y_i$ is the length of fully elongated branch terminal bud;

$A_b$ is initial the cross-sectional area of the branch;

$BL$ is initial the branch length;

$I_\tau$ is the indicator variable for treatment $\tau$ where $\tau = 1 – 9$;

$\varepsilon_i$ is the error.

**Results**

**Length of terminal leader**

Growth of the terminal bud at the end of the growing season was predicted from the cross-sectional area at the base of the branch, initial length of the branch, and the previous year’s leaf area carried on the branch (Fig 2-3, 2-4 and 2-5). The effect of previous year’s leaf area on growth of terminal leader was evaluated by adding treatments to the model. Treatment effect was significant in the model (p = 0.03). Significant effects were also observed from cross-sectional area of the branch (p < 0.01) and initial length of the branch (p < 0.01). The interaction between treatment and cross-sectional area, and treatment and branch length were also significant (Table 2-2). The model fit showed unbiased residuals (Fig 2-6).
Figure 2-3 Correlation between cross-sectional area of branch and the final length of terminal leader

Figure 2-4 Correlation between initial length of the branch and the final length of terminal leader
Figure 2-5 Correlation between initial leaf area of the branch and the final length of terminal leader

Figure 2-6 Residual plot of predicted length of terminal leader from model fit \( y_i = A_b + BL + I_{\tau i} + A_b \cdot I_{\tau} + BL \cdot I_{\tau} + \varepsilon_i \) where \( y_i \) is the length of fully elongated terminal bud (cm); \( A_b \) is the cross-sectional area of the branch; \( BL \) is the branch length; \( I_{\tau i} \) is the indicator variable for treatment \( \tau \) where \( \tau = 1 - 9 \); and \( \varepsilon_i \) is the error.
Table 2-2 Fixed effects of initial branch cross-sectional area, length, leaf area and their interactions on the final length of terminal bud. Values obtained from fitting the model: \( y_i = A_b + BL + I_\tau + A_b \cdot I_\tau + BL \cdot I_\tau + \varepsilon_i \) where \( y_i \) is the length of fully elongated terminal bud (cm); \( A_b \) is the cross-sectional area of the branch; \( BL \) is the branch length; \( I_\tau \) is the indicator variable for treatment \( \tau \) where \( \tau = 1 - 9 \); and \( \varepsilon_i \) is the error.

<table>
<thead>
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<th>DF</th>
<th>F Value</th>
<th>Pr &gt; F</th>
</tr>
</thead>
<tbody>
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<td>Cross-sectional area</td>
<td>1</td>
<td>84.57</td>
<td>&lt;.01</td>
</tr>
<tr>
<td>Branch length</td>
<td>1</td>
<td>47.53</td>
<td>&lt;.01</td>
</tr>
<tr>
<td>Treatment</td>
<td>8</td>
<td>2.23</td>
<td>0.03</td>
</tr>
<tr>
<td>Cross-sectional area x Treatment</td>
<td>8</td>
<td>2.51</td>
<td>0.01</td>
</tr>
<tr>
<td>Branch length x Treatment</td>
<td>8</td>
<td>3.67</td>
<td>&lt;.01</td>
</tr>
</tbody>
</table>

Table 2-3 Estimated difference in effect of treatments on the growth of the terminal bud between selected treatment groups and the control. \( H_0: u_1 - u_2 = 0 \).

| Label                          | Group 1 | Group 2 | Branch elongation (cm) | Standard Error | Pr > |t| |
|--------------------------------|---------|---------|------------------------|----------------|-------|---|
| Control vs treated neighbors   | CC      | CD CS   | -15.90                 | 18.73          | 0.39  |   |
| Control vs Defoliated target   | CC      | DC DD DS| -47.62                 | 24.56          | 0.05  |   |
| Control vs Shaded target       | CC      | SC SD SS| -65.44                 | 26.71          | 0.02  |   |

**Number of new leaves**

The number of new fascicles formed on the terminal bud followed a simple power law when plotted against the length of the terminal bud (equation 2.6). The model exponent shows a
decreasing number of leaves per unit increase in length of the terminal leader. The model explained 72% of the data in predicting number of fascicles (Fig 2-7).

Figure 2-7 Distribution of number of new fascicles as predicted by the length of fully elongated terminal leader

The fitted model is

$$\hat{y} = 10.45 x^{0.69},$$

where $\hat{y}$ is the number of fascicles a fully elongated terminal bud and $x$ is the length of fully elongated terminal bud.

For trees with treated target branches and untreated neighbors (DC and SC) the number of new fascicles on the terminal leader was significantly lower than the number on untreated controls (CC) (Fig 2-8). Defoliation of neighbor branches in addition to a treated target (DD and SD) also resulted in significant reduction in the number of new fascicles. The number of new fascicles in the next growth season appeared to be sensitive to defoliation. Treatments with a shaded target and untreated or defoliated neighbor (SC and SD) had significantly less number of new fascicles than the control. Shading neighbor branches appeared to enhance the number of
new fascicles on the target irrespective of the treatment on the target as demonstrated in treatments CS, DS, and SS as compared to CC, DC, and SC respectively, though not significantly different.

Figure 2-8 Mean number of fascicles on the first flush of branch terminal leader in the next season following treatments. Treatments with different letters are significantly different (alpha=0.05)

Discussion

The initial values of current leaf area, cross-sectional area at the base of the branch, and length of the branch predicted the extension of the terminal bud. The cross-sectional area is related to sapwood, the actively conducting section of the branch diameter. Though the initial length of the branch had a weak correlation, it was significant in predicting final length of terminal leader. The branch length correlates with path length in conducting water, hence is a factor in building resistance to water conduction (West et al., 1999). The branch cross-section and length are a measure of branch size or volume. In this regard, branch size is also a measure of available
substrate in reserves that can act as a buffer to a stressed branch and supplement photosynthesis when photosynthates are in short supply (Eyles et al., 2009).

Leaf area has a controlling effect on how branches grow. Treatments represented varying levels of leaf area on the branch as the leader elongated. Contrast groups estimates in table 3 show that the length of leader of the untreated target branches (CS, and CD) did not differ from the control irrespective of the neighbor treatment (p=0.39). It was therefore assumed that defoliation or shading of the neighbor branches does not significantly alter extension of the terminal bud of target branches. Contrast group estimates that compared control treatment to treatments with defoliated target branches recorded a reduction of 47.62 cm shorter that the control (p=0.05). Shaded target branches were significantly shorter (p=0.02) with a reduction of 65.44 cm compared to the control. Defoliated target branches suffered a sudden reduction in the photosynthetic surface area. This reduction in leaf area could have caused the shorter branches observed at the end of the growing season. However, the magnitude of reduction was less compared to shaded because the elongating bud could have mobilized reserves (Vanderklein and Reich, 1999) which acted as a buffer as the new leaves were still elongating.

There is overwhelming evidence that plants exhibit compensatory responses following defoliation events. First, trees increase the rate of photosynthesis in the residual or regrowth foliage (Reich et al., 1993) as they compensate for lost leaf area. Second, after loss of leaf area, plant biomass does not necessarily reduce by the same proportion as the lost leaf area (Bassman et al., 1982; Harris, 1974), and third, some partial defoliation events may lead to an increase in biomass of the affected plant as compared to undefoliated plants (McNaughton, 1983). These compensatory responses explain the continued growth, and similar growth responses between defoliated branches and the control.
In shaded branches (SC, SD, and SS), the branch carried covered leaves for a while. Shading blocked light hence the leaves could not photosynthesize. However, the covered leaves continued to respire, and therefore sustained the carbohydrate demand without external supply. This could have reduced the amount of carbohydrates available for growth of the terminal leader. The carbohydrate demand from covered but respiring leaves and the growth of reaction wood to counter weight of the shade cloth could have provided competing carbohydrate sinks leading to reduced extension of the terminal bud.

**Effect of treatments on new leaf area**

Loblolly pine buds that elongate in the spring were preformed in the previous year. In testing the effect of treatments on formation of new stem units, the number of new fascicles in the first flush of the season following treatments was analyzed. A simple power law predicted the number of new fascicles formed on the terminal leader (equation 2.7). Log-transformation of the power model gives the scaling factor and the exponent biological interpretation as intercepts and growth rates respectively, which makes it adaptable to forestry applications. The log-transformation of this model retained favorable model fit as it explained 70% of the data (Fig 2-9).

Terminal buds of treated branches were allowed to grow and establish while the previous year’s leaf area was subjected to artificial shade stress or completely removed from the branch. Growth of terminal buds was observed to be dependent on the availability of incident radiation. In the absence of photosynthates from leaves, the treated branches could have mobilized stored carbohydrate reserves (Da Silva et al., 2014) to sustain elongation of the bud and establish new leaf area. Defoliated (DC) or shaded (SC) target branches recorded significant reduction in the number of new fascicles (Fig 2-4). Defoliation stress on the target branches could have had an
effect on carbohydrate supply to the elongating buds in addition to interrupting supply of hormones and other substances manufactured or stored in the leaves (Kozlowski and Pallardy, 1997; Lanner and Connor, 1988). Defoliation of neighbor branches therefore, could have limited the resources available to be exported to the target, and increased the distance to the next available source.

Figure 2-9 Plot of number of fascicles on a terminal bud against the fully elongated bud on log-transformed scale (log = log base 10).

Artificial shade on the neighbor branches appeared to moderate the effect of the target treatments (DS and SS), resulting in similar number of fascicles to the control (Fig 2-4). This is reflected in a higher number of fascicles for treatments with a shaded neighbor as compared to defoliated ones. Generally, the effect of neighbors on number of fascicles was only detected when the target branch was treated, indicating that individual branches have local control over the setting of stem units in new buds.
The extension of the terminal bud was observed in all the treated branches. Treatments removed or covered last year’s foliage but terminal buds were able to grow new leaf area within the first flush. This emphasizes that trees prioritize shoot and leaf area growth even while under stress.

The extension of the leader was predicted from the initial cross-sectional area of the branch, amount of leaf area and the length of the branch, giving an indication of the influence of size of the branch and photosynthetic capacity on future growth. The number of stem units as indicated by number of fascicles carried on bud can be predicted from the length of a fully elongated bud using a simple power law. Shoot growth was reduced by defoliation and shading of previous year’s leaf area, but shoot extension was observed possibly supported by reserves and current year’s leaf area.

References


CHAPTER 3 EXAMINING BRANCH AUTONOMY AND HOW CROWN DYNAMICS INFLUENCE GROWTH OF TREES

Introduction

The relationship between tree architecture and the function of morphological units is important in understanding tree growth responses to changes in the environment and adaptability to pests, diseases, and competition. Plants demonstrate morphological plasticity in both shoot and root structures when responding to environmental changes (Ford, 1985; Sultan, 2000). For instance, plants have developed modules (such as branches) that function independent of each other but are linked together in an integrated body that allows flow of substances between them (Kawamura, 2010). While this structure gives plants flexibility when foraging for resources in a heterogeneous environment (Hardwick, 1986), it is unclear how differential growth and autonomy of modules is coordinated into a responsive organism.

The tree is considered modular organism due its unique structure, which has repetitive self-similar modules. Researchers somewhat subjectively define the size and extent of a functional module because of seemingly obvious organizational levels in a plant segment. For instance, based on gross morphological features, a tree crown is organized into branches, branches into shoots, shoots into ramnets and buds, each qualifying as a module (Godin and Caraglio, 1998; White, 1979). Studies on crown structure classify a branch as semi-autonomous module in regard to resource acquisition and supply (Marsal et al., 2003; Sprugel et al., 1991). However, there is no consensus on the mechanisms underlying functional relationships between branches and the main tree profile. Some studies have suggested that branches act autonomously in acquisition of resources (Lacointe et al., 2004; Sprugel et al., 1991) while others have proposed that there is interaction whether competitive or cooperative (Kawamura, 2010; Sprugel, 2002). According to
Kawamura (2010), modular responses may be enhanced by competitive exploitation of resources from a module in a poor condition by a module in a better condition or by a cooperative transfer of resources into a module under a poor condition from a module under a better condition.

Researchers are still divided on the concept of autonomy of branches in the crown and how it can be quantified in the functional crown and tree growth studies. Several studies have provided experimental evidence that supports autonomy of branches in carbohydrate fixation and utilization (Hasegawa et al., 2003; Lacointe et al., 2004; Sprugel et al., 1991; Watson and Casper, 1984). For example, in their study of Siberian alder (*Alnus hirsuta* var. *sibirica*), Hasegawa and others (2003) observed that the current year shoots were carbon autonomous for producing flowers and one-year-old shoot systems were carbon autonomous for producing fruits. Some other researchers have reported a lack of sufficient evidence to support autonomy of shoots (Henriksson, 2001; Sprugel, 2002). Sprugel (2002) observed that the principle of branch autonomy that characteristics of a branch’s carbohydrate economy are independent of the tree to which the branch is attached may not be true because carbohydrates are translocated from the stem to branches in the spring and that a positive carbon budget alone does not ensure branch survival. However, there is general agreement that understanding the role of branch autonomy is needed for better predictions in tree growth models, and understanding the growth allocation patterns of tree responses for ecological studies.

