Stand Density Management for Optimal Volume Production

Micky Gale Allen II

Dissertation submitted to the faculty of the Virginia Polytechnic Institute and State University in partial fulfillment of the requirements for the degree of

Doctor of Philosophy
In
Forestry

Harold E. Burkhart, Chair
Philip J. Radtke
Thomas R. Fox
Inyoung Kim

March 25, 2016
Blacksburg, Virginia

Keywords: growth-density relationship, periodic annual increment, Langsaeter's hypothesis, planting density, thinning intensity, loblolly pine

Stand Density Management for Optimal Volume Production

Micky Gale Allen II

ABSTRACT

The relationship between volume production and stand density, often termed the "growth-density relationship", has been studied since the beginnings of forestry and yet no conclusive evidence about a general pattern has been established. Throughout the literature claims and counterclaims concerning the growth-density relationship can be found. Different conclusions have been attributed to the diverse range of definitions of volume and stand density among problems with study design and other pitfalls. Using data from two thinning studies representing non-intensively and intensively managed plantations, one spacing trial, and one thinning experiment a comprehensive analysis was performed to examine the growth-density relationship in loblolly pine. Volume production was defined as either gross or net periodic annual increment of total, pulpwood, or sawtimber volume. These definitions of volume production were then related to seven measures of stand density including the number of stems per hectare, basal area per hectare, two measures of relative spacing and three measures of stand density index. A generalized exponential and power type function was used to test the hypothesis that volume production follows either an increasing or unimodal pattern with stand density. These patterns were tested using all combinations of the six definitions of volume production and the seven measures of stand density. Significance of the parameters indicated that different patterns existed depending on the type of management (intensive vs. non-intensive), if thinning is performed, and depending on the definitions of growth and density. The growth-density pattern was generally the same between gross and net production although different patterns emerged when comparing total, pulpwood, and sawtimber volumes. The definitions of stand density which used diameter as a measure of average tree size were more highly correlated with volume production and produced similar patterns while the number of stems per hectare was the least correlated. Further analysis was performed to evaluate Langsaeter's hypothesis which states that volume production is constant and optimal across a wide range of stocking. A mixed-model approach was used to test the equality in mean volume production across a range of planting densities and thinning intensities. To account for the effects of age, the equality in mean volume production was tested separately across a range of ages from 8 to 25 years within the spacing trial data and across a range of one to six years since thinning within the thinning experiment. A multiple comparison test indicate that pattern of volume production and stocking is highly related to the two stages of self-thinning. In young stands, within the distance-independent mortality stage, volume production increases with increasing planting density and therefor increasing stocking. During the distance-dependent mortality stage the assumption of constant and optimal volume production across a wide range of stocking is generally correct. However when mortality began to reduce canopy closure to the point that the residual stand could not recover gaps in the canopy a decline in volume production occurred resulting in a decreasing relationship with increasing stocking. Finally, a system of equations were constructed to describe volume production at the individual tree and stand levels. From this model it was determined that stand level volume production follow an increasing pattern with stand density.

Acknowledgements

I wish to express sincere thanks to my advisor Dr. Harold E. Burkhart for his guidance and support. The knowledge I have gained from our many conversations and discussions is priceless. I also wish to thank to the members of my graduate committee Drs. Thomas R. Fox, Inyoung Kim, and Philip J. Radtke. Their criticisms, suggestions, and overall comments helped improve the manuscripts in this dissertation. Furthermore, their guidance has helped my understanding of both statistical and biological concepts aiding in my professional development.

Financial support from the USDA National Needs Fellowship and the Forest Modeling Cooperative at Virginia Tech made the successful completion of my Doctoral program possible and to those I give thanks. I also wish to thank the Department of Forest Resources and Environmental Conservation at Virginia Tech whose administrative support and facilities provided the framework necessary for me to carry out my academic and research work.

Many thanks are owed to Ralph Amateis who provided information, datasets, software codes, and hands on training in growth and yield modeling studies. Additionally, his spiritual guidance was invaluable throughout the duration of my Doctoral program. I will never forget the many discussion we have had.

This work would not have been possible without the support of my family. To Micky and Rusti Allen who gave me life and encouraged me to do something with it. To Kenny and Glenda Allen, who believed in me above all else. To my siblings Tommy, Robby, Lonnie, and Alyssa Allen who looked up to me and held me to a higher standard. What an amazing family you all are and I am lucky to count you as friends. I thank God for allowing us to share our lives together.

Finally, to my partner in life, Paula J. Celis-Salazar who supported me through the entire process of this dissertation. Your love, support, encouragement, and, above all, patience made this possible and for that I am forever indebted.

Table of Contents

List of Tables

List of Figures

Chapter 1: Introduction and Objectives

1.1. Introduction

Over half of the pine type in the southeastern U.S. consists of planted stands. Southern pines provide more than 40% of the softwood timber harvested in the U.S. annually (McNulty et al. 1996). Because of increasing demand for wood products in the world one primary objective of southern pine plantation management is to increase tree growth and improve its quality on a sustainable basis. While this objective is still relevant today, many generations of foresters have manipulated forest stand dynamics in order to increase wood production and quality. For several centuries forest managers have observed that a reduction in stand density can increase individual tree growth. As a result, thinning is one of the oldest and most commonly used forest management techniques (Zeide 2002). However, the problem of optimizing growth and value by controlling stand density still exists today. Zeide (2001) provides a useful review of how the philosophy of thinning has changed since the 18th century. Initial beliefs were that undisturbed stands were the most productive. Gradually, foresters observed that canopy closure resulted in decreased individual-tree growth and the idea of reducing canopy closure by thinning in order to stimulate growth was born. From this time foresters have sought to uncover the relationship between stand density and tree growth. Despite much effort we are still lacking commonly accepted generalizations and models that are needed for density optimization (Zeide 2004). Clutter et al. (1983) attribute our lack of understanding to inconsistency among different studies due to confounding effects of stand age and merchantability limits used. Zeide (2004) details that the problem may be that the effect of density on tree growth is not always separated from tree size and age.

1.2. Growth-Density Relationship

With the population of the world increasing, the demands for forests and forest products are increasing as well. An important objective of southern pine plantation forestry is to meet the increasing demand for wood and fiber use. Lumber for construction, pulp for paper products, and biofuels are just a few examples of products that are needed and obtained from planation forestry. Intensive silviculture, including site preparation, weed control, and fertilization, has been applied to increases plantation productivity. While wood production in southern pine plantations was less than 90 cubic feet/acre/year in the 1950s, an increase in growth to more than 400 cubic feet/acre/year can be seen today. Increased production has also led to a reduction in rotation lengths by more than 50% (Fox et al. 2007). Intensive management increases the amount of available resources for crop trees; however, understanding the relationship between stand density and growth is imperative so that management treatments can be applied efficiently for maximum forest output.

Zeide (2001) summarized four different hypotheses concerning the relationship between total and merchantable volume growth and density. The first pattern, named increase-increase, says that both total and merchantable volume increments increase with density. By implication, any kind of thinning would diminish both types of volume and their increments. This was the view of European foresters in the early 19th century and most notably that of George Ludwig Hartig, chief of the Prussian forest service. He insisted that thinning should be limited to the periodic removal of dead or dying trees and only when they could be sold profitably. In no case should thinning break the canopy closure. This growth-density relationship was challenged in 1811 by wealthy Danish landowner Christian Reventlow. Through observations of oak and beech stands he concluded that frequent thinnings substantially reduced canopy closure while increasing merchantable volume and total production as well as volume per unit area. This gave rise to the second pattern, named optimum-optimum, which says both merchantable and total volume increment peak at an optimal density. The idea of an optimum density for merchantable volume growth seems reasonable because increased density can decrease tree size below a merchantable limit. With increasing density after a point merchantable growth should obviously decline. In 1932 Wiedemaan, manager of the Prussian Forest Experiment Station, used 50-year observations in beech stands to demonstrate total wood production is independent of thinning intensity. This led to the third pattern, named constant-optimum, where total volume growth decreases at low and high densities but remains constant over a wide range. Langsaeter's hypothesis states that the total volume production of a stand at a given age and composition on a given site is constant and optimum for a wide range of densities and total volume production can be decreased but not increased(Langsaeter 1941). In a study designed to identify the ends of Langsaeter's plateau in Douglas-fir stands Curtis et al. (1997) found that total volume increment increases with density. They found that there was no such thing as an "excessive" number of trees and thinning increases growth of individual trees at the expense of their number and the volume growth of the entire stand. This gives the fourth and final pattern, named increase-optimal, where total volume production increases with density and merchantable volume production is maximized at an optimal density. Based on these findings Zeide (2001) claims a full circle in the evolution of forester's views on thinning has occurred.

The growth-density relationship in loblolly pine has been reported in several studies, though no conclusive evidence of a general pattern has been found (Trincado et al. 2004). McClay (1955) studied the relationship between periodic annual growth per acre and residual stand density, measured as basal area, after thinning. Using linear regression analysis he found a trend of increasing growth with increasing residual stand density up to a point where growth was maximized. Because of a lack of data in high density stands he was unable to determine if growth declined beyond this point. Wenger et al. (1958) studied the effect of growing-space requirements for thinned and unthinned stands of natural loblolly pine for a period of 5 years after treatment. The relationship between volume growth and density varied with site quality but not with stand age in thinned stands; however, both variables were significant for unthinned stands. Using data from the 5-year period (5-10 years after treatment) following Wenger et al. (1958), Nelson and Brender (1963) discovered no differences in volume increment between thinned and unthinned conditions. Using regression analysis they found that production in thinned stands increased with stand density on better sites and reached an optimum on poor sites. Trincado et al. (2004) used a long term thinning study in loblolly pine to determine the relationship between periodic annual increment (PAI) and density, measured as basal area. Their analysis indicated gross PAI in total volume and basal area for all site index classes follows an increasing pattern and in general net PAI in total volume follows an optimal pattern. Zeide (2004) developed a theoretical model for determining the 'optimal stand density' in loblolly pine. He concluded that maximum growth occurs at maximum stand density, supporting the observations reported by Curtis et al. (1997) for Douglas-fir. In an evaluation of the growth-density relationship in Norway spruce and European beech stands, Pretzsch (2005) determined the optimal density where periodic annual increment of merchantable volume is maximized, based on a standardized stand density index (SSDI). This SSDI relates SDI of stands with moderate and heavy thinnings to a control stand where only dead, dying, and unsound trees were removed. In general an optimum growth-density pattern occurred, but in some instances only an increasing or culminating portion of the curve was observed.

1.3. Defining Density

Within the literature there have been conflicting claims and counter claims dealing with the effects of thinning. Many researchers admit that these contradictions are the result of data inadequacies and differences in site quality among other pitfalls (Zeide 2001). While these problems can be addressed in the experimental design, one of the major concerns is the diversity of definitions of density. Zeide (1995) details that the relationship between tree size and their number is critical for estimating stand density and stocking, determining optimal thinning intensity, and calculating the degree of disturbance, rate of self-thinning, and other forestry processes. The problem is that stand density is not clearly defined and current “definitions” do not uniquely describe density. Zeide (2005) states that in an attempt to identify the single advancement that would be the most consequential to the science of forestry, the ability to measure stand density correctly would be the most likely candidate.

The first requirement for any density measure is that it should be identical in equally dense stands. This means that equal values of the measure in two different stands should imply equal site occupancy in the two stands (Zeide 2002). The number of trees per unit area cannot adequately describe the density of a forest. For example a stand with 800 one-year old seedlings per acre is not nearly as dense as a stand with 800 60-foot-tall trees per acre. One of the most common measures of density, basal area, is not sufficient either. A popular density guide developed by Ginrich (1967) shows that stands with the same basal area can be classified as overstocked, fully stocked, or understocked with increasing average diameter. For example a stand with basal area of 115 ft^2 per acre is overstocked for average diameters less than 10 inches and fully stocked for average diameters greater than 10 inches. Alternatively, if the number of trees per acre is held constant the trend of stocking with increasing diameter is reversed. Stands are understocked when trees are small and have relatively low basal areas and overstocked when trees are large. In an attempt to determine where these trends balanced one another Zeide (2002) recognized that both basal area and number of trees can be expressed as the product of number of trees (N) and mean diameter (D). The difference is that in basal area D is raised to a power of 2 and in number of trees D is raised to a power of 0. Because of the opposite stocking trends there should be some power, x, between 0 and 2 that produces an invariant combination of number of trees and their diameter. Zeide claims that this power, x, was found when Reineke (1933) plotted trees per unit area in fully stocked stands over their average diameter on the logarithmic scale. While Reineke's statistical methods were subjective his development of a stand density index (SDI) is of vast importance. The index is composed of the same components as basal area but it is more reasonable because stands with the same index for a given species and region will be consistently classified as to stocking. However, it has been shown that SDI changes with age and tree size (Bickford et al. 1957). Zeide (1991) attributes this change to the natural decrease of density in undisturbed stands. As a stand ages the size of gaps created in the canopy by fallen trees increases, while the ability of the residual stand to close the gaps decreases due to decreasing growth rates. Despite this fallback Pretzsch (2005) found that SDI gave a more adequate and stable measure of density than basal area.