Testing independence of branches can be done using direct carbon tracing or indirect methods. Previous studies have used indirect methods which involve application of artificial stress like defoliation and shade (Cregg et al., 1993; Sprugel et al., 1991), or pruning (Långström and Hellqvist, 1991; Mediene et al., 2002; Stiell, 1969) to test tree growth responses when the natural state is disrupted as indication of autonomy of plant parts. The major setback is that some of the
treatments applied do not occur in nature. It is also difficult to isolate the secondary effects of artificially imposed stress to a plant. For example pruning and defoliation injure plants and therefore may elicit hormonal responses to injury. It is a difficult task to isolate compensatory responses from those of treatments.

Direct methods involve the use of labeled carbon isotopes to trace movement of carbohydrates within the tree and record allocations, or utilization of carbohydrates (Cregg et al., 1993; Lacointe et al., 2004). Direct carbon measurement is however used in combination with some form of artificial stress as a way of determining a tree’s response when the natural state is distorted. Direct methods, though effective, are expensive and are restricted to controlled experimental setups due to regulatory and environmental concerns.

The main challenge in designing experiments for studying autonomy of branches has been how to isolate the target branch from the effects of neighbors. Previous studies have not successfully isolated treated branches from the direct influence of their neighbors. Cregg and others (1993) selected three branches randomly from mid to upper crown for use in their experiment. The influence of immediate neighbors and the other branches sharing a node with the experimental branch was not accounted for. Lacointe et al (2004) while working on Juglans regia L. debudded branches except for two branches that were measured. The lower branch was shaded while the upper one was not. The positional effect of branches in the crown and secondary effects of debudding other branches were not accounted for in the design of the experiment. Arguments on the autonomy of branches are hinged on demonstrating that a branch can be isolated from the influence of its neighbors and that the observations account for positional effects. The height position of shoots in the crown has been shown to affect shoot growth pattern independent of light exposure (Osada, 2006; Sumida et al., 2013; Takahashi et al., 2006).
Previous studies on branch autonomy have focused on independence of individual branches and survival in terms of leader growth, and fruit development with respect to carbohydrate supply. In the current study, a new method of studying the independence of branches in the crown of trees is presented. This design provides a unique way of quantitatively measuring the net effect of neighboring branches on net growth. A series of treatments are employed to confer artificial defoliation and shade stress on branch whorls. The position of branches in the crown is accounted for, and the target branches are isolated by treating neighbors to minimize their influence. Growth of target branches is then assessed from the elongation of the terminal leader, and growth in diameter at the base of branches.

**Materials and methods**

**Description of the study site**

This study was conducted at the Louisiana State University’s Lee Memorial Forest in southeastern Louisiana, USA (30° 52’52.5” N 89° 58’ 43.4” W) (Fig 3-1). The general site conditions were described by Dicus and Dean (2008). Lee Forest has subtropical climate with average daily temperature range of 12.5°C to 25°C and mean annual rainfall of 1600 mm. The average monthly temperature and rainfall during the study period were recorded a weather station at the site (Fig 3-2). The soil at the study site is well drained, fine loamy, siliceous, thermic typic Paleudult (Ruston series) with a high level of exchangeable aluminum. There is North-South soil fertility gradient at the site (Dicus and Dean, 2008), and therefore blocks are established to reflect the site specific variations.
Figure 3-1 Location of Lee Memorial Forest in southeastern Louisiana, USA

Figure 3-2 Average monthly rainfall (mm) and temperature (°C) recorded at Lee Forest (30°52’16.096” N 89°59’ 49.916” W) between 2013 and 2015
Experimental design and treatments

The trees used in this study were planted in 2012 at Lee Memorial forest in five isolated field plots measuring 27 m x 27 m. The field plots constitute experimental blocks for this study. Trees were planted at the spacing of 3 m x 3 m in three of the blocks and at 1.59 m x 1.59 m in two blocks. The trees were considered to be open grown in all the blocks at the start of the study. Healthy vigorous trees of good form were carefully selected along the outer boundary of the plots. Experimental trees were located on East-West and North-South orientation of each plot to maximize light interception. On each tree, branch whorls were numbered from the top and individual branches on the fourth whorl were selected for treatment and are referred to as the target branches. The immediate upper and lower neighboring branches to the fourth whorl were also selected and are referred to as the neighboring branches. Ten trees were randomly assigned one of the nine treatments. Treatments consisted of three levels of two factors. The three levels were an untreated control, current and second-year foliage removed, or current and second-year foliage covered with shade cloth. Foliage was covered with 90% shade cloth to block light. The two factors were whether the first factor was applied to the target branch or the upper and lower neighboring branches (Fig 3-3). Removal of foliage eliminates the local carbohydrate source to the branch, and probably triggers plant hormonal response to injury (Haukioja, 1982). Covering branches with shade cloth eliminates light thus reduces photosynthesis rates on the branch without injury. This in effect limits carbohydrate supply. I assumed that shading would not produce an injury response that defoliation would. Shading of leaves maintains hormonal balance as opposed to defoliation, but respiration demand from covered leaves is unaffected. Each treatment combination was replicated twice in each of the five blocks in the field. The isolation of treatment effects is shown in Table 3-1.
Defoliation treatments were done by carefully removing previous year’s needles from selected branches in the spring. The buds were left to produce new needles. In the following spring, the new needles were carefully removed and the buds left intact to grow fresh needles for the next year. Shading was also done by covering previous year’s needles but terminal buds were left exposed to allow growth of new leaf area. In the following spring, shade was extended to cover the previous year’s needles. The new terminal buds were left exposed to continue growing.

Figure 3-3 Vertical profile of treatments on branch whorls 1, 2, 3, 4, and 5. Branch whorl 4 is the target experimental unit, branch whorl 3 and 5 are treated neighbors. There are 3 treatments: defoliated branches (D), covered branches (S) or untreated branches (C), applied to the target or neighbor branches represented by first and second letter respectively.
Table 3-1 Treatment combinations and effects included in treatments

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Abbreviation</th>
<th>treatment effect</th>
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<tr>
<td>Control</td>
<td>CC</td>
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</tr>
<tr>
<td>Defoliated neighbors</td>
<td>CD</td>
<td>0+d</td>
</tr>
<tr>
<td>Shaded neighbors</td>
<td>CS</td>
<td>0+s</td>
</tr>
<tr>
<td>Defoliated target branch whorl</td>
<td>DC</td>
<td>D+0</td>
</tr>
<tr>
<td>Defoliated target and defoliated neighbors</td>
<td>DD</td>
<td>D+d</td>
</tr>
<tr>
<td>Defoliated target branch and shaded neighbors</td>
<td>DS</td>
<td>D+s</td>
</tr>
<tr>
<td>Shaded target branch whorl</td>
<td>SC</td>
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</tr>
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<td>Shaded target branch and defoliated neighbors</td>
<td>SD</td>
<td>S+d</td>
</tr>
<tr>
<td>Shaded target branch and shaded neighbors</td>
<td>SS</td>
<td>S+s</td>
</tr>
</tbody>
</table>

C-control, D-defoliation, S-shade. First and second letter represent the treatment on target and neighbor branches respectively. D and S are primary effects of defoliation and shade treatments on target branches respectively, while d and s are secondary effects of defoliating or shading neighboring branches.

**Measurements**

From each tree, the pretreatment values of height, diameter of the stem at the root collar (15 cm above ground), branch lengths of the target and neighbor branches, diameters at the base of target branches, and length of terminal leaders of the target branches.

The lengths of the terminal leaders of target branches were measured weekly from April 2015 until elongation slowed down in August. Subsequent measurements of growth of the terminal leaders was recorded biweekly until elongation ceased. Weekly measurement of the elongation of terminal leaders resumed in the spring of 2016 immediately after the buds started to elongate. The diameter at the base of treated target branches was also measured above the branch collar.
using a digital caliper in April and December of 2015, and in March, May, and August of 2016. The tree water status was monitored regularly by measuring midday water potential using a Scholander pressure bomb. The midday water potential was used to monitor the possible effects of defoliation on the water relations within the tree. The tree midday water potential did not vary significantly between treatments hence there was no need for watering the trees in the field.

Data Analysis

Branch growth

The data for growth in length of branches showed sigmoid-like, asymptotic curves when plotted as a function of date (Fig 3-4). Several asymptotic candidate growth models were considered such as Weibull, logistic, Chapman-Richards, Bailey and Clutter, and Gompertz models. Initial screening led to three models that were evaluated for selection of the best model to fit the data based on their flexibility, complexity, and mathematical limitations such as inflection point, limitation to a specific stage of growth, and biological interpretation of the parameters.

The logistic function, Bailey and Clutter model (Bailey and Clutter, 1974) , and Chapman-Richards models (Chapman, 1961; Richards, 1959) were evaluated for fitting the branch growth data. The model with unbiased residuals and lowest value based on the Akaike information criterion (AIC) was selected as the best model to fit the data (Table 3-2). The Chapman-Richards model was selected for subsequent use in branch growth analysis.
Figure 3-4 Growth of branch terminal leaders in the first year following treatments

<table>
<thead>
<tr>
<th>Model</th>
<th>AIC</th>
<th>BIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bailey and Clutter</td>
<td>9434.5</td>
<td>9456.1</td>
</tr>
<tr>
<td>Logistic</td>
<td>9446.5</td>
<td>9468.1</td>
</tr>
<tr>
<td>Chapman-Richards</td>
<td>9433.4</td>
<td>9455.5</td>
</tr>
</tbody>
</table>

The difference in growth of the terminal leaders due to treatment combinations was analyzed using nonlinear, mixed effects models. Data from each target branch were analyzed by fitting the data to the Chapman-Richards growth model (equation 3.1).
\[ y_i = b_1[1 - e^{(-b_2 t)}]^{b_3} + \varepsilon_i, \quad (3.1) \]

where \( y_i \) is incremental growth of the terminal leader for tree \( i \);

\( t \) is time in weeks;

\( \varepsilon_i \) is the error;

\( b_1, b_2, \) and \( b_3 \) are parameters to be estimated. Parameter \( b_1 \) denotes maximum asymptotic value, \( b_2 \) is related to intrinsic growth rate, and \( b_3 \) depends on shape of the curve.

Nonlinear, mixed-effects model allows the use of both fixed and random parameters simultaneously in the model, thus accounting for variations due to random effects. Random effects vary from tree to tree and give information about the population of the experimental trees. The Chapman-Richards model was evaluated for the significance of adding random variables to each parameter. The model with one random variable on \( b_1 \) was selected for use because fitting more complex models with two and three random parameters presented difficulties with convergence in SAS. The model specified the covariance structure, and unique tree subject identifiers to account for within subject correlation.

The model with one random variable is

\[ y_i = (b_1 + u)[1 - e^{(-b_2 t)}]^{b_3} + \varepsilon_i, \quad (3.2) \]

where the random variable \( u \) is normally distributed with a mean of zero and unknown variance.

Growth increment of the branches was determined by fitting the weekly data to equation (3.2) above. Treatments were added to the model as indicator variables on \( b_1 \) (equation 3.3).
Let

\[ \beta = \sum_{i=1}^{9} b_i l_i + u, \]

where random \( b_i \) is the upper asymptotic value, for treatment \( i, i = 1,2 \ldots, 9, \)

\[ l_i = \begin{cases} 
1 & \text{if treatment } i, \\
0 & \text{otherwise}
\end{cases} \]

The model for predicting growth of individual branches for each treatment is therefore

\[ y_i = \beta [1 - e^{-b_2 t_i}] b_3 + \varepsilon_i \] (3.3)

**Diameter of branches**

The diameter growth at the base of target branches from each treatment combination was analyzed for differences with the untreated controls using mixed-model analysis of variance. The average measured values for diameter increment was analyzed by analysis of variance. The general mean model for diameter increment data analysis is

\[ y_i = \mu + \tau_i + \beta_j + \gamma_{ij} + \varepsilon_{ijk} \] (3.4)

where \( \mu \) is the overall mean,

\( \beta_j \) is the jth block effect,

\( \tau_i \) is the ith treatment effect,

\( \gamma_{ij} \) is the interaction effect from the ith treatment and jth block, and

\( \varepsilon_{ijk} \) is the experimental error assumed to be normally distributed with uniformity of variance.

Pair-wise contrasts were used to test the treatment groups for primary and secondary effects of treatments.
Results

Growth of branches

In the first year of growth, shaded target branches experienced significant reduction in growth of the terminal shoots. Shaded neighbors acting alone did not appear to affect the growth of the untreated target branches, but defoliated or shaded target branches experienced significant reduction in growth when the neighbor branches were shaded. Defoliation treatments had significant reduction in growth of terminal buds when both the target and neighbor branches were defoliated or when the target was shaded and the neighbor defoliated (Table 3-3).

Table 3-3 Mean difference in length of the branch terminal leader between the control and other treatments at the end of first year following treatment application. Values generated by fitting Chapman- Richards model ($y_i = \beta [1 - e^{(-b_2 t)}]^{b_3} + \epsilon_i$) to the data ($H_0 \mu_1 - \mu_2 = 0$)

| Treatment | Mean growth of leader (cm) | Std error | Pr > |t|
|-----------|---------------------------|-----------|------|
| CC        | 14.97                     | 1.62      | <.01 |
| CD        | -1.4457                   | 2.28      | 0.53 |
| CS        | -0.4199                   | 2.28      | 0.83 |
| DC        | -2.4466                   | 2.28      | 0.29 |
| DD        | -4.6650                   | 2.28      | 0.04 |
| DS        | -0.5772                   | 2.28      | 0.81 |
| SC        | -8.0589                   | 2.29      | <.01 |
| SD        | -8.8796                   | 2.29      | <.01 |
| SS        | -8.2141                   | 2.28      | <.01 |
**Primary and Secondary effects of treatments**

Examination of treatment effects shows that primary effects due to treatments on the target branches had greater reduction of branch growth (Table 3-4) than untreated control. In the first year following treatment, shading treatment had greater magnitude of reduction in growth of the target terminal leader than defoliation treatments. The primary effects of defoliation were not significant in the first year. Indirect effects on target leader extension due to treatment of neighbor branches had minimum effects. In the second year of growth, primary effects were stronger for both defoliation and shading treatments. No significant treatment effect was detected for secondary effects in the second year.

**Branch diameter**

Plot of branch diameters increment against time showed a linear curve (Figure 3-5) and the fit data to equation 3-4 produced unbiased residuals (Figure 3-6). There was significant treatment effect on the growth of branch diameters (p<0.05). Growth in branch diameter was significantly reduced by defoliation or shading of target branches, or by both shade and defoliation combinations on the same tree. Significant reduction in branch diameter growth was also recorded when the neighbor branches were defoliated or shaded in addition to a treated target. Shading or defoliating neighbor branch whorls alone did not detect a significant effect on the growth in diameter of untreated target branches (Table 3-5).
Table 3-4  Primary and Secondary effects of treatment combinations on growth of terminal buds of selected branches for two growth seasons. Primary effects are estimated from treated target branches while secondary effects are from treated neighbor branches. Estimated values are the difference between treatment groups that reflect the net effect, t –value tests if the estimate is different from zero (See Appendix II).

| Treatments | Net effect | Estimate year 1 (cm) | Std error | Pr > |t| | Estimate year 2 (cm) | Std error | Pr > |t| |
|------------|------------|----------------------|-----------|------|----------------|----------------------|-----------|------|----------------|
| **Primary effects** | | | | | | | | | |
| **Defoliation** | | | | | | | | | |
| CC - DC | D1 | 2.5 | 2.3 | 0.27 | 7.6 | 2.7 | <0.01 |
| CD - DD | D2 | 3.2 | 2.3 | 0.16 | 6.4 | 2.4 | 0.01 |
| CS - DS | D3 | 0.2 | 2.3 | 0.94 | 5.9 | 2.4 | 0.02 |
| **Shading** | | | | | | | | | |
| CC - SC | S1 | 8.1 | 2.3 | <0.01 | 7.9 | 2.5 | <0.01 |
| CS - SS | S2 | 7.8 | 2.3 | <0.01 | 6.1 | 2.4 | 0.01 |
| CD - SD | S3 | 7.4 | 2.3 | <0.01 | 8.9 | 2.4 | <0.01 |
| **Secondary effects** | | | | | | | | | |
| **Defoliation** | | | | | | | | | |
| CC - CD | d1 | 1.5 | 2.3 | 0.52 | -0.6 | 2.4 | 0.81 |
| DC - DD | d2 | 2.2 | 2.3 | 0.33 | -1.7 | 2.6 | 0.51 |
| SC - SD | d3 | 0.8 | 2.3 | 0.72 | 0.4 | 2.6 | 0.87 |
| **Shading** | | | | | | | | | |
| CC- CS | s1 | 0.4 | 2.3 | 0.85 | -1.2 | 2.4 | 0.63 |
| DC - DS | s2 | -1.9 | 2.3 | 0.42 | -2.8 | 2.6 | 0.27 |
| SC - SS | s3 | 0.2 | 2.3 | 0.95 | -3.0 | 2.5 | 0.23 |

D and S direct effects due to defoliation and shading of target branch respectively. d and s are indirect effects due to defoliation and shading of neighbor branches respectively.
Figure 3-5 Predicted curves for mean growth in diameter of branches for two growth cycles grouped by treatments.

Figure 3-6 Residual plot of predicted diameter growth from analysis of variance model fit
Table 3-5 Estimated direct and indirect effects of treatment combinations on mean diameter increment of branches for two growth seasons. Primary effects are associated with treated target branches while secondary effects are from treated neighbor branches. Estimated values obtained from post hoc paired comparison of treatment groups (alpha=0.05)

| Effect combinations | effect | Estimate (mm) | Std error | Pr > |t| |
|---------------------|--------|---------------|-----------|-------|-----------|
| **Primary effects** |        |               |           |       |           |
| **Defoliation**     |        |               |           |       |           |
| CC - DC             | D1     | 2.53          | 1.05      | 0.02  |           |
| CD - DD             | D2     | 1.36          | 0.98      | 0.18  |           |
| CS - DS             | D3     | 2.44          | 0.91      | 0.01  |           |
| **Shading**         |        |               |           |       |           |
| CC - SC             | S1     | 2.64          | 0.98      | 0.01  |           |
| CS - SS             | S2     | 3.26          | 1.00      | <0.01 |           |
| CD - SD             | S3     | 2.66          | 1.06      | 0.02  |           |
| **Secondary effects** |     |               |           |       |           |
| **Defoliation**     |        |               |           |       |           |
| CC - CD             | d1     | -0.42         | 0.96      | 0.66  |           |
| DC - DD             | d2     | -0.75         | 1.07      | 0.49  |           |
| SC - SD             | d3     | 0.45          | 1.08      | 0.68  |           |
| **Shading**         |        |               |           |       |           |
| CC - CS             | s1     | -0.16         | 0.90      | 0.86  |           |
| DC - DS             | s2     | -0.25         | 1.06      | 0.82  |           |
| SC - SS             | s3     | 0.47          | 1.08      | 0.67  |           |

**Discussion**

**Effect of treatments on growth of branch length**

All the treatments caused some reduction of the target branches when compared to the control. Growth of artificially shaded target branches was significantly reduced when artificial shade stress was applied to a target branch irrespective of the treatment on the neighbors (Table 3-3).
Shading of leaf area limits the photosynthetic potential of branches and complete darkness can lead to mortality of foliage and branches (Sevanto et al., 2014). Shoots growing in darkness cannot photosynthesize and will therefore exhaust the available carbohydrates. Covered needles persisted for a while; therefore, continued to respire. However, branches continued to grow because the terminal buds were exposed to incident radiation and were able to grow and establish new leaf area. Applying shade stress on neighbor branches had little effect on target branches. Intervening shaded neighbor branches may have been constrained by local stress and could not confer influence on the target branches as evidenced in CS treatment and the magnitudes of treatments SC and SS (Table 3-3). The covered neighbor branches may have been stressed by local effects of the treatments and their own survival was given priority in allocation of limited resources.

Defoliation of the target branch only (DC) did not cause significant reduction in the growth of the treated branch. However, defoliation of the target branches and their immediate upper and lower neighbors (DD) did result in significant reduction in the growth of the target branches when compared to the control. The removal of leaf area on one branch whorl may have had a short term effect, and the branches may have benefitted from local reserves and export from immediate neighbors to sustain growth of the terminal bud thereby putting on new leaf area. However, on defoliating neighbors, more strong sinks were created and the local reserves may have been insufficient to keep up with the demand of the growing terminal buds which are strong carbohydrate sinks (Kozlowski, 1992). Local supply from reserves and imports may have been insufficient to support initial elongation and the new leaf area was not fully established to support early season elongation.
The series of treatments were designed to isolate the effects on the target branch in relation to the various treatment combinations. Autonomy of the target branch from the neighbors was assessed from set of *a priori* contrasts set up to test primary effects due to treated target and secondary effects from treated neighbors (Table 3-4). The paired contrasts did not detect significant primary effects from defoliated target branches when the neighbor was untreated, defoliated, or shaded in the first year. However, significant reduction in growth was detected in the second year following treatments. Initial growth of defoliated branches may have benefited from a buffer of previous year reserves but subsequent growth into the second growing season happened after decline in labile carbohydrates (Deslauriers et al., 2015; Ericsson et al., 1980). Though secondary effects caused a reduction in growth of the target branch leader, the reduction was not statistically significant when compared to the untreated control. Stressed neighbors were designed to prevent export of carbohydrates to the target branches. Some studies have observed that severely stressed branches import small amounts of carbohydrates (Cregg et al., 1991), though other studies using labeled carbon have observed movement of labile carbohydrates between branches even at natural state (Zimmerman and Brown, 1971).

**Effect of treatments on diameter of branches**

Growth in diameter of branches was significantly reduced due to direct effects resulting from defoliation of the target branches (Table 3-5). Untreated target branches were not significantly affected when the neighbor branches were subjected defoliation stress. Removal of previous year and current year foliage from trees has been reported to reduce diameter growth (Ericsson et al., 1980; O'Neil, 1962).
Primary effects due to shade on the target branch were significant regardless of the treatment on the neighbor branches. Shaded branches may have had additional carbohydrate cost and thus had greater effect on diameter growth of the branches. Secondary effects due to shading or defoliating neighbors failed to reject the null hypothesis of no treatment effect.

Diameter growth correlates well with leaf area and leaf mass. Various studies have documented the functional relationship between sapwood area and leaf area or leaf mass (Dean et al., 1988; Shinozaki et al., 1964a). Leaf area depends on sapwood area for supply of water and nutrients while the leaf synthesized carbohydrates are supplied to the branch for radial growth, respiration demands, and storage. Removal of foliage or severe shade on the branch therefore disrupts this functional relationship. Shading limits the photosynthetic capacity of leaf area. Therefore, covered leaves could have relied on local carbohydrates for survival but they become an additional carbohydrate sink due to cell respiration. Removal of leaf area also eliminates the local supply of carbohydrates and other substances supplied by leaves. Defoliation and shade stress imposes limitations on the supply of available carbohydrates, and therefore affects cambium activity. Sone and others (2005) observed that diameter growth of branches is determined by the balance between supply of photosynthates, the activity of the cambium, and shoot elongation. Therefore, in a constrained supply of carbohydrates the cambium has to compete with the growing terminal buds for the limited carbohydrates thereby limiting diameter growth.

References


CHAPTER 4 GROWTH RESPONSE OF TREE ANNUAL RINGS TO CHANGES IN LEAF AREA OF SELECTED BRANCHES

Introduction

Growth in diameter of trees and stem form is a function of many factors, among them the size of the crown and ratio of live crown to total tree height. Diameter growth results from the work of the cambium, which divides to form phloem on the outside and xylem in the interior and is renewed regularly to ensure perennial existence of the functional xylem and phloem. Stem growth is modified by changes to the live crown due to defoliation, pruning, and mechanical stress from wind sway (Kellogg and Steucek, 1980) but how the distribution of growth is affected by the interaction of these responses is yet to be determined.

Tree responses to changes in the live crown can be detected in radial growth, form, and taper of the stem. Trees respond differently to these changes depending on the proportion of live crown that is affected (Kulman, 1971; Långström and Hellqvist, 1991). In a review of the effects of insect defoliation on growth of Kulman (1971) found that growth responses in tree height and diameter varied depending on the proportion of leaf area affected, the timing of defoliation and tree species. Långström and Hellqvist (1991) deprived Scot’s pine trees 50 – 75 % of their needle biomass and observed a total volume loss of 24 – 33 % compared to control trees.

The work of Duff and Nolan (1953) is but one example of investigations into the pattern of annual increment within the tree. While working on trees in even-aged stands, Duff and Nolan (1953) observed that dominant and codominant trees recorded approximately equal cross-sectional area growth within the stem, but the width of growth rings decreased downwards to the base. Their work examined annual increment on the entire tree. Few authors have looked at the
pattern of growth in width and cross-sectional area of growth rings within the upper stem, in the vigorously growing section of the crown.

The rate of diameter growth is influenced by site quality, tree vigor, leaf area, density of trees, among other factors. Yeh and Wensel (2000) observed that temperature and precipitation accounted for 67% of variation in annual increment in pines and 74% of the annual increment variation in other species, for annual increment witnessed in growth rings. Moist and cooler years record greater diameter growth than drier and warmer years. Duff and Nolan (1953) observed that the maximum width of growth rings was wider in rapidly growing trees than slowly growing ones. Diameter growth therefore responds to the prevailing site, tree, and environmental conditions.