Basal area and the SDI of Reineke (1933) are based on the average diameter of the stand but other measures have been developed that include variables such as height and volume. Since stand density is determined by tree size, it seems intuitive that total tree mass or stem volume would be a good predictor of stand density. Yoda (1963) developed the 3/2 rule of self-thinning by plotting the logarithm of mean tree volume or weight against the logarithm of the number of stems per unit area. He determined that in pure, even-aged stands that are sufficiently crowded and competition-induced mortality is occurring the slope of the line of the logarithm of mean volume versus the logarithm of trees per unit area is approximately -3/2; however, the intercept of the line varies by species. Zeide (1987) found that Reineke's SDI predicted mortality more accurately than the 3/2 rule of self-thinning. He attributed this result to mortality being driven by increasing crown width, which is more related to stem diameter than volume. Zeide also found that the 3/2 rule is not constant but varies with species, age, and more generally shade tolerance (Zeide 1987, 1991).

Relative spacing is a measure of density that uses the average distance between trees divided by the average height of the dominant canopy. Zhao et al. (2010) noted that relative spacing is a useful measure of stand density for developing thinning specifications in managed plantations because it uses number of trees and incorporates both site quality and age through dominant height. In an examination of spacing indices Bredenkamp and Burkhart (1990) show algebraically that Rieneke's SDI, the 3/2 power rule, and relative spacing produce the same slope and by extension are interrelated. Burkhart (2013) evaluated three stand density indices based on average diameter, height, and tree volume. He confirmed the expectations of Zeide (2002) in that average diameter was most effective in predicting number of trees and growth, height was least effective, and stem volume, which incorporates both height and diameter, was intermediate.

1.4. Objectives

The purpose of this research was to analyze data from several studies of loblolly pine in the southeast U.S. to determine the general relationship between stand density and stand productivity and average tree size. When evaluating the effects of stand density and stand productivity a major issue within the literature is how to define stand density. Zeide (2001) notes that many claims and counterclaims about the effects of thinning on volume production are due to the wide range of definitions of stand density that exist in the literature. Throughout Zeide's work in describing the relationship between stand density and stand productivity many of the pitfalls of commonly-used definitions of stand density are described, however, no direct comparison is made among the definitions. The pitfalls are described theoretically and, although good points are made, it would be useful to know how each definition compares in respect to showing a relationship between density and stand productivity. Several definitions of density including basal area, relative spacing, and stand density index based on average diameter, height, and volume were analyzed to determine if the relationship differed among alternate definitions and if one definition showed a stronger relationship than others.

A common generalization of the stand density-productivity relationship, commonly known as the Langsaeter's hypothesis, states that essentially the same volume production can be obtained over a wide range of stand densities and that thinning merely redistributes a constant volume increment among varying numbers of trees. This result would be very beneficial because stand density could be managed to obtain production in a desired product class without reducing volume production. Using a model developed from 40 research plots of loblolly pine in Arkansas, Zeide (2004) hypothesized that volume production had an optimum instead of constant pattern. Although, no direct observations of this optimum were made and the result could be due to the form of the model used. While Langsaeter's hypothesis has been tested for other species, this topic has not been addressed in the literature for loblolly pine. In addition to thinning study data, data from a spacing trial in loblolly pine, which covered a wide range of densities and only one treatment (initial planting spacing), Langsaeter's hypothesis was evaluated to determine if volume production is constant over a wide range of Stocking.

The final part of this research aimed to develop a model that describes the relationship between stand density and stand productivity. Understanding this relationship is important for determining planting densities and thinning schedules and currently a reliable model has yet to be developed. This model has the potential of defining the density that maximizes volume growth. Such a model would be useful for calculating thinning schedules and could be incorporated into forest stand growth simulators.

Literature Cited

Bickford, C.A., F.S. Baker, and W. F.G. 1957. Stocking, normality, and measurement of stand density. Journal of Forestry 55:99-103.

Bredenkamp, B.V., and H.E. Burkhart. 1990. An examination of spacing indices for Eucalyptus grandis. Canadian Journal of Forest Research 20(12):1909-1916.

Burkhart, H.E. 2013. Comparison of maximum size–density relationships based on alternate stand attributes for predicting tree numbers and stand growth. Forest Ecology and Management 289(0):404-408.

Clutter, J.L., J.C. Fortson, L.V. Pienaar, G.H. Brister, and R.L. Bailey. 1983. Timber management: a quantitative approach. John Wiley & Sons, inc, New York.

Curtis, R.O., D.D. Marshall, and J.F. Bell. 1997. LOGS: A pioneering example of silvicultural research in coast Douglas-Fir. Journal of Forestry 95(7):19-25.

Fox, T.R., E.J. Jokela, and H.L. Allen. 2007. The development of pine plantation silviculture in the southern United States. Journal of Forestry 105(7):337-347.

Ginrich, S.F. 1967. Measuring and evaluating stocking and stand density in upland hardwood forests in the central states. Forest Science 13(1):38-53.

Langsaeter, A. 1941. Om tynning i enaldret gran-og furuskog. Medd. Nor. Skogforsosves 8:131-216.

McClay, T.A. 1955. The relation of growth to site and residual density in loblolly pine pulp stands. USDA For. Ser., Southeast. For. Exp. Stn., Research Note No. 78. 2p.

McNulty, S.G., J.M. Vose, and W.T. Swank. 1996. Potential climate change effects on loblolly pine forest productivity and drainage across the southern United States. Ambio 25(7):449-453.
Nelson, T.C., and E.V. Brender. 1963. Comparison of stand density measures for loblolly pine cubic-foot growth prediction. Forest Science 9:8-14.

Pretzsch, H. 2005. Stand density and growth of Norway spruce (Picea abies (L.) Karst.) and European beech (Fagus sylvatica L.): evidence from long-term experimental plots. Eur J Forest Res 124(3):193-205.

Reineke, L.H. 1933. Perfecting a stand-density index for even-aged forests. Journal of Agricultural Research 46:627-638.

Trincado, G., H.E. Burkhart, and R.L. Amateis. 2004. Volume increment and stand density relationship: Hypothesis testing of patterns and modeling approach. Department of Forestry, Virginia Polytechnic Institute and State University, Blacksburg, VA., Loblolly Pine Growth and Yield Research Cooperative, Report No. 137.

Wenger, K.F., T.C. Evans, T. Lotti, R.W. Cooper, and E.V. Brender. 1958. The relation of growth to stand density in natural loblolly pine stands. USDA For. Ser., Southeast. For. Exp. Stn., Paper No. 97. 10p.

Yoda, K. 1963. Self-thinning in over-crowded pure stands under cultivated and natural conditions.(In-traspecific competition among higher plants.XI.). J Biol Osaka City Univ 14:107-129.

Zeide, B. 1987. Analysis of the 3/2 Power Law of Self-Thinning. Forest Science 33(2):517-537.

Zeide, B. 1991. Self-thinning and stand density. Forest Science 37(2):517-523.

Zeide, B. 1995. A relationship between size of trees and their number. Forest Ecology and Management 72(2–3):265-272.

Zeide, B. 2001. Thinning and growth: A full turnaround. Journal of Forestry 99(1):20.

Zeide, B. 2002. Density and the growth of even-aged stands. Forest Science 48(4):743-754.

Zeide, B. 2004. Optimal stand density: A solution. Canadian Journal of Forest Research 34(4):846-854.

Zeide, B. 2005. How to measure stand density. Trees 19(1):1-14.

Zhao, D., M. Kane, and B.E. Borders. 2010. Development and applications of the relative spacing model for loblolly pine plantations. Forest Ecology and Management 259(10):1922-1929.

Chapter 2: Literature review

2.1. Individual Tree Models

The following literature review covers component models at the whole-stand and individual tree levels as well as studies on changing stand dynamics due to thinning. The purpose is to review the general models and methods previously developed to describe changes loblolly pine exhibits after thinning.

2.1.1. Height-diameter Models

Utilizing data from a loblolly pine thinning study Zhang et al. (1997) fit the following model to unthinned, lightly thinned, and heavily thinned plots to determine if there were height differences for given diameters among treatments:

$$H = b_1 HD^{b_2} * exp\left(\frac{b_3}{A} + \left(\frac{1}{D} - \frac{1}{D_{max}}\right)\left(b_4 + b_5\left(\frac{\ln(N)}{A}\right)^{b_6}\right)\right) \qquad (1)$$

where,

H	=	individual tree height (feet),
HD	=	average height of dominants and codominants (feet),
A	=	stand age (years),
D	=	individual tree diameter (inches)
D_{max}	=	maximum tree diameter (inches) in a stand,
N	=	surviving number of trees (stems/acre), and
b_i	=	parameters to be estimated.

They found that parameter estimates from this model differed significantly among treatments indicating that thinning had significant effects on tree height growth. To account for the effect of thinning, and using equation (1) as a baseline model, the following thinning responses were evaluated:

$$T_1 = \frac{BA_a}{BA_b} \tag{2}$$

$$T_2 = \left(\frac{BA_a}{BA_b}\right)^{\left(b_1\left(\frac{A_t}{A}\right)\right)} \tag{3}$$

$$T_2 = \left(\frac{BA_a}{BA_b}\right)^{\left(\frac{b_1\left(-(A-A_t)^2+b_2(A-A_t)\right)}{A^2}\right)} \tag{4}$$

where

T_i = thinning response,

BA_a = stand basal area (square feet) after thinning,

BA_b = stand basal area (square feet) before thinning,

A_t = stand age (years) at time of thinning, and

all other variables as previously defined.

The thinning response of equation (2) is proportional to thinning intensity and is independent of time from thinning. Equations (3), originally proposed by Short III and Burkhart (1992), and (4), originally proposed by Liu et al. (1995), account for both thinning intensity and time from thinning. Also, these two response variables can describe a delay in the response due to thinning. Using Mean Square Error (MSE) as a selection criterion the authors found that including thinning response variables (equations 2-4) did not improve the precision of the base model (equation 1). They attribute this to regressors in the base model accounting for the effects of thinning on tree height growth.

Using data from the same study as Zhang et al. (1997), with additional measurements, Trincado et al. (2007) fit the following mixed effects height-diameter model to data from thinned and unthinned plots:

$$ln(H_{ki}) = b_0 + b_1 ln(d_{ki}) + a_{0k} + a_{1k} ln(d_{ki}) \quad (5)$$

where

H_{ki} = total height of tree *i* in plot *k*,

d_{ki} = diameter of tree *i* in plot *k*,

$a_{1,2}$ = random effect parameters for plot *k*, and

all other variables as previously defined.

The random effect parameters allow the model to be calibrated to individual plots, which removes the assumption that the height-diameter relationship is constant through the data. This calibration process indirectly accounted for the effects of stand density on the height-diameter relationship and therefore additional responses to thinning were unnecessary in the model.

Russell et al. (2010) incorporated variables for latitude and longitude into equation (1) with the thinning response of equation (3) to determine if geographic location could improve the accuracy of modeling height-diameter relationships. Their model has the form:

$$H = b_1 HD^{b_2} {T_2}^{b_3} * exp\left(\frac{b_4}{A} + \left(\frac{1}{D} - \frac{1}{D_{max}}\right)\left(b_5 + b_6\left(\frac{\ln(N)}{A}\right) + b_7 LAT + b_8 LONG\right)\right) \quad (6)$$

where

LAT = latitude (decimal degrees),

LONG = longitude (decimal degrees), and

all other variables as previously defined.

The parameters for LAT and LONG were significant in the model indicating that geographic coordinates can aid in predicting total tree height. The authors found similar results as Zhang et al. (1997) in that including a thinning response function did not effectively reduce the MSE of the model.

2.1.2. Diameter Increment

Amateis et al. (1989) presented an equation for predicting annual diameter growth of thinned loblolly pine plantations:

$$DIN = PDIN * b_1 CR^{b_2} * exp\left(b_3\left(1 - \frac{QMD}{ID}\right) + b_4 A_t + b_5\left(\frac{BA_a}{BA_b}\right)\right) \quad (7)$$

where

DIN = annual diameter growth (inches),

PDIN = potential diameter increment (inches),

CR = crown ratio,

QMD = quadratic mean diameter of stand (inches),

ID = initial diameter at start of growing period (inches), and

all other variables as previously defined.

Because the treatment plots were measured every three years it was assumed that annual diameter growth was the same over a three year period.

Westfall and Burkhart (2001) incorporated a thinning response variable into a diameter growth model to improve the accuracy of predicting diameter growth in thinned stands. Their model has the form:

$$DIN = PDIN * T_4 * \left(b_1 CR^{b_2} * exp(b_3 CI^{b_4})\right) \tag{8}$$

$$T_4 = \left(\frac{BA_b}{BA_a}\right)^{\frac{A-A_t}{HD^2}} * exp\left(\frac{(A-A_t)^2}{(A/A_t)^{b_1}}\right) \tag{9}$$

where

CR = $1 - exp\left((b_1 - b_2 A^{-1}) D/H\right)$,

CI = competition index from Daniels (1976), and

all other variables as previously defined.