The distribution of leaf area within the crown vertical profile has a controlling effect on stem form. The functional relationship between crown leaf area and stem form was quantified by Shinozaki and others (1964) when they proposed the pipe model theory. According to the pipe model, a unit of leaf mass is serviced by a continuation of conducting tissue of constant cross-sectional area. Following this relationship, stem diameter at base of the crown can be used to calculate tree leaf area or leaf mass. This phenomenon is attributed to the crown length, which approximates the progressive increase amount of leaf area from the tip of the stem downwards. Therefore, defoliation or pruning drastically reduces the leaf area or leaf mass within the crown and could alter the ratio of leaf mass to sapwood cross-sectional area.

The form and taper of the upper stem is modified by the crown environment, owing to its proximity to sources of carbohydrates and growth regulators. The upper stem therefore experiences large rates of diameter growth (Courbet and Houllier, 2002), with a maximum point of diameter increase located at the base of the crown (Larson, 1963). Pruning that drastically
reduces leaf mass stimulates increased diameter growth in upper stem thus reducing overall stem taper (Larson, 1965). However, studies have shown that reduction in foliage due to defoliation could lead to reduction in diameter growth (Hoogesteger and Karlsson, 1992). In a study that used artificial defoliation to simulate insect attack, (Hoogesteger and Karlsson, 1992) observed that severe defoliation strongly reduced formation of growth rings for at least 3 years after defoliation. This was attributed to severe reduction in photosynthetic production that could not be overcome by short-term compensation from stored reserves or increased photosynthesis in the remaining foliage.

Primary data from 5-year old loblolly pine trees is used to evaluate the hypothesis that seasonal growth in tree diameter and stem form correlates with minor changes in leaf area on branch whorls in the active crown. A series of artificial defoliation and shade treatments on selected branch whorls were used to confer carbohydrate and growth restraints on diameter growth. The treatments were intended to quantify the net contribution of individual branch whorls to growth of annual rings in adjacent internodes. The width and cross-sectional area of growth rings from treated trees at relative heights at which they were measured was then compared to the values of untreated control trees.

**Materials and methods**

**Data**

This study was conducted at Lee Memorial Forest East of Franklinton, Louisiana (30°52’52.5” N 89°58’43.4” W). The data was collected from 4-year-old loblolly pine (Pinus taeda L.) trees that were planted in 5 blocks. All the blocks were planted within the same year at spacing of 1.5 m x 1.5 m and 3 m x 3 m. and were established with a common protocol. Trees of good form
were carefully selected from each block on the North-South and East-West boundaries of the plots for use in this study. Eighteen trees per block were then selected from among the preselected trees and marked. On each tree, the fourth order branch whorl from the top was marked as the target whorl. Immediate lower and upper neighbor whorls to the target were also marked. Each marked tree was assigned one of the nine treatments designed to effect carbohydrate and growth factors on branches. Treatments were applied on the target whorl and neighbor whorls, each with three treatment levels. The treatment levels were untreated control, foliage removed, and foliage covered with shade cloth (Table 4-1). Treatments were randomized to give possible nine combinations that were applied on selected trees.

Table 4-1 Arrangement of treatments. Treatments Control (C), foliage removed (D), and foliage covered with shade cloth (S) were applied on the target branch and neighboring branches represented by first and second letters, respectively.

| Target | Neighbor |  |  |  |
|--------|----------|  |  |  |
| C      | C        | D | S |
| D      | DC       | DD | DS |
| S      | SC       | SD | SS |

**Measurements**

Initial measurements of tree height, root collar diameter, and internode diameters were measured in April 2015. The root collar diameter (RCD) was measured at 0.15 m above the ground. The heights of internode mid-points \( h_1 \) - \( h_4 \) were marked and measured below the lower neighbor branch, below the target branch whorl, above the target branch whorl, and above the upper neighbor respectively (Figure 4-1). Subsequent measurements included height to base of live
crown, which were measured in December 2015, March 2016, May 2016, and August 2016, and the length of live crown affected by treatments (Table 4-2).

![Diagram](image)

Figure 4-1 Relative position of mid-section of internodes

Table 4-2 Summary of tree height, live crown, effective live crown and percent of live crown that was treated for 45 trees recorded at the end of two growth seasons (Year 1 and Year 2) following treatments

<table>
<thead>
<tr>
<th>Variable</th>
<th>Year 1</th>
<th>Year 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total height at end of the year (m)</td>
<td>3.36 0.55</td>
<td>4.28 0.62</td>
</tr>
<tr>
<td>Live crown length (m)</td>
<td>2.93 0.53</td>
<td>3.83 0.63</td>
</tr>
<tr>
<td>Effective live crown length* (m)</td>
<td>2.40 0.59</td>
<td>3.30 0.69</td>
</tr>
<tr>
<td>Percent of live crown length removed or shaded* (%)</td>
<td>18.36 11.41</td>
<td>14.10 8.88</td>
</tr>
</tbody>
</table>

*Effective live crown length refers to portion of live crown from the tip to bottom of the crown that was not affected by treatments

*Percent live crown length defoliated or shaded is the proportion of live crown length that was affected by treatments
Derived value of live crown length was calculated as the difference between total tree height and height to the base of live crown. Effective live crown length was calculated as the difference between live crown length and the length of live crown affected by treatments (shaded or removed). The percent live crown length defoliated or shaded represents the proportion of live crown length that was affected by treatments.

At the end of the growing season in December 2016, nine trees were harvested from each of the five blocks in the field, corresponding to one tree per treatment per block. Stem discs were cut from the midsection of each internode, and labelled (Fig 4-2). The discs were stored separately for each tree in brown bags and transported to the lab for further measurements.

The stem discs were sanded until growth rings were clearly visible, and tracheid cells were visible under dissecting microscope. The diameter of growth rings that corresponds to years 2014, 2015, and 2016 were then measured in two perpendicular planes, the average was then calculated and used in the analysis. The cross-sectional area of each year’s growth ring was calculated for each disc.

**Data Analysis**

Derived values of the annual increment in cross-sectional area at a relative height calculated with the height at the end of the year the increment occurred were obtained from diameter and height measurements described above.

Let

\[ \gamma_{ijk} = \frac{\pi D_{ijk}^2}{4}; \]

where \( \gamma_{ijk} \) is the cross-sectional area of the \( k^{th} \) growth ring of the \( j^{th} \) internode on the \( i^{th} \) tree,
$D_{ijk}$ is the diameter of cross-section enclosed by the $k^{th}$ growth ring of the $j^{th}$ internode on the $i^{th}$ tree, and

$\pi$ is a constant of value 3.1416.

Let

$$RA_{ijk} = \gamma_n - \gamma_{n-1}, \quad (4.1)$$

where $RA_{ijk} =$ cross-sectional area of $k$th growth ring at the $j^{th}$ location on the $i^{th}$ tree,

$n = 1, 2 \text{ years}$.

Figure 4-2 Measurement of tree heights for three successive years ($H_0, H_1,$ and $H_2$) and corresponding cross-sectional area of growth ring column for each year $A_0, A_1,$ and $A_2$ respectively, measured at four internodes of heights $h_1, h_2, h_3$ and $h_4$ along the trunk. $H_0$ and $A_0$ denote initial values measured before treatment.
The cross-sectional area of annual growth rings was then related to the relative height of the corresponding internode during the year the ring grew (equation 2).

Let

\[ x_{ijk} = \frac{h_{ijk}}{H_{jk}}, \]

where \( x_{ijk} \) = relative height at the end of growth year,

\( h_{ijk} \) = height of the \( i \)th tree at the \( j \)th location, and

\( H_{ij} \) = total height of the \( i \)th tree at time \( j \) at the end of the growth year.

Let

\[ RA_{ijk} = f(x_{ijk}) + \epsilon_{ijk}. \quad (4.2) \]

Linear, mixed-effects model was used to analyze diameter growth data and to test for the effects of treatments on the annual increment of the cross-sectional area at different heights on a stem. The internode height on a stem for an individual tree in each year was expressed as relative height (eq 2). The response variable in the linear mixed model was the cross-sectional area of a growth ring at a given stem internode on the tree for the year \( Y_1 \) and \( Y_{1+1} \) after treatment. The data used was restricted to the segment of the tree stem within which treatments were applied. The top conical part and lower stem below the crown base were excluded. Treatments, relative height, and their interactions were employed as explanatory variables in the full model. The year was included as additional explanatory variable. Several possible combinations of treatment, relative height, year and their interactions were tested as explanatory variables in combination with random effects in the intercept, slope or both. The model with random components in the intercept and random slope was selected based on AIC and the distribution of residuals.
model \( \text{Log} \ RA = \log(x) + \text{treatment} + \text{year} + \log(x) \times \text{treatment} \) was fit using a linear mixed model algorithm (Proc Mixed in SAS 9.4)

**Results**

**Radial Increment**

When the plot of mean width of growth rings was plotted along the vertical stem profile as a function of height of the internode midpoints, a pattern of increasing width of growth rings with height was observed (Fig 4-3). The widths of growth rings on internode 4 had wider growth rings while that of internode 1 have relatively thinner rings during the same year.

![Graph showing mean width of growth rings](image)

**Figure 4-3** Mean width of growth rings of young loblolly pine trees measured at mid points of successive internodes within the crown for two growth seasons following treatment.

Radial increment was differentially affected by treatments depending on the year of observation. The radial increment was significantly reduced when target and neighbor whorls were treated (Fig 4-4). The reduction in radial increment for treatments DD, DS, SD, and SS was more pronounced in the second year of growth following treatment. Treatment of the target branches
only (DC and SC) or neighboring whorls only (CD and CS) did not significantly affect the width of growth rings when compared to the control.

**Cross-sectional area of growth rings**

Growth in tree diameter responded to reduction in the amount of leaf area in the crown. There was reduction in cross-sectional area of growth ring with increase in proportion of crown length that was subjected to treatments (Fig 4-5)

When the cross-sectional area of the growth ring was plotted against the relative height of each internode, a pattern of decreasing cross-sectional area with increasing internode height was observed (Fig 4-6). The cross-sectional area gives the actual surface area used in transport or mechanical support. The stem tapers and carries less branches and leaf area with increasing height. This pattern is consistent with the expected taper form and requirements for mechanical stability.

![Figure 4-4 Mean difference in growth ring width between the control (CC) and other treatments for year 1 (2015) and year 2 (2016) following treatment, values averaged across all internodes (* Means significant LSD, \( \alpha = 0.05 \))](image)
Figure 4-5 Cross-sectional area increment of annual rings in the internodes of young loblolly pine trees in response to percent of live crown removed or shaded for two growth seasons following treatment.

Figure 4-6 Vertical profile of mean cross-sectional area of two outer growth rings of young loblolly pine trees measured at successive internodes within the active crown.
The scatter plot of the cross-sectional area of annual growth rings with the relative height for the current year followed what appeared to be a negative exponential curve (Fig 4-7).

Initial examination of the data revealed that the residual error was not normally distributed. The data was therefore log-transformed to be linear. Plotting the cross-sectional area against relative height on log-scale gave a linear curve (Fig 4-8) and normal distribution of the error based on Shapiro-Wilk test of normality (W = 0.9946, p-value = 0.2349).

A simple linear model with random components added to both the intercept and slope showed better fit than fixed model based on the lowest value of AIC and unbiased residuals (Fig 4-9). The mixed-effects model results showed significant effect of treatments, relative height, and age in predicting the cross-sectional area of growth rings (Table 4-3). Treatment effects on ring cross-sectional area varied significantly with change in relative height. The ring cross-sectional area increment demonstrated sensitivity to changing crown environment at the branch whorl level.

Figure 4-7 Scatter plot of cross-sectional area of growth rings against relative height grouped by year of growth rings.
Figure 4-8 Linear plot of log-transformed data for cross-sectional area of growth ring against relative height.

Table 4-3 Results of fixed effects of linear mixed effects model used to fit growth ring data. The response variable was the cross-sectional area of growth ring at specified height in a given year.

<table>
<thead>
<tr>
<th>Effect</th>
<th>DF</th>
<th>F Value</th>
<th>Pr &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Log (relative height)</td>
<td>1</td>
<td>142.60</td>
<td>&lt;.01</td>
</tr>
<tr>
<td>Year</td>
<td>1</td>
<td>373.79</td>
<td>&lt;.01</td>
</tr>
<tr>
<td>Treatment</td>
<td>8</td>
<td>2.64</td>
<td>0.01</td>
</tr>
<tr>
<td>Log (relative height) x Treatment</td>
<td>8</td>
<td>3.01</td>
<td>0.01</td>
</tr>
</tbody>
</table>
Pairwise contrasts of predetermined treatment groups were set up and the results are shown in table 4-4 below. Test of pairwise contrasts of fixed effects showed that the cross-sectional area of trees that were treated was significantly lower than the untreated control (p < 0.01). The cross-sectional area of trees that received a defoliation treatment (CD, DD, and DC) was significantly lower than that of the control (p < 0.01). The same was observed for trees on which shade and defoliation treatment combinations were applied (DS and SD) (p < 0.01). The slope of trees that received a shading treatment on selected branches (CS, SC and SS) was significantly different from the control trees (p = 0.04), and that of the defoliated trees (p = 0.03) (Table 4-4).
Table 4-4 Test of pairwise contrasts between treatment groups on the slope from mixed effects model. (H₀: \( \mu_1 > \mu_2 \)) where \( \mu_1 \) is the mean of group 1 and \( \mu_2 \) is the mean of group 2.

<table>
<thead>
<tr>
<th>Label</th>
<th>Group 1</th>
<th>Group 2</th>
<th>F Value</th>
<th>Pr &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control vs other treatments</td>
<td>CC</td>
<td>CD, CS, DC, DS, SC,</td>
<td>11.95</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SD, SS</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Control vs defoliated</td>
<td>CC</td>
<td>CD, DD,DC</td>
<td>13.65</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Control vs shaded</td>
<td>CC</td>
<td>CS, SS, SC</td>
<td>4.15</td>
<td>&lt;0.04</td>
</tr>
<tr>
<td>Control vs D&amp;S</td>
<td>CC</td>
<td>DS, SD</td>
<td>13.84</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Control vs target</td>
<td>CC</td>
<td>DC, SC</td>
<td>9.04</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Control vs neighbor</td>
<td>CC</td>
<td>CS, CD</td>
<td>6.07</td>
<td>&lt;0.02</td>
</tr>
<tr>
<td>Target vs neighbor</td>
<td>DC, SC</td>
<td>CD, CS</td>
<td>0.41</td>
<td>&lt;0.52</td>
</tr>
<tr>
<td>Shaded vs defoliated</td>
<td>CS, SC, SS</td>
<td>DC, CD, DD</td>
<td>4.77</td>
<td>&lt;0.03</td>
</tr>
</tbody>
</table>

**Discussion**

A predictable pattern in width of growth rings and the cross-sectional area of growth rings along the vertical profile of the tree was observed. The average width of annual rings decreased downwards from the highest measured internode down the lowest internode (Fig 4-3). The annual rings at the upper stem portions enclose fewer rings inside compared to lower portions of the tree where outer growth rings are laid on top of older rings and therefore enclose a wider stem. The tapering of the stem gives annual rings this unique pattern whereby the young top wood that enclosed the pith is wider in ring width but as the tree tapers downwards the ring width decreases in proportion to cover the increasing tree diameter. Generally, diameter growth is large in upper part of the stem and around the crown but is also more tapered (Duff and Nolan, 1953).
Growth in width of annual rings was affected by treatments (Fig 4-4). Trees on which treatments were applied on more than two branch whorls (DS, DD, SD, and DD) experienced significant reduction in annual ring width compared to untreated control. This observation was consistent with the observation in Fig 4-5 that showed proportionate reduction in the cross-sectional area of annual growth rings with reduction in the amount of leaf area on the tree quantified as percent live crown length treated.

The ring cross-sectional area is a better parameter to quantify the actual amount of new xylem formed during the period of observation than ring width because it estimates the surface area increment. The cross-sectional area also quantifies the available conducting tissue within the segment of the stem being observed. Stem cross-sectional area or sapwood-cross-sectional area is generally considered as a better predictor of the functional relationship between leaf area and stem conducting tissue (Baldwin, 1989). Therefore, the reduction in increment in cross-sectional area of annual rings with reduction in leaf area (Fig 4-5) appears to follow established relationships of the pipe model theory (Shinozaki et al., 1964a). Growth in diameter correlates with total crown length (Larson, 1963) being an approximation of progressive increase in leaf area from the tip of the tree downwards. This also has physiological implications because leaf area is a source of carbohydrates and growth regulators which are synthesized at the apices of branches.

The ring cross-sectional area increased from the top downwards (Fig 4-6). The increase in cross-sectional area of annual rings was in response to increasing tree diameter downwards. Though radial increment is thinner in lower internodes (Fig 4-3), they actually cover a larger circumference compared to internodes at the top, increasing ring area plays a role in the mechanical stability of the stem to withstand lateral forces that impose mechanical stress on the
tree. Trees form and taper is also modified by these forces, and the stem is thought to distribute mechanical stress uniformly in an attempt to achieve optimal stable form (Dean et al., 2002; Long et al., 1981; Metzger, 1893).

Individual treatments had varying degrees of effect on diameter growth of the stem as reflected in the test of fixed effects (Table 4-3 and 4-4). The effect of reducing the efficiency of branches by removal of leaf area was detected in the profile of the main stem. This emphasizes that cambial activity of the stem is sensitive to the effect of local branches. The profile of the tree taper varied significantly with treatments, and from year to year. The effect of treatments also varied with change in height, an indication of the local effect of treated branches to the stem profile. Yearly changes in the relative height of trees are attributable to periodic increase in total tree height. Thus the area of the outer annual growth ring corresponds to the current year tree height.

Removal of leaves and shading reduced photosynthetic capacity of the treated branches. Defoliation significantly reduced diameter increment compared to control (Table 4-4). By eliminating leaf area, photosynthesis was eliminated and branches could not effectively contribute the carbohydrate substrate needed for cambial activity. Studies have shown that diameter growth of a branch is determined by the balance between supply of photosynthates and its demand in the cambial zone (Sone et al., 2005).

The action of cambium is also controlled by growth regulators that are synthesized in shoot tips. The vertical distribution of cambial activity along the stem profile has also been found to correlate with the activity of auxin (Funada et al., 2001). Funada and others (2001) observed that seasonal variations in cambial activity correlated with fluctuations in the quantities of IAA and abscisic acid. The growth of stem diameter and taper within the crown also correlates with
increasing leaf area downwards, an attribute that is linked to increased availability of growth regulators.

The response of the stem to treatments by increment in ring width, ring cross-sectional area, and the effect on stem profile of the trees illustrates that growth in tree diameter is sensitive to minor changes in the crown. There is evidence of the functional role of leaf area to stem formation (Larson, 1965) and variations in stem diameter are consistent with proportionate reduction in crown length.

References


CHAPTER 5  GROWTH OF TREE DIAMETER AND STEM TAPER AS AFFECTED BY REDUCED LEAF AREA ON SELECTED BRANCH WHORLS

Introduction

Crown dimensions are commonly used in tree growth predictions based on the findings of previous studies that established a relationship between stem form and crown structure (Larson, 1963). These relationships inform the general application of silvicultural practices intended to control growth of forest trees. For instance, pruning of lower branches has been observed to increase diameter growth in upper stem thus reducing overall stem taper (Larson, 1965). Similarly the effect of wind forces acting on the tree stimulate radial growth at the base of the stem, alongside formation of reaction wood (Kellogg and Steucek, 1980). While it is reasonable to anticipate that reduced leaf area will have somewhat detrimental effect on tree growth, the counteracting effect from mechanical stimulation of stem growth present uncertain predictions on how the tree will respond.

Studies on how the crown and branches influence growth of trees are often described by pruning experiments which give an insight into the value of branch whorls to the stem growth. Most pruning studies have not established a significant change in the growth of the stem with removal of lower branches (Pinkard and Beadle, 1998; Underwood, 1967). However, few studies have recorded an increase in growth of the stem following pruning operations (Stein, 1955; Stiell, 1969). Increase in growth of the stem following pruning could be attributed to availability of more substrate for growth that would otherwise be used by pruned branches, or a change in the distribution of mechanical stress along the stem due to changes in the loading profile (Larson, 1965). Variations in tree responses to pruning are expected due to the different environmental and tree specific factors such as morphologies, resistance to injury, age of the tree, vigor, or...
intensity of pruning. To avoid the secondary effect of pruning, similar growth response can be achieved from less destructive approaches like defoliation and shade treatments on branches.

It is not clear which branches on the tree are not contributing to stem growth, but as a general rule for describing the functional crown, Roberts (1994) observed that the lower third of the crown had reduced physiological activity due to shading, or aging, and therefore does not produce growth rings on branches.

Growth of the main stem follows a predictable model of growth in which the terminal leader gives rise to and is maintained by branches and leaf area distal to it. The terminal leader develops new branches and leaf area annually, and maintains a pattern of growth where the previous year branches are relegated a number of ranks lower depending on the number of new flushes per growth season. Each set of branches have biomass and leaf area differences depending on how long they have survived on the tree. Previous year branches will therefore be lower on the tree and are longer and bigger in size with variations controlled by the degree of exposure to light and other factors. It therefore occurs that older branches in the lower crown are prone to self-shading from upper branches, and will only persist on the tree if they are able to access light. The series of events that control the structure of a tree’s crown allude to coordinated action at the tree level that produce an efficient functional crown (Fisher and Honda, 1979; Smith and Stitt, 2007).

In studying stem form, it is important to discriminate stem shapes in a tree in the regions within the crown, below the crown base, and the butt because of the difference in growth patterns. For instance, the stem region within the crown records greater rates of diameter growth and is more tapered than the region below the crown (Courbet and Houllier, 2002; Funada et al., 2001; Van Laar and Akça, 2007). The pattern of growth within the crown strongly correlates with the
progressive increase in leaf area down the stem. However, some researchers have been able to generalize stem taper for the entire stem. In their study of mature trees and saplings of *Pinus contorta*, Dean and Long (1986) observed that the constant stress model adequately described the taper for the stem above the butt swell for both ages. According the constant-stress model, a stem tapers to equalize stress produced by wind pressure along the stem (Dean and Long, 1986a; Metzger, 1893).

Coordinated growth between leaf area, main stem and branches is based on the established functional relationships that allow movement of substrates, water, and growth regulators within the tree. The functional relationship between leaf area and stem sapwood was described by Huber (1928). This relationship was then expanded into the pipe model theory (Shinozaki et al., 1964a) which quantified the functional link between leaf area and stem transport. Subsequent studies established the relationships between tree sapwood-cross-sectional area and leaf mass (Grier and Waring, 1974) or leaf area (Dean et al., 1988; Kaufmann and Troendle, 1981). The action of leaf area held on branches therefore affects cambial activity and stem transport.

The mechanism on how leaf area affects growth in form and taper of stem segment within the crown could be controlled by carbon relations (Långström et al., 1990), physiological responses (Larson, 1963), or distribution of mechanical stress (Dean and Long, 1986a). The cross-sectional area of the stem at a given point in the crown is directly related to the amount of leaf area above that point times the distance to the median of leaf area raised to the 1/3 power (Dean and Long, 1986b). Stem growth therefore responds to changes in crown leaf area. Stein (1955) observed that diameter growth is significantly reduced when over 40% of the live crown is removed during pruning. Since branches carry synthesis sites, it can be postulated that supply of growth
regulators and carbohydrates follows the same relationship, and may increase with crown length. Conversely, reduced leaf area could lead to limited supply and therefore reduced growth.

The current study was designed to test whether growth of tree diameter varies predictably with changes in leaf area on actively growing branches in the mid-crown of young loblolly pine trees. The study examines the contribution of individual branch whorls to growth of the stem by manipulating the carbohydrate sources on branches. It is postulated that a reduction in the photosynthetic capacity of individual branches on a whorl will be reflected in diameter growth of the main stem. The objectives of the study were to (1) describe the changes in the stem profile of young loblolly pine trees in response to different combinations of artificial defoliation and shade treatments, (2) quantify the growth impact of defoliated and shaded branch whorls on diameter growth, and (3) examine growth distribution along stem profile in response to reduced leaf area on branches.

Materials and methods

Data

The data for this study is from 4-year old loblolly pine (*Pinus taeda* L.) trees. The trees were planted in five isolated blocks at spacings of 1.5 m x 1.5 m and 3 m x 3 m. Eighteen trees of good form were carefully selected from exterior rows of each block for use in this study and assigned one of the nine treatments expected to effect carbohydrate and growth factors on branches. Treatments were applied on vigorous branches in the middle of the crown of selected trees. The branches on the fourth whorl from the top of each tree were marked and treated as the target. The immediate higher and lower neighboring whorls to the target were also treated to limit their influence on the target branches. Treatments were applied on one target branch whorl.
its neighboring whorls or both. The treatment levels were a control, foliage removed, and foliage covered with shade cloth to achieve complete darkness (Table 5-1).

Table 5-1 Arrangement of treatments. Treatments Control (C), foliage removed (D), and foliage covered with shade cloth (S) (90% shade) were applied on target and neighbor represented by first and second letters respectively.