Fit statistics were nearly identical for this model with and without the thinning response variable T_4 indicating that the effects of thinning were accounted for in the independent variables of the model and an additional response variable was not needed.

2.1.3. Mortality

Using data from a loblolly pine thinning study Amateis et al. (1989) developed the following individual tree survival equation:

$$P = b_1 CR^{b_2} * exp(b_3 DD^{b_4}) \tag{10}$$

where

P = probability of living on an annual basis

DD = ratio of QMD to diameter, and

all other variables as previously defined.

This model assumes that the probability a tree remains alive in a given year is a function of its competitive status and individual tree vigor or photosynthetic potential.

Avila and Burkhart (1992) developed the following distance-dependent and distance-independent models, respectively, to predict the probability of survival in thinned loblolly pine plantations:

$$P = 1/\left(1 + exp\left(-(b_1 + b_2 CR^{1.5} + b_3 HH + b_4 CI)\right)\right) \tag{11}$$

$$P = 1/\left(1 + exp\left(-(b_1 + b_2 CR^{1.5} + b_3 HH + b_4 DD)\right)\right) \tag{12}$$

where

HH = ratio of total tree height to stand dominant height, and

all other variables as previously defined.

Equations (11) and (12) were then compared to the distance-independent model of Amateis et al. (1989) (equation 10) and to the distance-dependent model of Burkhart et al. (1987):

$$P = b_1 CR^{b_2} * exp(-b_3 CI^{b_4}) \tag{13}$$

where,

all variables as previously defined.

Equations (11) and (12) only showed slight improvements over those of Burkhart et al. (1987) and Amateis et al. (1989).

2.1.4. Crown-Height Increment

Short III and Burkhart (1992) incorporated the thinning response variable T_2 (equation 3) into the following distance-independent and distance-dependent individual tree crown-height increment models:

$$\Delta HLC = b_1 T_2^{b_2} H^{b_3} * exp(b_4 CR^{0.5} + b_5 DD + b_6 A) \tag{14}$$

$$\Delta HLC = b_1 T_2^{b_2} H^{b_3} * exp(b_4 CR^{0.5} + b_5 CI + b_6 A) \tag{15}$$

where,

ΔHLC = annual crown-height increment,

equations (14) and (15) are distance-independent and distance-dependent, and

all other variables are as previously defined.

Because plots were measured every three years it was assumed that annual crown-height increment was the same over the three year measurement period. The authors observed that by including a thinning response variable in the crown-height increment models there was an improvement in fit statistics and predictions of independent data. Liu et al. (1995) modified equation (15) by including the thinning response variable of equation (4) in both the crown-height increment model and the CR model. They found that using this alternative thinning response variable increased the prediction accuracy of the model.

2.2. Whole Stand Models

2.2.1. Basal Area

By removing trees in thinning one of the immediate results is a reduction in basal area. Pienaar (1979) theorized that trees in thinned stands grow similar to trees in unthinned stands of the same age, site index, and number of stems per unit area. Using data from permanent plots in old field slash pine, Pienaar developed an index of suppression which relates the basal area growth of thinned stands to that of a similar unthinned stand. This index of suppression can be used to project basal area growth of thinned stands.

Bailey and Ware (1983) tested two thinning responses based on a ratio of QMD before, to removed, and to after in a basal area growth equation. The two ratios are:

$$R_t = \frac{D_t}{D_b} \tag{16}$$

$$R_a = \frac{D_a}{D_b} \tag{17}$$

where,

D_t = QMD of trees removed in thinning,

D_a = QMD of trees remaining after thinning, and

D_b = QMD of trees before thinning.

To define response to thinning with desirable properties, the authors changed the ratios R_t and R_a into indexing variables. These variables have the properties of increasing from negative to positive when thinnings change from removing larger to smaller trees and equaling zero when there is no thinning or when thinning is indifferent to diameter, such as row thinning. The indexing variables have the form:

$$X_t = \begin{cases} 1 - R_t, & if\ R_t \neq 0 \\ 0, & if\ R_t = 0 \end{cases} \tag{18}$$

$$X_a = R_a - 1 \tag{19}$$

To compare these indexing variables Bailey and Ware incorporated the basal area growth model of Clutter (1963) to include the response to thinning while at the same time retaining the properties of the model. After including the indexing variables the model has the form:

$$BA_2 = BA_1^{(A_1/A_2)} * exp\left(b_1 \frac{1-A_1}{A_2} + b_2 X \frac{\frac{1}{A_2} - \frac{1}{A_1}}{A_1 A_2} + b_3 S \frac{1-A_1}{A_2}\right) \tag{20}$$

where,

$BA_{1,2}$ = stand basal area at ages A_1 and A_2,

S = site index,

X = indexing variable X_t or X_a, and

all other variables as previously defined.

The authors found that the parameter associated with X when $X=X_a$ was not significant in the model, however, X_t was significant for slash and loblolly pine. When X_t was incorporated in the model, the model had lower prediction error for thinned stands than the base model without a thinning response variable.

Pienaar et al. (1985), expanding on the work of Pienaar (1979), determined that thinned stands can exhibit different basal area growth patterns than unthinned stands of the same age, site index, and stems per acre. After determining that separate models are needed to project growth of thinned stands they developed the following basal area growth equation that includes response to thinning intensity:

$$BA_2 = BA_1^{\left({A_1}/{A_2}\right)^{b_1+b_2\frac{N_t}{N_a}}} * exp\left(b_3\left(1-\left({A_1}/{A_2}\right)^{b_1+b_2\frac{N_t}{N_a}}\right)\right) \tag{21}$$

where,

N_t = trees per unit area removed in thinning,

N_a = trees per unit area remaining after thinning, and

all other variables as previously defined.

This model significantly decreased prediction bias as compared to a baseline model without the inclusion of a response to thinning.

Pienaar and Shiver (1986) developed a basal area prediction model that modifies the basal area of unthinned stands of a given age, dominant height, and trees per unit area to that of comparable thinned plantations. Their model has the form:

$$\ln(BA) = b_0 + b_1 \frac{1}{A} + b_2 \ln(N) + b_3 \ln(HD) + b_4 \frac{\ln(N)}{A} + b_5 \frac{\ln(HD)}{A} + b_6 \frac{N_t A_t}{N_a A} \tag{22}$$

where,

all variables as previously defined.

This equation can be used for thinned and unthinned stands because the base model is simply modified by the last term to include the effect of thinning intensity. Pienaar and Rheney (1993) modified equation (22) by using the number of trees before thinning (N_b) instead of the number of stems after thinning (N_a) in the last term of the model, although no direct comparison is given between the two models.

Hasenauer et al. (1997) recognized the effect of hardwood competition on basal area development in loblolly pine stands and included a component for hardwood competition along with a thinning response variable similar to equation (3) to model basal area growth in thinned plantations:

$$BA_{P2} = BA_{P1}^{HD_1/HD_2} * exp\left(\left(\frac{BA_{P1}}{BA_{T1}}\right)^{b_1} b_2 S^{b_3} T_5 \left(1 - \frac{HD_1}{HD_2}\right)\right) \tag{23}$$

$$T_5 = \left(\frac{BA_{Pa}}{BA_{Pb}}\right)^{b_4(HD_T/HD_2)} \tag{24}$$

where,

$BA_{p1,p2}$ = pine basal area at times 1 and 2,

BA_{T1} = total basal area (including hardwoods) at time 1,

BA_{Pa} = pine basal area after thinning,

BA_{Pb} = pine basal area before thinning,

$HD_{1,2}$ = stand dominant height at times 1 and 2,

H_T = stand dominant height at thinning, and

all other variables as previously defined.

The parameter b_4 in the thinning response variable was negative, indicating that the basal area of thinned plots converges to that of unthinned plots. The authors found that including the thinning response function increased the coefficient of determination (R^2) slightly from 0.97 to 0.98 but reduced the MSE from 2.09 to 1.42. Thus, ignoring the response to thinning could cause biased estimates of basal area projections.

To model the development of basal area growth in thinned plots of loblolly pine relative to an unthinned control, Amateis (2000) proposed the following equation:

$$BT_t - BC_t = (BA_a - BA_b) + ln\big(\alpha(A_{st} + 1)\big)\gamma A_{st}^{b_1} \tag{25}$$

where,

$$\alpha = \left(\frac{A}{10}\right)^{b_2} \left(\frac{BA_a}{10}\right)^{b_3} \left(\frac{N_b}{100}\right)^{b_4} \left(\frac{N_b - N_a}{100}\right)^{b_5} \left(\frac{N_a}{N_b}\right)^{b_6} + b_7\theta$$

$$\gamma = \left(\frac{BA_b - BA_a}{10}\right)^{b_8} \left(\frac{N_a}{100}\right)^{b_9} \left(\frac{N_a}{N_b}\right)^{b_{10}}$$

$$\theta = \begin{cases} 0, & if\ first\ thinning \\ 1, & if\ second\ thinning \end{cases}$$

BT_t = basal area of thinned stand at future age t,

BC_t = basal area of unthinned stand at future age t,

A_{st} = years since thinning, and

all other variables as previously defined.

The logarithmic portion of equation (25) models growth suppression following thinning while the power function models the increased growth of thinned stands after the suppression period. Heavier thinned plots had more growth suppression immediately after thinning which caused a longer time for basal area in these plots to converge with that of the unthinned control.

2.2.2. Mortality

Using data from plots in thinned old-field loblolly pine plantations Lemin and Burkhart (1983)compared the survival models of Clutter and Jones (1980)(Eq. 26) and Pienaar and Shiver (1981)(Eq. 27) with two proposed models that relate survival to basal area and QMD (Eq. 28) and to spacing as a percent of height (SPH) (eq. 29):

$$N_2 = \left(N_1^{b_1} + b_2\left(A_2^{b_3} - A_1^{b_3}\right)\right)^{1/b_1} \quad (26)$$

$$N_2 = N_1 * exp\left(-b_1\left(A_2^{b_2} - A_1^{b_2}\right)\right) \quad (27)$$

$$N = BA/(0.005454 * QMD) \quad (28)$$

$$N = 43560 * \left(\frac{107.4}{SPH*HD}\right)^2 \quad (29)$$

where,

$N_{1,2}$ = number of trees per acre at ages A_1 and A_2, and

all other variables as previously defined.

They found the Clutter and Jones (1980) and Pienaar and Shiver (1981) models (equations (26) and (27), respectively) behaved similarly and were relatively unbiased with R^2 values about 0.97 for both models. Equation (28) also performed well, however, equation (29) performed poorly and produced some illogical values such as predicting increasing number of stems with time in lower densities.

Bailey et al. (1985) incorporated a response to thinning, specifically the diameter ratio R_t of Bailey and Ware (1983), into the survival model of Clutter and Jones (1980). However, the formulated model did not have the property of projection path invariance where projections from ages A_1 to A_2 and then from ages A_2 to A_3 would equate to direct projections from ages A_1 to A_3. Modifying this model to preserve the path invariance property the following model was proposed:

$$N_2 = N_1 \left(\frac{A_2}{A_1}\right)^{b_1} * exp\left(b_2 S(A_2 - A_1) + \frac{b_3 X_t Z\left(A_2^{-1} - A_1^{-1}\right)}{A_t}\right) \tag{30}$$

where,

$$Z = \begin{cases} 1, & A_2 < \omega \\ 0, & A_2 \geq \omega \end{cases}$$

ω = age where thinning no longer affects survival, and

all other variables as previously defined.

Equation (30) had comparable fit statistics to equation (26) at older ages but performed better in younger ages where there was still an effect of thinning on survival.

Amateis et al. (1997) developed a survival equation for thinned loblolly pine to account for the effects of thinning by including a ratio of basal area before and after thinning and to account for hardwood competition. Their model has the form:

$$N_2 = \alpha \left(\frac{N_1}{\alpha}\right)^{exp\left(\gamma\left(A_2^{b_4} - A_1^{b_4}\right)\right)} \quad (31)$$

where,

$\alpha = b_1 \left(\frac{1 - BA_H}{BA_T}\right)^{b_2}$,

$\gamma = b_3 \left(\frac{BA_{Pa}}{BA_{pb}}\right) S \left(\frac{1 + BA_H}{BA_T}\right)^{b_2}$,

$BA_H =$ basal area of hardwoods, and

all other variables as previously defined.

Equation (31) is conditioned such that the effect of thinning is zero when there is no thinning allowing the prediction of survival in both thinned and unthinned stands. The effect of hardwood competition is also conditioned to be zero when there are no hardwoods competing with the pine overstory.

Similar to the basal area growth equation (25), Amateis (2000) also developed a survival model that relates survival of thinned plots to that of an unthinned control:

$$NT_t - NC_t = (N_a - N_b) * exp(-\alpha A_{ST}) \quad (32)$$

where,

$$\alpha = \left(\frac{S}{10}\right)^{b_1} \left(\frac{N_a}{N_b}\right)^{b_2} \left(\frac{BA_a}{10}\right)^{b_3} \left(\frac{N_b}{100}\right)^{b_4} \left(\frac{N_b - N_a}{100}\right)^{b_5}$$

NT_t = number of trees of thinned stand at future age *t*,

NC_t = number of trees of unthinned stand at future age *t*, and

all other variables as previously defined.