<table>
<thead>
<tr>
<th>Target</th>
<th>Neighbor</th>
</tr>
</thead>
<tbody>
<tr>
<td>C</td>
<td>D</td>
</tr>
<tr>
<td>C</td>
<td>CC</td>
</tr>
<tr>
<td>D</td>
<td>DC</td>
</tr>
<tr>
<td>S</td>
<td>SC</td>
</tr>
</tbody>
</table>

**Measurements**

Pretreatment measurements of tree height, root collar diameter, and internode diameters were recorded for each tree in April 2015. The root collar diameter (RCD) was measured at 0.15 m above the ground. The average size of trees was 4.28 m in height and 8.14 cm at root collar diameter (Table 5-2). The diameters \( d_1 \) - \( d_4 \) were measured in the middle of the internodes located below the lower neighbor branch, below the target branch whorl, above the target branch whorl, and above the upper neighbor respectively (Figure 5-1). Subsequent measurements were taken in December 2015, March 2016, May 2016, and August 2016.

Table 5-2 Summary attributes of 90 trees recorded in August 2016

<table>
<thead>
<tr>
<th>Variable</th>
<th>Mean</th>
<th>Minimum</th>
<th>Maximum</th>
<th>Standard deviation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tree height (m)</td>
<td>4.280</td>
<td>3.048</td>
<td>5.505</td>
<td>0.623</td>
</tr>
<tr>
<td>Root-collar diameter (cm)</td>
<td>8.135</td>
<td>5.404</td>
<td>10.416</td>
<td>1.071</td>
</tr>
</tbody>
</table>
Data Analysis

Taper

The stem profile of the trees was predicted by relating relative diameter to relative height (Figure 2). Relative diameter is the ratio of internode diameter ($d_i$) at a certain height along the stem to the collar diameter (RCD) measured at 0.15 m (eq 5.1). The relative height is the ratio of the height of an internode ($h_i$) to the total height (H) of the tree (eq 5.2).

Let

$$y_{ijk} = \frac{d_{ijk}}{D_{ij}} = \text{relative diameter},$$

and

$$x_{ijk} = \frac{h_{ijk}}{H_{ij}} = \text{relative height},$$

where $d_{ijk}$ = bole diameter of measurement $k$ for tree $j$ in treatment $i$, $h_{ijk}$ = height from root collar to diameter measurement $k$ for tree $j$ in treatment $i$, $D_{ij}$ = root collar diameter of tree $j$ in treatment $i$, and $H_{ij}$ = height from root collar to the tip of tree $j$ in treatment $i$. 

Figure 5-1 Illustration of the relative position of internodes measured from young loblolly pine trees. The root-collar diameter (RCD) was measured at 0.15 m.
Model selection

Linear regression was sufficient to model stem profile in log scale (Fig 5-2).

![Figure 5-2 Residual plot of predicted values of relative diameter (Yhat) derived from fitting data to equation 5.3.](image)

The fixed model is given by equation 3:

\[
\log(y_{ij}) = a + b \log(x_{ij}) + \varepsilon_{ij},
\]

(5.3)

where \(y_{ij}\) is the relative diameter of the \(j^{th}\) internode of the \(i^{th}\) tree;

\(x_{ij}\) is the relative height of the \(j^{th}\) internode of the \(i^{th}\) tree;

\(a\) is the intercept and \(b\) the slope of the regression line for treatment \(I\);

\(\varepsilon_{ij}\) is the error.

To account for tree to tree random variation, regression models were examined for addition of random variable to the intercept, the slope, or both. The log-transformed data was fit separately to each of the models with different random parameters. The fit statistics are provided in Table 5-3.
Table 5-3 Fit statistics in terms of Akaike Information Criterion (AIC) and Bayesian Information Criterion (BIC) for models with random parameters $u_1$ and $u_{12}$ are random components for the intercept $(a_i + u_1)$ and slope $(b_i + u_2)$ respectively. Underlined value denotes the smallest value for each criterion.

<table>
<thead>
<tr>
<th>Random Parameters</th>
<th>AIC</th>
<th>BIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>None</td>
<td>-747.6</td>
<td>-743.8</td>
</tr>
<tr>
<td>$a_i + u_1$</td>
<td>-934.1</td>
<td>-934.1</td>
</tr>
<tr>
<td>$b_i + u_2$</td>
<td>-906.5</td>
<td>-906.5</td>
</tr>
<tr>
<td>$(a_i + u_2)$ and $b_i + u_2$</td>
<td><strong>-996.9</strong></td>
<td><strong>-996.5</strong></td>
</tr>
</tbody>
</table>

The model that random components were added to the intercept $a_i$ and slope $b_i$ had the lowest values of AIC and BIC, and was therefore selected for use in subsequent analyses. The selected model form was:

\[
\log (y_{ijk}) = (a_i + u_1) + (b_i + u_2)\log(x_{ijk}) + \varepsilon_{ijk}, \quad (5.4)
\]

where $u_1$ and $u_2$ are bivariate normal random variables with mean zero, variances $\sigma_1^2$ and $\sigma_2^2$, and covariance $\sigma_{12}^2$.

**Fitting the model to the data**

The stem profiles were analyzed by fitting equation (6) above to the log-transformed tree data using a linear mixed model approach as implemented in SAS 9.4 (Proc Mixed). In the model, the intercept and slope were specified as random with tree as subject and treatment nested within tree. *A priori* contrasts were specified for various treatment groups to determine treatment effects as compared to the control. The treatment groups were whether the control was different from all the other treatments (control vs all), defoliated treatments (control vs defoliated), shaded...
treatments (control vs shaded), or defoliation-shade treatments (control vs D&S) for target and neighbors. Contrasts were also specified to determine whether treatments applied on the target (control vs target) or neighbor (control vs neighbor) branches affected stem profile.

Let

\[ A = \sum_{i=1}^{9} a_i I_i + u_1, \]

and

\[ B = \sum_{i=1}^{9} b_i I_i + u_2, \]

where random \( a_i \) and \( b_i \) are intercept and slope respectively, for treatment \( i, i = 1, 2, ..., 9, \)

\[ I_i = \begin{cases} 1 & \text{if treatment } i, \\ 0 & \text{otherwise}. \end{cases} \]

The model for describing the taper for individual treatments is

\[ \log y_{ijk} = A + B (\log x)_{ijk} + \epsilon_{ijk}. \]  \hfill (5.5)

Details on constructing the likelihood ratio test for contrasts are shown in the Appendix I.

**Effect of treatments on growth of stem internodes**

Growth of the stem was determined from diameter measurements from internodes within the treated portion of the crown and the root-collar diameter. The treatment effect was analyzed as split plot with the internodes within the treated crown as the sub plots. The unstructured covariance structure was used in the model to account for intercorrelation between the four internode measurements occurring on the same tree subject and separated by space. The general model for the effects on internodes is given by equation 5.6.
\[ y_{ijk} = \mu + \beta_i + \tau_j + (\tau\beta)_{ij} + e_{ijk} + \gamma_k + (\tau\gamma)_{jk} + \epsilon_{ijkl} \] (5.6)

Where

- \( y_{ijk} \) is the tree diameter at the kth internode location of the jth treatment in the ith block;
- \( \mu \) is the overall mean;
- \( \beta_i \) is the effect of ith block;
- \( \tau_j \) is the effect of the ith level of treatment;
- \( (\tau\beta)_{ij} \) is the interaction effect of the ith block and the jth level of treatment;
- \( e_{ijk} \) is the error associated with main treatment effect;
- \( \gamma_k \) is the effect of kth location of internode;
- \( (\tau\gamma)_{jk} \) is the interaction effect of the jth level of treatment and the kth location of the internode;
- \( \epsilon_{ijkl} \) is the random error component which is assumed to be independently and normally distributed.

**Results**

The diameter of internodes was negatively correlated with percent of crown length that was defoliated or shaded (Fig 5-3)

![Graph showing correlation between diameter and defoliation](image)

Figure 5-3 Correlation between diameter at mid-section of internodes and the proportion of live crown that was treated
Stem taper

The Wald’s test for random variance components showed significant intercept and slope variance estimates. The effect of treatments on relative diameter varied between trees. Treatment effect on relative diameter also varied with change in relative height, and slope. The intracorelation class coefficient (ICC) was used to determine the proportion of the total random variance attributable to the tree to tree effect (equation 5.7).

\[
ICC = \frac{\sigma^2_{tree}}{\sigma^2_{tree} + \sigma^2_{slope} + \varepsilon_{ijk}}
\] (5.7)

Where \(\sigma^2_{tree}\) is the tree specific variance, \(\sigma^2_{slope}\) is the variance for slopes, and \(\varepsilon_{ijk}\) is the unexplained variation in the model.

The tree to tree variation accounted for 61.62% of the random variation in this model while 3.12% of the random variance remained unexplained (Table 5-4).

There was strong evidence of treatment effects on taper (p < 0.0001). Evidence of significant interaction between relative height and treatment existed (Table 5-5). The slope and intercept were significantly different from zero. The effect of treatments on relative diameter changed both the overall size and the change in diameter with relative height of trees.

Table 5-4 Partitioning of random variance based on ICC

<table>
<thead>
<tr>
<th>Component</th>
<th>ICC</th>
<th>Percent variance</th>
</tr>
</thead>
<tbody>
<tr>
<td>(\sigma^2_{tree})</td>
<td>0.61623</td>
<td>61.62</td>
</tr>
<tr>
<td>(\sigma^2_{slope})</td>
<td>0.3526</td>
<td>35.26</td>
</tr>
<tr>
<td>(\varepsilon_{ijk})</td>
<td>0.0312</td>
<td>3.12</td>
</tr>
</tbody>
</table>
Table 5-5 Fixed effects of treatment, relative height and interactions on relative diameter derived from mixed effects linear model \( \log y_{ijk} = A + B(log x)_{ijk} + \epsilon_{ijk} \)

<table>
<thead>
<tr>
<th>Effect</th>
<th>Num DF</th>
<th>Den DF</th>
<th>F Value</th>
<th>Pr &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Treatment</td>
<td>9</td>
<td>104</td>
<td>370.92</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td>Log(relative height)</td>
<td>1</td>
<td>97.2</td>
<td>1170.47</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td>log(relative height) x treatment</td>
<td>8</td>
<td>97</td>
<td>2.04</td>
<td>0.0492</td>
</tr>
</tbody>
</table>

In testing a priori contrasts, Type I error was set at 0.1 considering the relative effect of treatments applied on branches to the main stem. Pairwise contrasts between treatment groups and untreated control showed that relative diameter for groups of treatments with defoliation, shade, or both shade and defoliation combination were significantly different from the relative diameter of the control \((p < 0.1)\) (Table 5-6). Growth in stem internode diameters was significantly reduced when treatments were applied on target branches \((p = 0.084)\), or neighbor branch whorls \((p = 0.0693)\). The contrasts also detected significant reduction in internode diameter when shade and defoliation treatments were applied on one, two, or three whorls. Therefore defoliation or shading stress on one or more branch whorls within the active crown significantly reduced diameter growth. The analysis did not detect significant differences \((p > 0.1)\) when comparing among shaded, defoliated, or combined defoliation and shade treatments. There was no detectable difference on taper when the effect of treated neighbors was compared to treated target branches \((p = 0.60)\). The slopes of the tree profiles for individual treatment combinations were different from that of control trees. His indicates that defoliation and shade treatments on branch whorls affected internode diameters.
Table 5-6 Test of pairwise contrasts between treatment groups on the slopes from mixed effects model. (H₀: 𝜇₁ = 𝜇₂) where 𝜇₁ is the mean of group 1 and 𝜇₂ is the mean of group 2.

<table>
<thead>
<tr>
<th>Contrast group</th>
<th>Group 1</th>
<th>Group 2</th>
<th>Pr &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control vs all other treatments</td>
<td>CC</td>
<td>CD, CS, DC, DD, DS, SC,</td>
<td>0.0136</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SD, SS</td>
<td></td>
</tr>
<tr>
<td>Control vs defoliation treatments</td>
<td>CC</td>
<td>CD, DC, DD</td>
<td>0.0219</td>
</tr>
<tr>
<td>Control vs shading treatments</td>
<td>CC</td>
<td>CS, SC, SS</td>
<td>0.0418</td>
</tr>
<tr>
<td>Control vs Defoliated + Shaded branches</td>
<td>CC</td>
<td>DS, SD</td>
<td>0.0114</td>
</tr>
<tr>
<td>Control vs treated target branches</td>
<td>CC</td>
<td>DC, SC</td>
<td>0.0615</td>
</tr>
<tr>
<td>Control vs treated neighbor branches</td>
<td>CC</td>
<td>CD, CS</td>
<td>0.0134</td>
</tr>
<tr>
<td>Control vs one whorl treated</td>
<td>CC</td>
<td>DC, SC</td>
<td>0.0615</td>
</tr>
<tr>
<td>Control vs 2 whorls treated</td>
<td>CC</td>
<td>CD, CS</td>
<td>0.0134</td>
</tr>
<tr>
<td>Control vs 3 whorls treated</td>
<td>CC</td>
<td>DD, SS, DS, SD</td>
<td>0.0188</td>
</tr>
<tr>
<td>Treated target vs treated neighbor branches</td>
<td>DC, SC</td>
<td>CD, CS</td>
<td>0.4371</td>
</tr>
<tr>
<td>Defoliated vs shaded</td>
<td>CD, DC, DD</td>
<td>CS, SC, SS</td>
<td>0.7017</td>
</tr>
<tr>
<td>Defoliated vs D&amp;S</td>
<td>CD, DC, DD</td>
<td>DS, SD</td>
<td>0.6176</td>
</tr>
<tr>
<td>Shaded vs D&amp;S</td>
<td>CS, SC, SS</td>
<td>DS, SD</td>
<td>0.3993</td>
</tr>
</tbody>
</table>

Plots of the stem profile of individual treatments compared to the profile of the control trees showed a clear pattern of reduced diameter at the internodes where branch whorls were shaded or defoliated (Figure 5-5). The stem profiles show treated tree profiles to appear to diverge from the control profile when approaching a treated whorl, then remain wide below the control within the internodes that were affected by treatments, then converge back to the control profile beyond
the treated internodes. Stem profiles with a defoliation treatment combination (Fig 5-5 a, b, and c) representing CD, DC and DD showed reduced diameter growth compared to the control. Treatments where branch whorls were shaded also showed reduction in diameter growth consistent with the observation described above (Fig 5-5 d, e and f). These observations underscore the fact that growth contribution of branch whorls to diameter growth of the stem is localized to immediate internodes adjoining the whorls.