As the number of years since thinning increases, the number of trees for a thinned stand asymptotically approaches the number of trees for an unthinned stand. This convergence occurs sooner in lighter thinnings and higher site indices.

2.2.3. Whole-Stand Volume

Burkhart and Sprinz (1984) used the volume prediction model of Sullivan and Clutter (1972) to model volume growth in old-field loblolly pine plantations:

$$ln(V) = b_0 + b_1 S + \frac{b_2}{A_2} + b_3 \left(\frac{A_1}{A_2}\right) \ln(b_1) + b_4 \left(\frac{1-A_1}{A_2}\right) + b_5 S \left(\frac{1-A_1}{A_2}\right) \quad (33)$$

where,

V = stand volume per unit area, and

all other variables as previously defined.

The model is conditioned such that when A_1=A_2 the projection period is zero years allowing for predictions at an initial or future time.

Pienaar and Rheney (1993) proposed the following volume prediction and projection equations for thinned plantations of slash pine:

$$\ln(V) = b_0 + b_1\left(\frac{\ln(HD)}{A}\right) + b_2\ln(N) + b_3\ln(B) \tag{34}$$

$$\ln(V_2) = \ln(V_1) + b_1\left(\frac{\ln(HD_2)}{A_2} - \frac{\ln(HD_1)}{A_1}\right) + b_2(\ln(N_2) - \ln(N_1))$$
$$+b_3(\ln(BA_2) - \ln(BA_1)) \tag{35}$$

where,

$V_{1,2}$ = stand volume at ages A_1 and A_2 and

all other variables as previously defined.

2.3. Changes in Stand Dynamics

Many changes are exhibited in stands that have been subjected to thinning. Most notably are changes in number of stems per unit area, basal area, and standing volume. Immediately following thinning the residual trees have more light and nutrients available and thus changes in growth can be expected, though the nature of the changes in growth can vary depending on shade tolerance, age, and type and intensity of thinning.

Utilizing data from a spacing trial and unthinned control plots from a fertilization study in Douglas-fir plantations, Harrington and Reukema (1983) found that immediately following thinning height growth was significantly reduced. After 10 years height growth was similar in thinned and control plots indicating that the negative effect was no longer a factor. Improved growth in thinned plots was then sufficient in overcoming the effect of thinning and projections indicated that total height in thinned plots would be greater than that of unthinned plots. Diameter growth was increased immediately following thinning and the magnitude of the response increased with wider spacings. There was a sharp increase in basal area and volume growth after thinning, however, the increased growth rates were not sufficient in overcoming the reduction in total plot basal area and volume due to thinning.

Baldwin et al. (1989) analyzed data from a thinning study in loblolly and slash pine plantations in Louisiana. They observed that mean heights between thinned and unthinned plots were not different following thinning, but 10 years after thinning mean heights were greater for thinned plots of loblolly pine. Also, 10 years after treatment basal area and volume growth rates were higher in thinned plots, however, net basal area and volume were higher in unthinned plots.

In a thinning study of red alder, Hibbs et al. (1989) found that height growth was reduced by as much as 56% in thinned plots as compared to unthinned plots and diameter growth increased by 100%. Because of the reduction in height, on thinned plots, volume growth was similar between thinned and unthinned plots.

Ginn et al. (1991) evaluated growth responses of loblolly pine thinned at age eight in southwest Virginia. After the first growing season following thinning, thinned plots exhibited a decrease in height growth and an increase in live crown diameter as compared to unthinned plots. At the end of the second growing season trees in thinned plots had an increase in live crown diameter and tended to decrease less in live crown ratio. In the second growing season diameter growth was increased and as a result basal area growth. Unthinned plots had more basal area after 2 growing seasons; however, basal area growth in thinned plots was 82% of the basal area growth in unthinned plots. Continuing the study, Peterson et al. (1997) found that after the first growing season thinning had no effect on height growth or on cumulative height. Even though diameter growth increased after thinning, significant differences in diameters were not exhibited between thinned and unthinned plots until after the fourth growing season. By the sixth growing season live crown ratios decreased by 30% in unthinned plots as compared to a decrease of 14% in thinned plots. The authors attribute the slower rate of decrease in thinned stands to the higher survival rate of lower branches and not to an increase in height growth. Additionally live crown diameters increased 82% and 20% for thinned and unthinned plots, respectively.

Using data from a loblolly pine thinning study Sharma et al. (2006) found that heights in heavily thinned plots (50% basal area removed) were significantly smaller than in unthinned plots three years after treatment. By the sixth year after treatment heavily thinned plots were not significantly different in height from unthinned plots and eighteen years after treatment heights of heavily thinned plots were significantly larger than those in their unthinned counterpart. Lightly thinned plots (30% basal area removed) were not significantly different in height from heavily thinned or unthinned plots throughout the duration of the study.

By reviewing these studies a pattern seems to emerge among the changes in stand dynamics due to thinning. There is generally a decrease in height growth due to thinning. Ginn et al. (1991) attributed the decrease in height growth to trees allocating growth to expansion of the lower crown diameter. In comparison to other studies this seems a reasonable explanation as height growth rates generally increase several years after thinning and dominant heights of thinned plots eventually approach or exceed those of unthinned plots. Due to increased growing space individual tree diameter growth rates tend to increase for several years after thinning. Changes to height and diameter growth from thinning have a direct effect on volume growth of a stand and the effects of thinning should be incorporated into growth and yield models to accurately reflect these changes in growth.

Literature cited

Amateis, R.L. 2000. Modeling response to thinning in loblolly pine plantations. Southern Journal of Applied Forestry 24(1):17-22.

Amateis, R.L., H.E. Burkhart, and J. Liu. 1997. Modeling survival in juvenile and mature loblolly pine plantations. Forest Ecology and Management 90(1):51-58.

Amateis, R.L., H.E. Burkhart, and T.A. Walsh. 1989. Diameter increment and survival equations for loblolly pine trees growing in thinned and unthinned plantations on cutover, site-prepared lands. Southern Journal of Applied Forestry 13(4):170-174.

Avila, O.B., and H.E. Burkhart. 1992. Modeling survival of loblolly pine trees in thinned and unthinned plantations. Canadian Journal of Forest Research 22(12):1878-1882.

Bailey, R.L., B.E. Borders, K.D. Ware, and E.P. Jones. 1985. A compatible model relating slash pine plantation survival to density, age, site Index, and type and intensity of thinning. Forest Science 31(1):180-189.

Bailey, R.L., and K.D. Ware. 1983. Compatible basal-area growth and yield model for thinned and unthinned stands. Canadian Journal of Forest Research 13(4):563-571.

Baldwin, J., V. C., D.P. Feduccia, and J.D. Haywood. 1989. Postthinning growth and yield of row-thinned and selectively thinned loblolly and slash pine plantations. Canadian Journal of Forest Research 19(2):247-256.

Burkhart, H.E., K.D. Farrar, R.L. Amateis, and R.F. Daniels. 1987. Simulation of individual tree growth and stand developement in loblolly pine plantations on cutover, site-prepared areas. FWS-1-87 Virginia Polytechnic Institute and State University, School of Forestry and Wildlife Resources.

Burkhart, H.E., and P.T. Sprinz. 1984. Compatible cubic volume and basal area projection equations for thinned old-field loblolly pine plantations. Forest Science 30(1):86-93.

Clutter, J.L. 1963. Compatible growth and yield models for loblolly pine. Forest Science 9(3):354-371.

Clutter, J.L., and E.P. Jones. 1980. Prediction of growth after thinning of old-field slash pine plantations. USDA Forest Serv Res Pap SE-217, 19 p. Southeast Forest Exp Stn, Asheville, NC.

Ginn, S.E., J.R. Seiler, B.H. Cazell, and R.E. Kreh. 1991. Physiological and growth responses of eight-year-old loblolly pine stands to thinning. Forest Science 37(4):1030-1040.

Harrington, C.A., and D.L. Reukema. 1983. Initial shock and long-term stand development following thinning in a Douglas-fir plantation. Forest Science 29(1):33-46.

Hasenauer, H., H.E. Burkhart, and R.L. Amateis. 1997. Basal area development in thinned and unthinned loblolly pine plantations. Canadian Journal of Forest Research 27(2):265-271.

Hibbs, D.E., W.H. Emmingham, and M.C. Bondi. 1989. Thinning red alder: Effects of method and spacing. Forest Science 35(1):16-29.

Lemin, R.C., and H.E. Burkhart. 1983. Predicting mortality after thinning in old-field loblolly pine plantations. Southern Journal of Applied Forestry 7(1):20-23.

Liu, J., H.E. Burkhart, and R.L. Amateis. 1995. Projecting crown measures for loblolly pine trees using a generalized thinning response function. Forest Science 41(1):43-53.

Peterson, J.A., J.R. Seiler, J. Nowak, S.E. Ginn, and R.E. Kreh. 1997. Growth and physiological responses of young loblolly pine stands to thinning. Forest Science 43(4):529-534.

Pienaar, L.V. 1979. An approximation of basal area growth after thinning based on growth in unthinned plantations. Forest Science 25(2):223-232.

Pienaar, L.V., and J.W. Rheney. 1993. Yield prediction for mechanically site-prepared slash pine plantations in the southeastern coastal plain. Southern Journal of Applied Forestry 17(4):163-173.

Pienaar, L.V., and B.D. Shiver. 1981. Survival functions for site-prepared slash pine plantations in the flatwoods of georgia and northern florida. Southern Journal of Applied Forestry 5(2):59-62.

Pienaar, L.V., and B.D. Shiver. 1986. Basal area prediction and projection equations for pine plantations. Forest Science 32(3):626-633.

Pienaar, L.V., B.D. Shiver, and G.E. Grider. 1985. Predicting basal area growth in thinned slash pine plantations. Forest Science 31(3):731-741.

Russell, M.B., R.L. Amateis, and H.E. Burkhart. 2010. Implementing regional locale and thinning response in the loblolly pine height-diameter relationship. Southern Journal of Applied Forestry 34(1):21-27.

Sharma, M., M. Smith, H.E. Burkhart, and R.L. Amateis. 2006. Modeling the impact of thinning on height development of dominant and codominant loblolly pine trees. Annals of Forest Science 63(4):349-354.

Short III, E.A., and H.E. Burkhart. 1992. Predicting crown-height increment for thinned and unthinned loblolly pine plantations. Forest Science 38(3):594-610.

Sullivan, A.D., and J.L. Clutter. 1972. A simultaneous growth and yield model for loblolly pine. Forest Science 18(1):76-86.

Trincado, G., C.L. VanderSchaaf, and H.E. Burkhart. 2007. Regional mixed-effects height–diameter models for loblolly pine (Pinus taeda L.) plantations. Eur J Forest Res 126(2):253-262.

Westfall, J.A., and H.E. Burkhart. 2001. Incorporating thinning response into a loblolly pine stand simulator. Southern Journal of Applied Forestry 25(4):159-164.

Zhang, S., H.E. Burkhart, and R.L. Amateis. 1997. The influence of thinning on tree height and diameter relationships in loblolly pine plantations. Southern Journal of Applied Forestry 21(4):199-205.

Chapter 3: The Relationship between Volume Production and Stand Density in Loblolly Pine Plantations

3.1. Abstract

The relationship between volume production and stand density has received much attention and yet no conclusive evidence on a general pattern has been established. Contradictory conclusions on the growth-density relationship have been attributed to the diverse range of definitions of growth and stand density. Using data from multiple growth and yield studies a comprehensive analysis of the growth-density relationship in loblolly pine was performed. A combination power and exponential type model was used to test the hypothesis that volume production followed either an increasing or unimodal pattern with stand density. Patterns were compared between six measures of volume production, including gross and net periodic annual increment of total, pulpwood, and sawtimber volume, in relation to seven measures of stand density. Results indicated that stand density measures basal area per hectare and relative spacing which uses diameter as a measure of average tree size were more correlated with volume production. Based on these measures the results of the hypotheses tests indicated that an increasing pattern held for thinned and unthinned non-intensively managed plantations, regardless of the definitions of volume production. Alternatively, in intensively managed plantations an increasing or a unimodal pattern generally held for thinned and unthinned stands, respectively.

3.2. Introduction

Advancements of forest management tools in the past century have led to large improvements in growth and yield of plantation forest throughout the world. Research in herbicide and fertilizer applications offer increased production, new machinery and planting techniques ensure increased survival rates, and genetically enhanced seedlings are developed to be resistant to diseases and to offer increased growth rates. Yet after these many advancements the oldest and most commonly used forest management tool is the control of stand density. Management guides detailing thinning regimes and schedules can be found readily throughout the literature but, surprisingly, finding a definitive relationship between growth and density can be difficult.

Since the beginnings of forestry, forest managers have searched for a stand density in which volume production is maximized (Zeide 2004). Early beliefs were that undisturbed stands produced the highest maximum yields and that any decrease in the number of trees would result in a loss of volume growth (Zeide 2001). These beliefs were challenged in the late 18^{th} century most notably by one of the first “fathers of modern forestry” George Ludwig Hartig. Hartig (1795) advocated for the removal of dead and dying trees, when they could be sold profitably, in order to follow and support nature in its effects. Reventlow (1879) considered this view of thinning as too light and was convinced of an unimodal relationship whereby volume production is maximized when the number of trees is less than what is carried naturally in a stand. In contrast, Langsaeter (1941) hypothesized that cubic-volume production was constant and optimal across a wide range of density of stocking for a stand of a given age and composition on a given site. Under this hypothesis volume production can be decreased but not increased by altering levels of growing stock outside of this range. This pattern between volume production and stand density is often called the ‘Langsaeter Hypothesis’ and has been confirmed in many countries vary various species (Zeide 2001).

More recently, in an experiment designed to examine the effects of thinning on Douglas-fir stands, Curtis et al. (1997) determined that the assumption of constant gross total cubic-volume production across a wide range of stocking levels is incorrect. Contradictory to the Langsaeter Hypothesis, cubic-volume production increased with numbers of stems per acre, though at a decreasing rate. Comparing the findings of Curtis et al. (1997) to the stagnation of lodgepole pine at unusually high densities, Zeide (2001) suggests that volume production must culminate but at a higher density than is commonly observed and that the increasing pattern is simply the left portion of the entire relationship. In an evaluation of the growth-density relationship in Norway spruce and European beech stands Pretzsch (2005) determined the optimal density where periodic annual increment of merchantable volume is maximized, based on a standardized stand density index (SSDI). This SSDI relates Reineke's stand density index (SDI) of stands with moderate and heavy thinnings to a control stand where only dead, dying, and unsound trees were removed. In general a unimodal growth-density pattern occurred, but in some instances only an increasing or culminating portion of the curve was observed.

The growth-density relationship in loblolly pine has been reported in several studies, though no conclusive evidence of a general pattern has been found (Trincado et al. 2004). McClay (1955) studied the relationship between periodic annual growth per acre and residual stand density, measured as basal area, after thinning. Using linear regression analysis he discovered a trend of increasing growth with increasing residual stand density up to a point where growth was maximized. Because of a lack of data in high density stands he was unable to determine if growth declined beyond this point. Wenger et al. (1958) studied the effect of growing-space requirements for thinned and unthinned stands of natural loblolly pine for a period of 5 years after thinning treatments. The relationship between volume growth and density varied with site quality but not with stand age in thinned stands; however, both variables were significant for unthinned stands. Using the 5-year period (5-10 years after thinning treatments) following Wenger et al. (1958), Nelson and Brender (1963) discovered no differences in volume increment between thinned and unthinned conditions. Using regression analysis they found that production in thinned stands increased with stand density on better sites and reached an optimum on poor sites. Trincado et al. (2004) used a long-term thinning study in loblolly pine to determine the relationship between periodic annual increment (PAI) and density, measured as basal area. Their analysis indicated gross PAI in total volume and basal area for all site index classes follows an increasing pattern and in general net PAI in total volume follows a unimodal pattern. Zeide (2004) developed a theoretical model for determining the stand density index (Reineke 1933) where total net volume PAI is maximized. He concluded that volume production is maximized at the very edge of maximum SDI reversing the conclusions of Trincado et al. (2004).

One reason for contradictory results on the growth-density relationship in the literature is because the terms “growth” and “density” vary. For instance, Zeide (2004) related gross total volume increment to stand density index while Pretzsch (2005) related a standardized merchantable volume increment to a standardized stand density index. Aside from the differences in approaches used to describe the relationship between volume productions and stand density, the difference in conclusions between these two studies may be simply due to different definitions of volume production and density. There has yet to be a study that determines if different relationships between growth and density exists among different measures of growth and density.

The purpose of the research presented in this work was to comprehensively examine the relationship between periodic annual cubic-volume production and stand density in loblolly pine. The first objective was to determine if different relationships between volume production and stand density exists. Seven measures of stand density were chosen for comparison, including the number of stems per hectare, basal area per hectare, two measures of relative spacing that use either mean tree diameter or height as a measure of average tree size, and three measures of stand density index that use either mean tree diameter, height, or volume as a measure of average tree size. Additionally, several measures of volume production were chosen for comparison, including total volume and merchantable volume based on two commonly used merchantability specifications. Volume production was further defined as either gross production, which includes mortality, or net production, which excludes mortality. In order to avoid confounding of model type a similar equation form was used to test the hypothesis that volume production follows either an increasing or unimodal pattern with stand density. A secondary objective was to examine the effects of management to determine if different relationships between growth and density can occur depending on different management strategies. Several studies in loblolly pine that cover a range of management strategies including thinned or un-thinned, non-intensively and intensively managed plantations were used to test the hypotheses on the relationship between growth and density.

3.3. Data

Data used for this work came from two observational growth and yield studies, a spacing trial maintained by the Forest Modeling Research Cooperative (FMRC) at Virginia Polytechnic Institute and State University, and an additional experimental study installed jointly by the Forest

Productivity Cooperative and the FMRC. The first observational study was a region wide thinning study established in nonintensively managed plantations (NIMPs) with 186 initial permanent plot locations throughout the piedmont and Atlantic coastal plain regions of the southern United States (Burkhart et al. 1985). The study was established in the dormant seasons of 1980-1982 in plantations that ranged in age from 8 to 25 years. The NIMPs were characterized by cutover site-prepared lands, non-genetically improved planting stock, and no intermediate fertilization or competition control treatments. Each installation consisted of one unthinned control plot and two plots with thinning treatments. Plots were located to minimize differences in site quality and stand density prior to treatment. Thinning treatments included a light thinning removing approximately one-third of the basal area and a heavy thinning removing about one-half of the basal area with all thinnings from below. For each planted pine the following data were measured: dbh, total height, height to the base of live crown, and stem quality. Plots were remeasured at three years intervals for a 21-year period after establishment. Second thinnings were imposed at the fourth remeasurement on selected plots. By the end of the study, a total of eight measurements (including initial measurement) had been collected.

The second study was established in intensively managed plantations (IMPs) across the natural range of loblolly pine (Amateis et al. 2006). Permanent plots were installed at 170 locations during the dormant seasons of 1996-2000 in plantations with an initial age range from 3 to 8 years. Each installation consisted of one unthinned control plot and two plots with thinning treatments. A heavily thinned plot was also pruned, removing dead branches only. These plots are representative of contemporary silviculture of loblolly pine. Common management strategies of these plots include site-preparation, planting genetically improved stock, and applying fertilizer and competition control as needed. Each plot was measured at establishment and subsequently on a 2-year cycle. In contrast to the first thinning study that was designed to initiate thinning at a range of ages (8 to 25), this IMP study used a stand dominant height of approximately 13.7 meters (45 feet) as the point at which thinning was imposed. Thus, a common point in stand development was used, with age at the time of thinning being dependent on site quality.

The third set of data came from a spacing study established by the FMRC (Amateis and Burkhart 2012). The study design was nonsystematic, allowing the spacing to be varied in two dimensions on a factorial basis with a constant number of trees per plot. Data were available from four locations, two in the Coastal Plain (Cl and C2) and two in the Piedmont (Pl and P2) physiographic regions. At each location three replicates (blocks) were planted, and, in each replicate, 16 plots were planted allowing initial tree spacing to vary in all combinations of 1.2, 1.8, 2.4, and 3.6 meters. This design offered nine different initial tree spacings. Trees were measured annually for diameter and height until age 10 and annually for diameter and biannually for height thereafter. Diameter was measured at ground level from age 1 to age 5 and at breast height (4.5 ft, 1.37 m) from age 5 to age 25. Competing vegetation was chemically controlled up to age 3. Several plots were damaged at different ages by southern pine beetle attacks, ice storms, or anthropogenic factors. A severe ice storm heavily damaged the plots at Pl at age 11; data from those plots after the ice storm were notused. One of the plots at location P2, spacing 4.46 m^2 /tree (1.8X2.4 m), was abandoned at age 12 because of a southern pine beetle outbreak, and at age 19 the whole location was discarded because of thinning in the adjacent stand. At location C2 an ice storm after growing season 15 resulted in broken tops, which affected height. Data for age 16 were not used at that location for any analyses.

The final study was established jointly with the Forest Modeling Research Cooperative and the Forest Productivity Cooperative at Virginia Tech. This study was designed to examine the interaction of stand density and fertilization. Eight installations were established in the southern United States with each installation either a split-plot or randomized complete block design. Thinning treatments included four plots thinned to either 1235, 741, 494, or 247 stems per hectare. Fertilization treatments included a non-treatment control for each thinning treatment and a one-time fertilization of 224 kg/ha N + 28 kg/ha P at the time of installation for each thinning treatment (5 plots). At each installation these treatments were replicated four times. Planted trees were measured annually for diameter and either annually or biannually for total height. As this study was established over several years each installation had between one and five measurements.

The data were organized into six different subsets of data which represent a range of operational plantations in the southern United States. The first study which is representative of non-intensively managed pine plantations was separated into datasets of unthinned plots (NIMP) and once thinned plots (NIMP1t). The second study represents intensively managed pine plantations and was separated into datasets of unthinned plots (IMP) and once thinned plots (IMP1t). The third study which examines a range of thinning treatments was reduced to a dataset of only thinned plots (RW19) as only one measurement before thinning was available, and finally the spacing trial (Spacing Study). In all thinning datasets the measurement immediately after thinning was used as the beginning value of the growth period. Descriptive statistics for each of the six datasets are presented in Table 3.1.

3.3. Methods

3.3.1. Defining Density and Volume Production

The first objective of this research was to examine the relationship between density and growth. Within this work seven measures of density were compared to determine which were more highly correlated with growth. These seven measures were chosen for comparison based on their common use in forest management. The first definition chosen was the number of stems per hectare (SPH) which can be formulated as:

1) $SPH = k\sum_{i=1}^{n} 1_i$

where k is a constant used to convert to a per hectare basis, *n* is the total number of trees in each research plot, and *i* represents each individual tree in the plot. The value of *k* depends on the plot size and varies among studies.

The second measure of density used was basal area per hectare. Basal area is commonly used as a decision tool for determining the need for intermediate thinnings and can serve as a base for which to form thinning guidelines. Basal area per hectare (BPH) can be formulated as:

2) $BPH = g\sum_{i=1}^{n}(B_i)$

where *g* is a constant used to convert to a per hectare basis, B_i is the basal area (m^2) of the *i*th tree, and all other variables are defined as before. As in the previous measure, the constant *g* depends on the area of the research plot.

The third and fourth measures of density used in this work were relative spacing based on average diameter (RSD) and average height (RSH). These measures can be formulated as:

3) $RSD = \bar{d}_q / \sqrt{10{,}000/SPH}$

4) $RSH = \bar{H}_d / \sqrt{10{,}000/SPH}$

where $\bar{d}_q$ is quadratic mean diameter (m) and $\bar{H}_d$ is the average height (m) of all undamaged trees greater than $\bar{d}_q$. Measures (3) and (4) are normally presented with average diameter and average height in the denominator. As a result, when related to volume growth, the values of PAI become larger as the values of relative spacing becomes smaller. This relationship is opposite that of the other measures of density compared in this work. In order to compare all measures of density in a similar manner these measures were computed with average diameter and average height in the numerator. This results in increasing values of PAI with increasing values of relative spacing, a pattern similar to the other measures of density.

RSH is interesting because instead of being dependent on diameter it is dependent on height. As average dominant stand height is commonly used as a measure of stand productivity (i.e. site index) having a measure of density based on height rather than diameter could be useful in making management decisions. Measures (3) and (4) apply a common formulation to produce a unitless index based on two different measures of tree size, diameter and height.

The final three measures of density are based on the Stand Density Index (SDI) of Reineke (1933). The original formulation of Reineke's index is based on the relationship between number of trees per unit area and quadratic mean diameter, although, other measures of average tree size can be used. This study includes stand density index based on average diameter (SDID), average height (SDIH), and average total tree volume (SDIV). In this work SDI was calculated as in Burkhart (2013) and can be formulated as:

5) $SDID = SPH\left(25/\bar{d}_q\right)^{-1.43089}$

6) $SDIH = SPH(30/\bar{H}_d)^{-1.42324}$

7) $SDID = SPH(0.65/\bar{v})^{-0.48895}$

where $\bar{d}_q$ is quadratic mean diameter (cm), $\bar{v}$ is mean tree volume (m^3), and all other variables are defined as before. Measures (5), (6), and (7) are based on a common framework but are indexed at $\bar{d}_q$ of 25 cm, $\bar{H}_d$ of 30 m, or $\bar{v}$ of 0.65 m^3.