Figure 5-4 Residual plot of predicted values of log relative diameter ($\hat{y}_{ijk}$) derived from mixed effects linear model (equation 5.7)
Figure 5-5 Stem-profiles of shaded and defoliated trees compared to the profile of the control. The y-axis represents the average relative diameter per internode while the x-axis represents the corresponding mean relative height. Treatments with defoliated branch whorls are represented by figures a, b, and c while treatments with shaded branch whorls are shown in figures d, e, and f.
Growth of internodes

The mean increment in diameter of internodes d1 and d3 were significantly reduced by all treatments except CD, SC, and DC (Table 5-7). Growth in internode d2 was significantly reduced by all treatments except CD and DC. The diameter growth for internode d4 was only reduced significantly by treatment SD (Table 5-7). The presence of shading treatment on either target branches or neighbors resulted in significant reduction in growth of internodes adjacent to the treated branches. Reduced growth in internode diameters due to shade treatments occurred just below the target branches (d2) when only the target branch whorl was treated.

Table 5-7 Mean diameter growth (mm) of stem internodes d1, d2, d3, and d4 for different treatment combinations

<table>
<thead>
<tr>
<th>Treatment</th>
<th>d1</th>
<th>d2</th>
<th>d3</th>
<th>d4</th>
</tr>
</thead>
<tbody>
<tr>
<td>CC</td>
<td>9.88</td>
<td>10.19</td>
<td>9.12</td>
<td>8.84</td>
</tr>
<tr>
<td>CD</td>
<td>8.80</td>
<td>8.58</td>
<td>8.15</td>
<td>8.47</td>
</tr>
<tr>
<td>CS</td>
<td>7.51*</td>
<td>7.78*</td>
<td>7.16*</td>
<td>7.39</td>
</tr>
<tr>
<td>DC</td>
<td>9.85</td>
<td>8.35*</td>
<td>9.38</td>
<td>9.17</td>
</tr>
<tr>
<td>DD</td>
<td>7.31*</td>
<td>7.45*</td>
<td>7.07*</td>
<td>7.05*</td>
</tr>
<tr>
<td>DS</td>
<td>7.88*</td>
<td>6.83*</td>
<td>6.93*</td>
<td>7.52</td>
</tr>
<tr>
<td>SC</td>
<td>8.04*</td>
<td>7.63*</td>
<td>7.66*</td>
<td>8.39</td>
</tr>
<tr>
<td>SD</td>
<td>7.11*</td>
<td>5.94*</td>
<td>6.18*</td>
<td>6.09*</td>
</tr>
<tr>
<td>SS</td>
<td>6.61*</td>
<td>7.37*</td>
<td>7.21*</td>
<td>7.77</td>
</tr>
</tbody>
</table>

*significant at alpha=0.1
Discussion

Growth in diameter and taper were affected by treatments because of the effect of defoliation or shading of leaves on growth. The amount of leaf area available for photosynthesis on the treated branches was reduced. Growth of plants depends on amount of leaf area and the efficiency of the crown to display foliage and capture incident radiation (Monsi and Saeki, 2005). Pairwise comparison between control and trees that received a defoliation treatment (DC, CD, and DD) detected a significant effect on taper ($p = 0.02$) (Table 5-6). Defoliation eliminated leaf area from one two or three branch whorls. This was a significant amount of reduction in carbohydrate supply to the branches and subsequently to the region of the stem affected. Reduced supply from the branches, could have led to the reduction in growth of the stem. Trees may exhibit short term tolerance to defoliation due to their ability to mobilize labile carbohydrates (Eyles et al., 2009; Jacquet et al., 2014). Trees may also respond to defoliation by increasing the rate of photosynthesis in the remaining leaf area (Turnbull et al., 2007) and allocating resources to growth of new leaf area (Mediene et al., 2002; Strauss and Agrawal, 1999). The level of defoliation stress in this study affected growth of the stem, emphasizing that compensatory or tolerance effects by the trees were not sufficient to overcome the effect of defoliation on a whorl of actively growing branches.

Significant effect was also detected on taper of trees that received a shading treatment when compared to the untreated control ($p = 0.04$). Shade stress had a gradual effect of eliminating leaf area from the branches; the covered leaves persisted on the branches while still respiring. Leaf photosynthesis is necessary for plants to maintain cell respiratory demands. Experiments involving artificial shading show that light limited shoots have significant reduction in growth occasioned by reduced substrate supply from foliage (Cregg et al., 1991). Whereas constrained
shoots have the option to import carbohydrates from neighboring sources, the mechanisms that control supply from competing sources are unclear. Previous studies on differential shading (Henriksson, 2001; Lacointe et al., 2004) show that a tree can be viewed as a single whole unit organism, within which response to shade is global. Global response is attributed to a compensatory mechanism that ensures symmetric growth irrespective of differential shading. Shaded branches had additional weight of the shade cloth that conferred mechanical stress on the branches. This could have contributed to the higher magnitudes of reduction in stem growth from shading treatments. Shaded branches recorded mortality within the first growth season. The experiment subsequently recorded mortality of 60% of branches covered with shade cloth.

Comparing the slopes of stem profiles for treated and untreated control trees shows that the magnitude of effect on diameter growth varied predictably with the number of branch whorls that were treated (Table 5-6). Growth of the stem was not significantly affected when a single branch whorl was treated as demonstrated by target treatments on one branch whorl, whether shaded (SC) or defoliated (DC). Treatment of two branch whorls as demonstrated by neighbor treatments (CD, CS) showed significant effect on the stem profile. Treatments on three branch whorls (DD, SS, SD, DS) recorded significant effect on stem profile compared to control trees. Previous studies that related crown structure to stem diameter also observed that stem diameter at a given point in the crown coordinates with the amount of leaf area above it (Shinozaki et al., 1964a).

The growth of internodes d1, d2, and d3 was significantly affected when two or more branch whorls received defoliation or shade stress treatment except treatment CD (Table 5-7). Defoliation stress on one branch whorl significantly affected the diameters of the internode immediately below the treated whorl (DC) but shade stress on one branch whorl (SC)
significantly reduced the diameter of the internode above and below the stressed branch whorl. Only two treatments (DD and SD) recorded significant reduction in growth of diameter of the internode 4 (Table 5-7). The two treatments had defoliated neighbors and a treated target highlighting that removal of foliage on neighbor branches had a carry-over effect to the upper internode. DD, SD and SC treatments were the only treatments to record reduction in growth of diameter of internodes above treated branch whorls. Internode 4 was in the active crown, above the uppermost treated branch whorl. Previous studies have recorded that growth of an internode is influenced by the whorl immediately above it (Stiell, 1969).

Mechanisms that control development of stem form encompass physiological and mechanical relationships of the stem and the crown. The ‘pipe’ model proposed by (Shinozaki et al., 1964a) emphasizes a strong correlation between stem cross-sectional area at a particular height and foliage mass above that height. The pipe model theory forms the basis of several models of stem form that are driven by canopy structure and carbon partitioning, and therefore suggest a functional relationship between stem and transpiring or photosynthesizing foliage (Mäkelä, 1986; Thorney, 1976; Valentine, 1985, 1988). As demonstrated in taper and diameter responses to the treatments in this study, leaf area on branches has functional contribution to growth of the stem.

Though widely adopted, models based on pipe theory are limited in their applications (Rennolls, 1994). In a review of pipe models of stem form, Ronellis (1994) concluded based on empirical data that parameters of developed models are complex functions of local conditions and may not be adequate to model the development of complete tree geometry. However, the pipe model has been used successfully to predict canopy leaf area (Waring et al., 1982), model relationships
between sapwood cross-sectional area and leaf mass (Dean et al., 1988; Grier and Waring, 1974), and derive stem taper (Makela, 2002).

Mechanical models of stem formation arise from the understanding that changes in stem diameter can be attributed to changes in the lateral forces acting on trees (Jaffe and Forbes, 1993; Valinger et al., 1995). Mechanical models explain the function of the stem in supporting the crown. Studies show that mechanical stress is distributed uniformly along the stem profile and that stems taper to maintain a uniform bending curvature (Dean et al., 2002). Synonymous with predictive ability of pipe models, Dean and Long (1986) derived a regression model that predicts stem diameter at a given height on the stem as a power function of the bending moment acting on it at that height.

The mechanisms of stem formation have not been independently fully accounted for by either crown driven or mechanical models of stem formation but collectively explain pertinent portions of stem formation (Long et al., 1981). Long and others (1981) observed that sapwood cross-sectional area at any height related linearly to the amount of foliage above that point, consistent with the ‘pipe’ model, but in large trees the sapwood area needed to supply transpiring foliage with water was insufficient to provide mechanical support. However, the combination of sapwood (conducting tissue) and heartwood (mechanical support tissue) provided the stem form sufficient to provide uniform resistance to bending stress.

References


CHAPTER 6 SUMMARY AND CONCLUSIONS

The overall goal of this dissertation was to determine the role of leaf area and crown dynamics in growth of trees. Branch leaf area was reduced through defoliation and shade treatments to test the contribution of current and previous year’s leaf area to elongation of branches, growth of new leaf area, and increase in stem diameter. In summary, this dissertation has: (1) analyzed the interaction between leaf area and branch elongation, (2) proposed a unique method of quantifying the effect of neighbor branches on net growth of a branch in the crown (3) summarized the growth impact of loss of leaf area on diameter growth of trees, and (4) quantified the distribution of growth along the stem profile as contributed by selected branches.

The value of leaf area on extension of shoots and growth of new leaf area was determined by defoliation and shading of previous year’s foliage. The extension of the terminal bud was predicted from the size of the branch and the previous year’s leaf area curried on the branch. The initial cross-sectional area at the base of the branch and length of the branch determined the initial size which could approximate sapwood area and amount of stored carbohydrates for branch growth. The initial leaf area approximated the photosynthetic capacity of the branch for future growth. The number of new fascicles in the next growing season was significantly reduced by loss of previous year’s leaf area. This number approximates the number of new stem units formed and could be predicted from the length of a fully elongated bud using the power model.

The independence of branches in the crown was tested by defoliation and shade treatments on selected target branches and their immediate upper and lower neighbors. The influence of leaf area on target and neighbor branches was analyzed by isolating the primary effects due to treating of the target branches and the secondary effects due to treatment of neighbor branches.
Primary effects from defoliation and shading of target branches were quantified and were observed to have significantly reduced elongation of the terminal leader and growth in diameter of treated branches as compared to the control. Secondary effects due to defoliation or shading of neighbor branches were quantified but did not significantly affect elongation of branches or growth in diameter of target branches. The method presented here gives a unique way of quantifying the net contribution of neighbor branches to net growth of a target branch. It also proposes a unique way of isolating a target branch from the immediate neighbors when studying autonomy of branches as independent modules on the tree.

Reduction of leaf area in the crown from selected branches through defoliation and shade treatments elicited a response on the stem in terms of increment in ring width, ring cross-sectional area and the effect on stem profile. Diameter growth showed sensitivity to minor changes within the crown. The increment in cross-sectional area of growth rings was significantly affected by defoliation and shade treatments, age of treatments on the tree, and relative height in the year it was measured. The effect of treatments also varied with relative height. Defoliation and shade treatments affected the photosynthetic capacity reducing available carbohydrates. The reduced substrate supply from branches could have affected cambial activity in the stem leading to the observed effects in diameter increment.

Coordinated growth between leaf area on selected branches in the crown and growth in form and taper of the main stem was also investigated. The growth impact of individual branch whorls on the stem profile was tested using a linear mixed effects model relating relative diameter to the relative height of the internodes in the year of measurement. Defoliation and shade treatments on selected branches significantly affected the stem profile compared to untreated trees. The effect of reduced leaf area due to defoliation and shading of branch whorls was localized to internodes
immediately below or above treated whorls. This emphasizes the localized contribution of branches to stem growth.