Stand volume growth was defined as the periodic annual increment (PAI) based on: Gross productivity – standing volume + volume removed in thinning + volume of mortality; and Net productivity – standing volume + volume removed in thinning. Mortality volume was estimated as the volume of dead trees at the beginning of each growing period. Additionally, gross and net PAI were calculated for both total and merchantable volume which were determined using the volume equations developed by Tasissa et al. (1997). They found that different coefficients were needed for thinned and unthinned stands. Therefore, total tree volumes for trees in unthinned (V_u) and thinned (V_t) plots were calculated as:

8) $V_u = 0.21949 + 0.00238D^2H$

9) $V_t = 0.25663 + 0.00239D^2H$

where D is tree diameter at breast height (in) and H is total tree height (ft). Additionally, using the volume ratio equations of Tasissa et al. (1997), merchantable volumes were calculated for unthinned (MV_u) and thinned (MV_t) plots as:

10) $MV_u = V_u exp\left(-0.78579 * (d^{4.9206}/D^{4.55878})\right)$

11) $MV_t = V_t exp\left(-1.04007 * (d^{5.25569}/D^{4.99639})\right)$

where *d* is the upper stem diameter limit and all other variables are defined as before. As these equation were fit using English units, total and merchantable tree volumes were calculated in cubic feet and then converted to cubic meters. When calculating merchantable volumes an upper stem diameter limit must be specified. For the purposes of this work two common merchantability specifications were used when considering merchantable volume. Any tree in the 13 cm (5 inch) diameter class or larger was considered pulpwood with an upper diameter limit of 7.6 cm (3 in). All trees in the 20 cm (8 inch) diameter class and greater were considered sawtimber with an upper diameter limit of 15.2 cm (6 in).

3.4.2. Determining the Relationship between Volume Production and Stand Density

In order to examine the relationship between volume growth and stand density a regression analysis approach was used. Preliminary analysis suggested that the relationship between density and growth is either an increasing or unimodal pattern. An increasing pattern indicates that as density increases growth increases. An unimodal pattern indicates that there is a level of density where volume production is maximized. To test if the data empirically support these relationships a generalized exponential and power function was chosen. This function has the flexibility of modeling both increasing and unimodal patterns and thus a hypothesis test can be performed based on the significance of the parameters. The function used to test the hypothesis has the form:

12) $PAI = \alpha_0 Den^{\alpha_1} exp^{\alpha_2 Den}$

where *Den* is a measure of density; α_0, α_1, and $\alpha_2$are parameters to be estimated; and all other variables are defined as before. Using equation (12) the following hypothesis was tested for both gross and net PAI for total and merchantable volumes:

H_0: an “optimum” relationship exists between PAI and stand density, and

H_1: an “increasing” relationship exists between PAI and stand density.

If parameter α_2 is significantly negative (at the 0.05 level of significance) in equation (12) then the test fails to reject the null hypothesis and it can be concluded that there is evidence for a unimodal pattern between volume production and density. If parameter α_2 is not significant or significantly positive then the test rejects the null hypothesis suggesting an increasing pattern is present. Equation 12 was fit in R, using nonlinear least squares regression, to each of the seven datasets using each of the seven definitions of density for gross and net total and merchantable PAI. The coefficient of determination (R^2) was used to calculate the variation in volume production as explained by the seven different measures of density. Thus, within each dataset the measure of density that explained the most variation in volume production would be considered the "best" measure of stand density for determining the pattern. In addition to R^2, Akeike's Information Criterion (AIC) was used to compare the fit of equation (12) to each measure of stand density. AIC is a measure of the quality of a statistical model relative to other models for a given set of data and is often used for model selection. Since the only thing changing in equation (12) from each fit is the definition of density, AIC can be used as a comparison among density measures.

In the case that all parameter are significant in the model, the stand density where PAI is maximized (Dens*) can be found by calculating the first derivative of equation (12) with respect to Dens ($\partial PAI/\partial Dens$), setting equal to zero, and solving for Dens:

13) $Dens^* = -\frac{\alpha_1}{a_2}$.

3.5. Results and Discussion

In order to test the hypothesis of an increasing or unimodal pattern within each dataset and for all combinations of volume production and stand density, the parameter estimates and p-values were obtained in R from each fit of equation 12. Additionally, the data were plotted with the inclusion of a regression line from the fits of equation 12 in order to visually assess the general relationship between growth and density. Only figures that contributed to the discussion were included at the end of this chapter.

3.5.1. Testing a Hypothesis on the Relationship between Total Volume Production and Stand Density in Unthinned Stands

3.5.1.1. Total volume production in unthinned stands

Decisions regarding the hypotheses tests were made based on the approximate p-values for parameter α_2 which are presented in Table 3.2 for the NIMP, IMP, and Spacing Study datasets which are from unthinned stands. The results of the hypothesis test indicated that there were no differences between the conclusions of either a unimodal or increasing pattern between total gross volume PAI and total net volume PAI. However, different conclusions resulted among the seven measures of stand density depending on the dataset.

When related to the numbers of SPH, total volume PAI exhibited an increasing pattern in the NIMP and Spacing Study data and a unimodal pattern was indicated in the IMP data (Table 3.2). However, the approximate p-values from the fit of equation (12) to the IMP data was close to the 0.05 cutoff (0.044 and 0.041 for gross and net PAI, respectively). Plotting the data showed that total volume PAI was highly variable across the range of numbers of SPH in all three unthinned datasets (Figure 3.1). The relationship between total volume PAI and SPH within the Spacing Study data, which included a much larger maximum range of SPH, suggests that the unimodal pattern exhibited within the IMP data may due to a lack of observations at larger numbers of SPH. The NIMP data showed that when SPH approaches zero total volume PAI decreases, which is expected. However, the difference between the average volume production at

2000 SPH and 6700 SPH within the Spacing Study data was about 1 m^2/ha/year, indicating a very slight gain in production with increasing numbers of SPH (Table 3.2).

According to Langsaeter's hypothesis, volume production is constant and optimal across a wide range of stocking and any increase or decrease in stocking outside of this range results in reduced volume production. A decrease in volume production at low levels of stocking seems reasonable as the number of SPH can become such that the site is not fully occupied. Although, in the absence of data more extreme than the maximum range of SPH in the spacing study it is difficult to determine empirically if volume production does indeed decrease at higher levels of stocking as hypothesized by Langsaeter. Maximum-size density relationships show that as the number of trees carried on a given site increases then the average diameter must decrease. Due to competition induced mortality stands of loblolly pine will begin self-thinning, reducing the numbers of trees before the point of stagnated growth that is commonly seen in ponderosa pine. Therefore, in order for a given site to carry an excessive amount of trees the average diameter must be small enough that competition induced mortality has not occurred. From known height-diameter relationships in loblolly pine, trees of small diameters in general have smaller heights. Since individual tree volume is generally estimated from diameter at breast height (1.3 meters) it seems reasonable to assume that for a given stand there is a point where the relationship between SPH and average tree size results in tree heights less than 1.3 meters. When considering volume production as purely a function of the numbers of SPH, there should be a point where total volume production begins to decrease and eventually becomes zero. So by reasoning, Langsaeter's hypothesis would hold true for loblolly pine in total volume production. However, comparing the NIMP and IMP data to the Spacing Study data suggests that the maximum range of commonly planted densities in operational plantations is not large enough to exhibit any decline.

Relating total volume PAI to the three stand density measures that use diameter as a measure of average tree size (BPH, RSD, and SDID) resulted in conclusions of increasing patterns within the NIMP and IMP data and a unimodal pattern within the Spacing Study data. Unlike the numbers of SPH, due to maximum size-density relationships, stand density measures that use diameter as a measure of average tree size have maximum values that can be quantified. For loblolly pine the commonly accepted maximum value of SDID is taken to be 1110 (450 in English Units) which directly relates to a BPH of 57 m^2 or a RSD value around 8.3 (Reineke 1933). The maximum density that a site can carry is generally termed carrying capacity, although, stands have been observed to cross this threshold before self-thinning begins. For example, the calculated values of SDID in the spacing study data included values greater than 1110, which is larger than the theoretical maximum as defined by Reineke (1933). A visual inspection of the data showed that value of -1.43 used to calculate SDID in equation (5) resulted in some plots crossing the maximum size-density boundary line. Refitting the equation of Reineke (1933) to these data resulted in an estimated slope of -2.3. If this value is used in place of -1.43 then all SDID values are less than the theoretical maximum of 1110. However, the value has been shown to change depending on site conditions, management, and planting density and published values range from -1.03 to -2.2 (VanderSchaaf and Burkhart 2007). Because one objective of this work was to compare stand density measures, the value of -1.43 was used for all analysis to avoid confounding in the calculation of SDID.

Plotting the relationship between total volume PAI and BPH across all three datasets of unthinned stands indicated that both increasing and unimodal patterns can be exhibited in loblolly pine, depending on the management (Figure 3.2). Within the Spacing Study data, total gross volume PAI was maximized around 37 m^2/ha, however, there appeared to be little difference in the average total gross volume PAI from 25 m^2/ha to 60 m^2/ha (Table 3.3). Fitting a simple linear regression model to a subset of the Spacing Study data that included only BPH values greater than 25 m^2/ha resulted in a slope not significantly different from zero. Much like SPH, it appears that volume production can be constant and optimal across a wide range of values of BPH. Further inspection of the data indicated that all planting densities in the Spacing Study data had reached crown closure by a BPH of 25 m^2/ha. Collectively, these results suggests that total gross volume production is maximized soon after crown closure and after which remains constant up to densities approaching carrying capacity.

The increasing pattern between total gross volume PAI and BPH exhibited within the IMP data could be due to the limited maximum range in BPH. A visual inspection of the fit of equation (12) to the IMP data indicates that volume production is increasing at a decreasing rate after a BPH of 25 m^2/ha (Figure 3.2). This suggests the total volume PAI is approaching an asymptote, however, the maximum BPH in the IMP data was only 45 m^2/ha. It is possible that with additional measurements the unimodal relationships observed in the Spacing Study data may also be observed in the IMP data. The NIMP data did not incur the same limitations and had observations up to maximum density. However, due to a heavy amount of competition from hardwoods that occurred in the NIMP data, total volume PAI of the planted pines was decreased below the site potential at medium densities. This resulted in the concluded increasing pattern as total volume PAI could only increase with increasing BPH of the planted pines.

After stands enter the competition-induced stage of mortality where photosynthesis cannot satisfy the respiration demands, self-thinning will occur resulting in a broken canopy and a decrease in total net volume production (Oliver and Larson 1996). Because of the large range in planting densities in the Spacing Study data, the rate of mortality and size of the gaps in the canopy after a wave of mortality resulted in a large variation in total net PAI after crown closure. Again, fitting a simple linear regression model to a subset of the Spacing Study data that included only BPH values greater than 25 m^2/ha resulted in a significantly negative slope. Collectively, these results indicate that as the amount of BPH increases after crown closure, the gaps in the canopy due to mortality become larger resulting in the average total volume production of the standing trees decreasing up to the maximum BPH that can be carried in loblolly pine. Different results were observed for total net PAI in the NIMP and IMP data. Due to a low amount of competition and the restricted range in BPH total gross and net volume PAI followed a similar path with increasing BPH in the IMP data. Similar to the Spacing Study data, the regression lines from the fits of equation (12) to total gross and net volume PAI within the NIMP data began to diverge around a BPH of 25 m^2/ha (Figure 3.2). Again, due to heavy competition total net volume PAI exhibited an increasing pattern with increasing BPH. However, at the maximum range of BPH both the average total gross volume PAI and total net volume PAI were similar between the NIMP and Spacing Study datasets. This provides further evidence that the increasing pattern exhibited in the NIMP data is due to heavy competition.

When related to stand density measures RSH, SDIH, and SDIV the same patterns were concluded as in BPH RSD and SDID within the NIMP and Spacing Study data (increasing and unimodal, respectively). Alternatively, within the IMP data unimodal patterns were concluded in stand density measures RSH, SDIH, and SDIV. One explanation for unimodal patterns occurring in the stand density measures that use or include height as a measure of average tree size is the increased growth rates from intensive management. Larger total volume PAIs where observed in the IMP data, relative to the NIMP data, with means of 15 and 23 m^3/ha/y and maximums of 33 and 47 m^3/ha/y for the NIMP and IMP data, respectively. This could indicate that intensive management can increase site quality to that point that stand density measures based on height (RSH and SDIH) or include height (SDIH), as a measure of average tree size, have the ability to describe the negative impacts of density on height growth, which is related to volume growth.

Comparing the variation in total gross volume PAI as explained by each stand density variable indicated that measures that use diameter as a measure of average tree size (BPH, RSD, and SDID) performed the best across all three datasets (Table 3.4). All three measures explained a similar amount of variation within each dataset, although, the amount of variation explained varied across datasets. Within the NIMP and IMP data, SDIV explained about 5% less variation in total gross volume PAI than stand density measures BPH, RSD, and SDID and about 4% more variation than RSH and SDIH. Although, within the Spacing Study data stand density measures RSH, SDIH, and SDIV all explained about 2% less variation in total gross PAI than BPH, RSD, and SDID. Collectively, these results adhere to the reasoning put forth by Zeide (2010) in that crown diameter, which is associated with growth, is more closely related to tree diameter than tree height or stem volume.

In all cases, the number of SPH was explained the least amount of variation in total gross volume PAI. One issue with using SPH as a measure of stand density is that it does not uniquely describe a stand structure. For example 800 seedlings per hectare would not have the same structure as a 30-year-old stand with 800 SPH. Consequently, the volume production would be largely different between the stands described in this example. The problem with using the numbers of SPH as a correlate for growth have been widely documented (Oliver and Larson 1996).

3.5.1.2. Pulpwood volume production in unthinned stands

Many different merchantability specifications detailing the minimum diameter at breast height and minimum top diameter exists for loblolly pine depending on local markets. As such, trees entering some merchantability class specifications can change based on local market specifications which can also change with time. Within this work a common minimum diameter at breast height and minimum top diameter were chosen for pulpwood merchantability specifications. In the same fashion, specifications for higher valued product classes can also change depending on local markets. In some areas markets may not exists for certain higher valued product classes. Consequently, all trees that met the minimum diameter at breast height and top diameter specifications were classified as pulpwood in this work. Thus, the analysis presented here would be representative of stands managed for the purpose of producing pulpwood class products.

Relating pulpwood volume PAI to the numbers of SPH resulted in increasing patterns within the NIMP and IMP data and a unimodal pattern within the Spacing Study data (Table 3.2). Whereas total volume PAI was constant and optimal across the entire range of densities within the Spacing Study data, pulpwood gross volume PAI was maximized around 2100 SPH (Table 3.3). In comparison to the results found in total volume PAI, these results show that even a conservative constraint on the diameters of trees included in the calculation of volume production can result in a decrease in production at higher numbers of SPH. Comparing the relationships between pulpwood volume PAI and SPH within the Spacing Study data to the relationships in the NIMP and IMP data showed that maximum pulpwood volume production should occur in the largest planting densities that are commonly used for operational plantations (Figure 3.3).

Within the Spacing Study data, the same patterns were concluded between pulpwood volume PAI and all stand density measures except SPH, as were concluded in total volume PAI. Similar to total gross volume PAI, pulpwood gross volume PAI was maximized around a BPH of 37 m^2/ha within the Spacing Study data (Table 3.3). Additionally, there appeared to be very little difference in the average pulpwood volume PAI across the range of 25 m^2/ha to 60 m^2/ha BPH. Again, fitting a simple linear regression model to a subset of the Spacing Study data that included only BPH values greater than 25 m^2/ha resulted in a slope not significantly different from zero. This provides evidence that volume production can be maximized across a large range of densities.

Increasing patterns were concluded between pulpwood volume PAI and all stand density measures within the NIMP data. Again, due to the amount of hardwood competition that existed within the NIMP data volume production was decreased below the site potential at medium densities resulting in the concluded increasing pattern. In contrast to total volume production a unimodal pattern was concluded for all measures of density except SPH within the IMP data. This indicates that the pulpwood portion of the stand, represented by diameters larger than 13 cm, reaches a maximum average pulpwood volume PAI at densities lower than the total stand volume production. Plotting the relationship between pulpwood volume PAI and BPH showed that within the IMP data pulpwood volume production reached an average site growth potential of 30 m^2/ha/year around a BPH of 25 m^2 (Figure 3.4). Alternatively, total volume production reached the same average site growth potential around a BPH of 43 m^2, the maximum observed BPH in the data (Figure 3.2). Using data from an experiment designed to examine the effects of fertilization and irrigation in young loblolly pine stands, Campoe et al. (2013) showed that the largest 20% of trees were contributing on average about 3.4 times more total aboveground biomass production annually (measured in kg/tree/year) than the smallest 20% of trees, regardless of treatment (values calculated from their Table 4). In conjunction with the results from total volume PAI, these results suggest that when competition is reduced, pulpwood volume PAI will be maximized soon after crown closure. Additionally, the relatively lower volume production of smaller trees can reduce the average total stand volume production causing an increasing relationship with stand density.

Similar to total volume PAI, the stand density measures that explained the most variation in pulpwood volume PAI within the NIMP and IMP data were BPH, RSD, and SDID (Table 3.4). Alternatively, the R^2 values within the Spacing study data were all close to zero. The numbers of SPH explained the most variation in sawtimber gross volume PAI with a R^2 around 0.04. Because periodic annual increment is a rate, and due to varying numbers of trees growing into the pulpwood merchantability limits across the large range of planting densities, there was a large variation in pulpwood volume PAI across the range of observed densities. This resulted in almost no correlation between pulpwood volume production and stand density within the Spacing Study data.

3.5.1.3. Sawtimber Volume Production

Much like pulpwood, different merchantability specifications exists for sawtimber depending on local markets. For this analysis a common minimum diameter at breast height and minimum top diameter were chosen to represent the volume production in the sawtimber portion of the stand. As a direct result of the diameter limits the maximum range of the number of SPH in the Spacing Study data was reduced from about 6300 to slightly less than 4000 SPH. Due to the large variability in these data, convergence was not achievable for equation (12) fit to sawtimber gross and net PAI and SPH. However, plotting the relationship showed that sawtimber volume PAI is maximized around 1500 SPH (Figure 3.5). The hypotheses tests resulted in the conclusion of a unimodal pattern between sawtimber gross and net PAI and SPH within the NIMP data and a decreasing pattern in the IMP data (Table 3.2). An examination of Figure 3.5 showed that within the range of numbers of SPH within all three datasets, sawtimber gross and net PAI was highly variable. Much of this variability can be attributed to the highly variable number of trees growing into the sawtimber product specifications. However, when compared with the Spacing Study, sawtimber volume production in operational plantations would be greatly reduced after 2000 SPH.

Within sawtimber volume PAI, the first unimodal patterns were concluded for the NIMP data in stand density measures BPH and RSD (Table 3.2). However, the point where sawtimber volume PAI was maximized was either at the maximum range of BPH (58 m^2/ha) or outside the maximum range of RSD (9.0) (Tale 3.3). As such, sawtimber volume PAI can be concluded to have increasing patterns with BPH and RSD, although the rate of increase diminishes as density approaches the theoretical maximum. This results in the conclusion of increasing patterns with all measures of density except SPH in the NIMP data. Similarly, increasing patterns were concluded for all measures of density within the IMP data. With the exception of the non-convergence in SPH, the Spacing Study data were concluded to have unimodal patterns in all measures of density.

Examining the relationships between sawtimber volume PAI and BPH showed that production was greatly reduced after a BPH of 50 m^2/ha within the Spacing Study data (Figure

3.6). Further inspection of the data showed that these data points were located in plots of relatively large planting density (3363 SPH or greater) and were the first observations of sawtimber PAI for those plots. Following the stand development showed that by the second observation of sawtimber PAI within these plots a wave of mortality had reduced the BPH below 50 m^2ha. Furthermore, the sawtimber volume PAI had increased due to more trees growing into the merchantability specifications. In contrast to the Spacing Study data, the NIMP and IMP data did not have observed sawtimber PAIs at densities greater than 50 m^2/ha. The decrease in sawtimber volume PAI appears to be a product of some planting densities having trees growing into the sawtimber product class while simultaneously approaching maximum density. However, because operational plantations are not planted at relatively large numbers of SPH, as compared to those in the Spacing Study data, a decrease in sawtimber volume production at high densities may not occur in operational plantations.

Comparing the R^2 values indicated that BPH and RSD were explaining a similar amount of variation in sawtimber volume PAI within the NIMP and IMP datasets (Table 3.4). However, within the NIMP data, RSD explained about 4% more variation than SDID, performing third best among the density measures. Within the IMP data, SDID ranked third in explained variation, similar to the results in total and pulpwood volume PAI. Unlike the results in total and pulpwood PAI, where SDID explained a similar amount of variation as BPH and RSD, SDID was explaining about half the variation in sawtimber volume PAI as these measures of density. Alternatively, within the Spacing Study data, all three stand density measures based on stand density index explained the most variation in sawtimber volume PAI. Furthermore, SDID was explaining about twice as much variation as BPH and RSD.

3.5.2. Testing a Hypothesis on the Relationship between Volume Production and Stand Density in Thinned Stands

3.5.2.1. Total volume production in thinned stands

Within the data from thinned plots of loblolly pine, the hypotheses tests resulted in different conclusions about the pattern between total volume production and the seven measures of stand density compared in this analysis (Table 3.5). Although, there were no differences in in the concluded patterns between total gross volume PAI and total net volume PAI for any measure of stand density.

When total volume production was related to the numbers of SPH, an increasing pattern was concluded for the NIMP1t data and unimodal patterns were concluded for the IMP1t and RW19 data. The increasing pattern exhibited in the NIMP1t data was again due to the high level of competition reducing growth rates at medium densities. This competition resulted in total volume production increasing with increasing numbers of SPH. However, connecting the results with those from the Spacing Study suggests that only the left hand portion of the curve, the increasing portion, was observed due to the restricted range in numbers of SPH in the data. Alternatively, the unimodal patterns exhibited in the RW19 and IMP1t data indicate that intensive management can increase growth rates to the point that volume production is maximized within the range of numbers of SPH commonly planted in production forests. The values of SPH where volume production was maximized differed widely within the IMP1t and RW19 data, with values of about 700 and 1600 SPH, respectively (Table 3.6). Since the number of SPH does not uniquely describe a stand structure it appears that point where volume production is maximized can be highly dependent on the underlying data.

Within the NIMP1t data, unimodal patterns were concluded in BPH and RSD and increasing patterns were concluded in RSH, SDID, SDIH, and SDIV. However, the densities at which volume production was maximized, as calculated from equation (13), were 69.5 m^2/ha BPH and a RSD of 10.6, which are well outside of the range of maximum densities (Table 3.6). This results in a conclusion of increasing total volume PAI with increasing density, although the rate of increase decreased at higher values of BPH and RSD.

Alternatively, within the IMP1t data increasing patterns were concluded between total volume PAI and BPH and RSD and unimodal patterns were concluded in RSH, SDID, SDIH, and SDIV. Comparing the relationships between total volume PAI and BPH across all three datasets from thinned stands indicated that the increasing pattern exhibited in the IMP1t data may be due to the limited range in densities (Figure 3.2). The average total volume production within the RW19 data began to reach an asymptote between 40 and 50 m^2/ha BPH. As the largest values of BPH within the IMP1t data were around 40 m^2/ha, a unimodal pattern may exists but only the left hand portion of the curve was observed. Evidence for this resides in the unimodal patterns concluded in RSH and all three measures of density based on stand density index.

The RW19 data, which includes a range of thinning intensities, exhibited an optimal pattern in all measures of density compared in this work. This result is interesting as the RW19 study was designed to examine the effects of thinning across a wide range of densities by reducing the number of SPH to common values of 1235, 741, 494, and 247, whereas the IMP1t study was designed to reduce density in relative terms by a percentage of basal area (either 30% or 50% basal area reduction). For the purposes of determining the effects of thinning on volume production, experimental studies that reduce density to a common point may be better suited.

Comparing the R^2 values across all measures of density within the NIMP1t and RW19 indicated that measures that use diameter as a measure of average trees size explained the most variation in total volume increment, measures based on height explained the least variation, and the measure based on volume (SDIV) was somewhere in between (Table 3.7). Alternatively, within the IMP1t data, stand density measures BPH, RSD, and RSH explained a similar amount of variation in volume production (about 47%) while all measures based on stand density index similarly explained less variation (about 42%). The same results were seen in both total and merchantable volume PAI. It is interesting that both RSD and RSH, which use either diameter or height as a measure of average tree size, explained a similar amount of variation in total volume PAI but had opposite conclusions. This is a good indication that stand density measures which use height as a measure of average tree size could better describe the negative effects of density on height development and therefor volume production.

3.5.2.2 Pulpwood Volume Production

Within the data from thinned plots, the conclusions from the hypothesis tests on the growth-density relationship between pulpwood gross and net PAI and the seven measures of stand density were the same as the conclusions from total gross and net PAI, with one exception in the NIMP1t data. The hypothesis test resulted in the conclusion of an increasing pattern between pulpwood gross PAI and RSD, the opposite pattern that was found between total gross PAI and RSD (Table 3.4). However, the p-value (0.0502) was close to the cut-off value of α=0.05. Furthermore, the BPH value at which pulpwood volume was maximized was well outside the range of the maximum theoretical densities that exist in loblolly pine (Table 3.5).

This results in the conclusion of increasing pulpwood volume PAI with increasing density for all seven measures of stand density.

The IMP1t data indicated increasing patterns between pulpwood gross and net PAI and stand density measures BPH and RSD and unimodal patterns in SPH, RSH, SDID, SDIH, and SDIV. The RW19 data were concluded to have unimodal relationships between pulpwood gross and net PAI and all measures of stand density, the same results which were found in total gross and net PAI. The reason for the similarity between total volume PAI and pulpwood volume PAI in the data from thinned plots is fairly simple. The thinning treatments were from below, removing mostly smaller stems, resulting in the majority of observed diameters being greater than the threshold diameter of 13 cm, which defines the pulpwood merchantability specifications. Additionally, in the calculation of total PAI, trees smaller than 13 cm only contributed to a small percentage of total volume growth. This resulted in the similar patterns seen between total PAI and pulpwood PAI.

3.5.2.3 Sawtimber Volume Production

When sawtimber volume production was related to stand density different conclusion were found depending on the measure of density within the NIMP1t and IMP1t data (Table 3.5). ALternatively, the hypothesis test resulted in the conclusions of unimodal patterns in all measures of density within the RW19 data.