This study reconciles the concepts of independence of branches in the crown and the crown centered models of stem formation based on the functional link between leaf area and stem transport. Tree crown dynamics as observed in variations in leaf area and light conditions could be detected in the response of trees in terms of branch elongation, branch diameter increment, growth in diameter of the stem, and distribution of growth in profile of the stem.
APPENDIX I: TESTING FOR CONTRASTS

Test: Group 1 vs Group 2.

Data: only measurements from group 1 and group 2

Full model: \( y_{ijk} = A + Bx_{ijk} + \varepsilon_{ijk} \), where \( A = a_1I_1 + a_2I_2 + u_1 \), \( B = b_1I_1 + b_2I_2 + u_2 \).

\( a_g \) and \( b_g \) = intercept and slope, respectively, for group \( g \), \( g = 1 \) or \( 2 \), \( I_g = 1 \) if treatment \( g \), \( 0 \) otherwise.

Reduced model: \( y_{ijk} = (a_i + u_1) + (b_i + u_2)x_{ijk} + \varepsilon_{ijk} \), where \( a \) and \( b \) are intercept and slope respectively for both groups.

Likelihood ratio test statistic: \( \chi^2 = -2 \left( \ln L_o - \ln L_1 \right) \) follows the chi-square distribution with \( k \) degrees of freedom, where \( L_1 \) and \( L_o \) are likelihood values of the full and reduced model respectively, and \( k \) is the difference in number of estimated parameters from the full and reduced models.
APPENDIX II: SAS CODES

A: SAS code for nonlinear mixed effects models: Logistic, Chapman-Richards, and Bailey and Clutter

**********FIXED BASIC MODELS**************;
proc nlmixed data=fam2;
   parms b1=1 b2=1 b3=1;
   pred = b1*(1-exp(-b2*t))**b3;
model y ~ normal (pred,s2e);
title 'Chapman-Richards basic model';
run;

proc nlmixed data=fam2;
   parms b1=1 b2=1 b3=1;
   pred = b1/(1+exp(b2-b3*t));
model y ~ normal (pred,s2e);
title 'Logistic basic model';
run;

proc nlmixed data=fam2;
   parms b1=1 b2=1 b3=1;
   pred=exp(b1-b2*t**b3);
model y ~ normal (pred,s2e);
title 'Bailey and Clutter basic';
run;

Data fam2; set fam2;
if y=0 then y='.';
run;
quit;

/* MODELS WITH ONE RANDOM VARIABLE*/
proc nlmixed data=fam2;
   parms b1=10.196 b2=1.9455 b3=0.3536 s2u=32.2 s2e=1.8;
   num=b1+u;
   den=1+exp(b2-b3*t); pred=num/den;
model y ~ normal( pred, s2e);
random u ~ normal( 0, s2u) subject=tree; predict pred out=preddata;
Title "Logistic model with one random variable on b1";
run;
data preddata;
   set preddata ;
   resid=y-pred;
run;
proc sgplot data=preddata;;
scatter x=pred y=resid;
refline 0/axis=y;
XAXIS label="Yhat" labelattrs=( size=14pt ) valueattrs=( size=12pt );
YAXIS label="Residuals" labelattrs=( size=14pt ) valueattrs=( size=12pt );
title 'Residual plot logistic one random';
run;
proc nlmixed data=fam2;
parms b1=10.96 b2=0.18 b3=1.4 s2u=36.46 s2e=1.66;
num=b1+u;
den=(1-exp(-b2*t))**b3; pred=num*den;
model y ~ normal( pred, s2e);
random u ~ normal( 0, s2u) subject=tree; predict pred out=preddata2;
Title "Chapman-Richards model with with one random variable on b1";
run;
data preddata2;
  set preddata2 ;
  resid1=y-pred;
run;
proc sgplot data=preddata2;;
scatter x=pred y=resid1;
refline 0/axis=y;
XAXIS label="Yhat" labelattrs=( size=14pt ) valueattrs=( size=12pt );
YAXIS label="Residuals" labelattrs=( size=14pt ) valueattrs=( size=12pt );
title 'Residual plot chapman one random';
run;
proc nlmixed data=fam2;
parms b1=10.96 b2=0.18 b3=1.4 s2u=36.46 s2e=1.66;
pred=exp((b1+u)-b2*t**b3);
model y ~ normal( pred, s2e);
random u ~ normal( 0, s2u) subject=tree; predict pred out=preddata3;
title 'Bailey and Clutter model with one random variable on b1';
run;
data preddata3;
  set preddata3 ;
  resid2=y-pred;
run;
proc sgplot data=preddata3;;
scatter x=pred y=resid2;
refline 0/axis=y;
XAXIS label="Yhat" labelattrs=( size=14pt ) valueattrs=( size=12pt );
YAXIS label="Residuals" labelattrs=( size=14pt ) valueattrs=( size=12pt );
title 'Residual Bailey one random';
run;
quit;
B: SAS code for Charpman-Richards model, treatment coefficients, contrast statements and estimates

```sas
ods graphics on;
data loblolly;
input block tree treatment target neighbor replicate week y;
iTcNd=0;
 iTcNs=0;
 iTdNc=0;
 iTdNd=0;
 iTdNs=0;
 iTsNc=0;
 iTsNd=0;
 iTsNs=0;
if treatment=12 then iTcNd=1;
if treatment=13 then iTcNs=1;
if treatment=21 then iTdNc=1;
if treatment=22 then iTdNd=1;
if treatment=23 then iTdNs=1;
if treatment=31 then iTsNc=1;
if treatment=32 then iTsNd=1;
if treatment=33 then iTsNs=1;
datalines;
run;

Data loblolly; set loblolly;
if y=0 then y='.'; output;
run;
proc nlmixed data=loblolly;
parms b1=14.977 b2=1.256 b3=0.153 bTcNd=0 bTcNs=0 bTdNc=0 bTdNd=0 bTdNs=0
 bTsNc=0 bTsNd=0 bTsNs=0 s2u=28.616 s2e=1.703;
num=b1+bTcNd*iTcNd+bTcNs*iTcNs+bTdNc*bTdNd*iTdNd+bTdNs*iTdNs*bTsNc*iTsNc+bTsNd*iTsNd+bTsNs*iTsNs+u;
exp1= (1 - (exp(-b3*week)))*b2;
pred=num*exp1;
model y ~ normal( pred, s2e);
random u ~ normal( 0,s2u) subject=tree; predict pred out=preddata2;
Title "nlmixed test of treatment CHAPMAN RICHARDS MODEL";
Estimate "direct D1" 1*b1 - (1*b1+1*bTcNd);
Estimate "direct D2" 1*bTcNd - 1*bTdNd;
Estimate "direct D3" 1*bTcNs - 1*bTdNs;
Estimate "direct S1" 1*b1 - (1*b1+1*bTsNc);
Estimate "direct S2" 1*bTcNs - 1*bTsNs;
Estimate "direct S3" 1*bTcNd - 1*bTsNd;
**Indirect effects***********;
Estimate "indirect d1" 1*b1 - (1*b1+1*bTcNd);
Estimate "indirect d2" 1*bTdNc-1*bTdNd;
Estimate "indirect d3" 1*bTsNs-1*bTsNd;
Estimate "indirect s1" 1*b1 - (1*b1+1*bTsNc);
Estimate "indirect s2" 1*bTdNc-1*bTdNs;
Estimate "indirect s3" 1*bTsNs-1*bTsNs;
run;
```

data preddata2;
  set preddata2;
  resid=y-pred;
run;

proc sgplot data=preddata2;;
scatter x=y y=resid;
reline 0/axis=y;
title 'chapman richards residual plot';
run;
proc sgplot data=preddata2;;
scatter x=pred y=resid;
reline 0/axis=y;
title 'chapman richards residual plot with yhat';
run;
quit;
C: SAS code for mixed effects linear models with starting values and contrast statement

data reladiam_log2; set reladiam1;
  logy = log(y);
  logx = log(x);
run;

Proc HPMixed Data = reladiam_log2;
Class tree treatment;
Model logy = logx treatment(tree) x*treatment;
Random Intercept logx / Subject = tree(treatment) Type = UN;
ods output CovParms = UN;
Run; Quit;

ods select all;
Proc Mixed Data = reladiam_log2 covtest;
Class tree treatment;
model logy = treatment logx logx*treatment / ddfm = KR;
ods output SolutionF = BLUE(Rename = (Estimate = EBLUE));
ods output SolutionR = BLUP(Rename = (Estimate = EBLUP StdErrPred = SEP));
title 'null model';
run;

Proc Mixed Data = reladiam_log2 covtest;
Class tree treatment;
model logy = treatment logx logx*treatment / ddfm = KR;
Random intercept / Solution Subject = tree(treatment) Type = UN;
Parms (0.01920) (0.0128)/ noiter;
ods output SolutionF = BLUE(Rename = (Estimate = EBLUE));
ods output SolutionR = BLUP(Rename = (Estimate = EBLUP StdErrPred = SEP));
title 'intercept';
run;

Proc Mixed Data = reladiam_log2 covtest;
Class tree treatment;
model logy = treatment logx logx*treatment / ddfm = KR;
Random logx / Solution Subject = tree(treatment) Type = UN;
Parms (0.01920) (0.0128) / noiter;
ods output SolutionF = BLUE(Rename = (Estimate = EBLUE));
ods output SolutionR = BLUP(Rename = (Estimate = EBLUP StdErrPred = SEP));
title 'slope';
run;

Proc Mixed Data = reladiam_log2 covtest;
Class tree treatment;
model logy = treatment logx logx*treatment / ddfm = KR;
Random intercept logx / Solution Subject = tree(treatment) Type = UN;
Parms (0.01920) (0.0128) (0.01099) (0.000972)/ noiter;
ods output SolutionF = BLUE(Rename = (Estimate = EBLUE));
ods output SolutionR = BLUP(Rename = (Estimate = EBLUP StdErrPred = SEP));
title 'intercept and slope';
run;
Proc Mixed Data = reladiam_log2 covtest;
Class tree treatment;
model logy = treatment logx logx*treatment / Noint Solution ddfm = KR
outp=fixed;
Randome intercept logx / Solution Subject = tree(treatment) Type = UN;
Parms (0.01920) (0.0128) (0.01099) (0.000972) / noiter;
ods output SolutionF = BLUE(Rename = (Estimate = EBLUE));
ods output SolutionR = BLUP(Rename = (Estimate = EBLUP StdErrPred = SEP));
*Order of Treatment levels 11 12 13 21 22 23 31 32 33;
CONTRAST 'Control vs treated' treatment -8 1 1 1 1 1 1 1 1;
CONTRAST 'Control vs defoliated' treatment -3 1 0 1 1 0 0 0 0;
CONTRAST 'Control vs shaded' treatment 3 0 -1 0 0 0 -1 0 -1;
CONTRAST 'Control vs D&S' treatment 2 0 0 0 0 -1 0 -1 0;
CONTRAST 'Control vs target' treatment 2 0 0 -1 0 0 -1 0 0;
CONTRAST 'Control vs neighbor' treatment 2 -1 -1 0 0 0 0 0 0;
CONTRAST 'Control vs one whorl' treatment -2 0 0 1 0 0 1 0 0;
CONTRAST 'Control vs 2 whorls' treatment -2 1 1 0 0 0 0 0 0;
CONTRAST 'Control vs 3 whorls' treatment -4 0 0 0 1 1 0 1 1;
CONTRAST 'Target vs neighbor' treatment 0 -1 -1 1 0 0 1 0 0;
CONTRAST '1 whorl vs >1 whorl' treatment 0 1 1 -3 1 1 -3 1 1;
CONTRAST 'Shaded VS defoliated' treatment 0 1 -1 1 1 0 -1 0 -1;
CONTRAST 'Defoliated vs D&S' treatment 0 1 0 1 1 -1.5 0 -1.5 0;
CONTRAST 'Shaded vs D&S' treatment 0 0 1 0 0 -1.5 1 -1.5 1;
title "random effects model";
run;
quit;
VITA

Shannon Dumo Kidombo was born in Kenya. After completing high school at Lubinu High School in Kakamega County, he joined Moi University in Eldoret, Kenya and graduated in 2005 with a Bachelor of Science degree in Forestry (first class honors). His first major assignment after graduating, was working on community based forest restoration with the greenbelt movement, a non-profit founded by 2004 Nobel Laureate for peace and environment, the late Prof. Wangari Maathai. He later joined Kenya Wildlife Service as a warden, working on protected area management and community involvement in conservation. Shannon was admitted to Southern University and A&M College for master’s degree in urban forestry in 2012. Upon completion of the master’s program, he joined the School of Renewable Natural Resources at Louisiana State University to pursue a doctoral degree under the supervision of Dr. Thomas Dean. He will receive the degree of Doctor of Philosophy during the summer commencement in August, 2017.