When related to the number of SPH, unimodal patterns were concluded for all three datasets from thinned stand (Table 3.5). However, the number of SPH at which sawtimber PAI was maximized changed among datasets (Table 3.6). Within both the NIMP1t and IMP1t datasets, sawtimber volume PAI was maximized around a density of 700 SPH. Alternatively, within the RW19 data, sawtimber PAI was maximized at a density around 1300 SPH. Comparing the relationships between sawtimber PAI and SPH in thinned and unthinned stands suggests that these differences could be due to a lack of data at in larger numbers of SPH within the IMP1t and NIMP1t datasets (Figure 3.5). In addition, there is also the possibility that the different numbers of SPH at which volume production is maximized are due to differences in the underlying study designs. The NIMP and IMP studies were designed to examine thinning by removing either 30 or 50% of the basal area. Additionally, the NIMP study contains data from stands thinned across a range of ages (8 to 25 years) while the IMP study contains data from stands thinned at a common point in stand development (45 feet). As such, the structure of the residual stands after thinning may vary largely in the numbers of SPH as well as any vacancy created in the canopy due to thinning. This results in a large variation in sawtimber PAI across the range of numbers of SPH in these data. In general, the data suggests that regardless of management or thinning intensity, sawtimber production decreases at values of SPH less than 700 SPH in unthinned stands. Alternatively, The RW19 study was designed to examine different levels of thinning where stands were reduced to 1235, 741, 494, or 247 SPH resulting in stands of similar structures. As a result, comparing sawtimber PAI across numbers of SPH provides evidence of the effect of thinning intensity on sawtimber production. Since 1300 SPH, the density at which sawtimber PAI was maximized, is larger than the maximum range in observed densities in the RW19 data, the data suggests that sawtimber volume PAI increases with increasing numbers of SPH, although at a decreasing rate. In comparison to the results in unthinned stands, sawtimber volume production will eventually decrease, although, this decrease may not be observed in plantations thinned to operational densities. Since thinning is used as a management tool to capture mortality and increase tree diameters above a merchantable threshold, these results indicate that the increase in diameter growth from larger tree removals will not increase sawtimber production in thinned stands of loblolly pine.

When sawtimber PAI was related to stand density measures BPH, RSD, and RSH, unimodal patterns were concluded in the NIMP1t and RW19 data and an increasing pattern was concluded in the IMP1t data. Comparing the relationship between sawtimber PAI and BPH indicated that the differences in conclusion between the NIMP1t and IMP1t data could be due to management (Figure 3.6) The NIMP1t data suggest that sawtimber volume production is maximized close to the edge of maximum density, however, the IMP1t data indicate that if competition is reduced then sawtimber PAI will increase up to the maximum densities that can be carried on a site. The densities at which sawtimber PAI was maximized in the RW19 data were well outside the maximum range of densities for loblolly pine (Table 3.6). This provides further evidence that sawtimber volume production increases with increasing density when competition is controlled.

In contrast, unimodal relationships were observed between sawtimber PAI and all measures of stand density index within the IMP1t and RW19 data, while an increasing pattern was concluded in the NIMP1t data. However, the densities at which sawtimber PAI was maximized within the RW19 data were outside of the range of maximum density resulting in the conclusion of increasing sawtimber PAI with increasing stand density index, regardless of the measure of average tree size. Further inspection of the IMP1t data indicate that due to the restricted range of densities only the increasing portion of the curve was observed. Collectively, these results suggest that sawtimber volume production in thinned stands is maximized at the largest densities that can be carried on a site.

3.6. Conclusions

This study provides a comprehensive overview of the effects of different definitions of density on the growth-density relationship. The results indicate that different patterns emerge depending on the definition of growth, the definition of stand density, the type of management, and even the dataset used in determining the growth-density relationship when compared in a two-dimensional manner. That is, when comparing volume growth only as a function of density. For total volume production of unthinned loblolly pine stands the results from the NIMP and IMP data suggest that total volume production increases up to the maximum densities a given site can carry, which would agree with the findings of Curtis et al. (1997). Alternatively, the results from the Spacing Study data suggest that total volume production becomes optimal somewhere close to the edge of maximum density. Results from the studies with thinning treatments additionally suggest that unimodal patterns can occur in intensively managed plantations. Both of these results would agree with the findings of Zeide (2004).

These results shed light on how different conclusions can be found in the literature concerning the growth-density relationship. One problem may be in the general approach to quantifying the relationship. In most cases the function used in this study determined that the density at which volume production was maximized was just outside the range of observed densities. It is interesting that the same result can be found in the functions of both Zeide (2004) and Curtis et al. (1997), even though completely different populations were analyzed. One conclusion could be that a density where volume production is maximized exists but that this density would fall outside the range of normally observed densities. However, the densities where volume production was maximized as calculated in this study were often much larger than the theoretical maximum as determined by Reineke (1933). This suggests that the density could be a function of the model used in determining the growth-density relationship. However, this could be a function of the data as well, regardless of the tree population studied. Consider a forest with trees of equal size and a known observed volume growth rate. If the site quality is kept constant and no mortality is observed then an increase in number of stems will lead to an increase in total stand growth. In some cases, the underlying theory behind a unimodal pattern between volume production and stand density is that at some point the density will become so large that growth is affected negatively. This would be true if a given area of land could sustain a larger number of stems, however, trees are more than just objects in the ground growing to fill a geometric area. They are living beings that compete for resources such as light in the canopy and moisture and nutrients in the soil. After a certain point this competition leads to self-induced mortality as weaker trees are unable to compete. When relating stand volume growth to a density measure such as basal area, a slight decline in growth can be seen right at the very edge of maximal density. This decline is due to mortality which reduces the total number of trees available for volume production. Just as an increased number of stems leads to increased stand volume growth any reduction in stems will have the opposite effect. However, a reduction in number of stems allows for an expansion of branches in the crown and roots in the soil which can lead to increased volume production. Thus, after a wave of mortality and with more resources available a stand can continue to grow until it again reaches maximum density and the process is repeated. This leads to a circular pattern where the growth-density relationship is in a constant flux of increased growth from increased tree sizes and decreased growth from loss of stems, right at the edge of maximum density.

Based on this reasoning the growth-density relationship can be thought of as having two stages. The first stage includes stand growth up to the point before self-thinning. The data suggest that in this stage of growth will have either a power or an exponential increase with increasing density. The second stage includes stand growth after the point of self-thinning where a stand is constantly changing around the point of maximum density. In this stage the growth-density relationship would be much more variable depending on average tree size and age. In terms of self-thinning, these two stages are generally referred to as density-independent and density dependent mortality stages, respectively (VanderSchaaf and Burkhart 2008). It seems reasonable to believe that any even-aged forest would go through these two stages of the growth-density relationship regardless of species. Therefore, any model that is flexible enough to describe an increasing or an optimum relationship could potentially exhibit a unimodal pattern close to the maximum density. Any data in the first stage would cause the model to show an increasing pattern, while data from the second stage could cause the curve to bend down, bend up, or stay straight. Depending on the function used to model the relationship and the availability of data at the edge of maximum densities either an increasing or optimum pattern could be observed. This is a highly important result and highlights the complications of expressing volume growth as only a function of density.

One of the principle problems with describing volume growth only as a function of density is the procedure ignores the effect of age. Both height and diameter growth slow with age which affects the response to any additional growing space that results from self-thinning. Additionally, trees can become so large that a residual stand would be unable to completely fill all gaps in the canopy created by mortality. This would result in an incomplete canopy whereby maximum light interception would not be achieved. A stand such as this would have diminished growth compared to a stand with a full canopy at a similar density. However, this effect would also be a function of initial planting density, average tree size, and site quality in addition to age.

Just as density and average tree size are used as a proxy to describe the mechanisms of competition that exists within a forest, age may also be a proxy for describing the change in those competitive processes. This could partially be accounted for in the model by including a measure of average tree size. Knowing the current density and average tree size has the potential for describing a range of stand structures. However, including another variable related to different stand conditions, such as dominant stand height, would additionally describe a larger range in stand structures and may further account for the effects of age and additionally site quality.

Within this work the stand density measures that use average tree diameter as a measure of average tree size (BPH, RSD, and SDID) were consistently the most highly correlated with volume growth. According to Zeide (2002) this is due to diameter being more correlated with crown width, as compared to height or tree volume, which is highly correlated with volume growth. However, In some cases within the IMP1t data, stand density measure RSH performed similarly to BPH and RSD, while SDID performed poorly. Future work should continue to examine the effects of different density measures on the growth-density relationship. The results here were not conclusive as to which density measure is best and the analyses were subject to the same complications as those found in determining the overall relationship. It is possibility that an improved model that explains a wider range of stand conditions would exhibit similar relationships in all of the density measures compared here.

The exploratory nature of this work provided a comprehensive and unique comparison of different measures of density and growth with different datasets of loblolly pine. The results here pave a path for future work in developing a model that more accurately describes the growth-density relationship. The formulation of a model should take into account different stand structures and incorporate variables that describe the change in stand structure over time.

Literature Cited

Amateis, R.L., and H.E. Burkhart. 2012. Rotation-age results from a loblolly pine spacing trial. Southern Journal of Applied Forestry 36(1):11-18.

Amateis, R.L., S.P. Prisley, H.E. Burkhart, and J. Liu. 2006. The effect of physiographic region and geographic locale on predicting the dominant height and basal area of loblolly pine plantations. Southern Journal of Applied Forestry 30(3):147-153.

Burkhart, H.E. 2013. Comparison of maximum size–density relationships based on alternate stand attributes for predicting tree numbers and stand growth. Forest Ecology and Management 289(0):404-408.

Burkhart, H.E., D.C. Cloeren, and R.L. Amateis. 1985. Yield relationships in unthinned loblolly pine plantations on cutover, site-prepared lands. Southern Journal of Applied Forestry 9(2):84-91.

Campoe, O.C., J.L. Stape, T.J. Albaugh, H. Lee Allen, T.R. Fox, R. Rubilar, and D. Binkley. 2013. Fertilization and irrigation effects on tree level aboveground net primary production, light interception and light use efficiency in a loblolly pine plantation. Forest Ecology and Management 288:43-48.

Curtis, R.O., D.D. Marshall, and J.F. Bell. 1997. LOGS: A pioneering example of silvicultural research in coast Douglas-Fir. Journal of Forestry 95(7):19-25.

Hartig, G.L. 1795. Anweisung zu Taxation der Forsten oder zur Bestimmung des Holzertrags der Walder. In: KommiBion bei Buchhandler Heyer.

Langsaeter, A. 1941. Om tynning i enaldret gran-og furuskog. Medd. Nor. Skogforsosves 8:131-216.

McClay, T.A. 1955. The relation of growth to site and residual density in loblolly pine pulp stands. USDA For. Ser., Southeast. For. Exp. Stn., Research Note No. 78. 2p.

Nelson, T.C., and E.V. Brender. 1963. Comparison of stand density measures for loblolly pine cubic-foot growth prediction. Forest Science 9:8-14.

Oliver, C.D., and B.C. Larson. 1996. Forest stand dynamics. Wiley, New York.

Pretzsch, H. 2005. Stand density and growth of Norway spruce (Picea abies (L.) Karst.) and European beech (Fagus sylvatica L.): evidence from long-term experimental plots. Eur J Forest Res 124(3):193-205.

Reineke, L.H. 1933. Perfecting a stand-density index for even-aged forests. Journal of Agricultural Research 46:627-638.

Reventlow, C.D.F. 1879. Forslag til en forbedret Skovdrift grundet, paa Undersogelser over Traeernes Vegetation I Denmarks og Slesvigs Skove. In: Kjobenhavn, 1879, Ed. in English 1960: A treatise of forestry, Society of Forest History, Horsholm Denmark.

Tasissa, G., H.E. Burkhart, and R.L. Amateis. 1997. Volume and Taper Equations for Thinned and Unthinned Loblolly Pine Trees in Cutover, Site-Prepared Plantations. Southern Journal of Applied Forestry 21(3):146-152.

Trincado, G., H.E. Burkhart, and R.L. Amateis. 2004. Volume increment and stand density relationship: Hypothesis testing of patterns and modeling approach. Department of Forestry, Virginia Polytechnic Institute and State University, Blacksburg, VA., Loblolly Pine Growth and Yield Research Cooperative, Report No. 137.

VanderSchaaf, C.L., and H.E. Burkhart. 2007. Comparison of Methods to Estimate Reineke's Maximum Size-Density Relationship Species Boundary Line Slope. Forest Science 53(3):435-442.

VanderSchaaf, C.L., and H.E. Burkhart. 2008. Using Segmented Regression to Estimate Stages and Phases of Stand Development. Forest Science 54(2):167-175.

Wenger, K.F., T.C. Evans, T. Lotti, R.W. Cooper, and E.V. Brender. 1958. The relation of growth to stand density in natural loblolly pine stands. USDA For. Ser., Southeast. For. Exp. Stn., Paper No. 97. 10p.

Zeide, B. 2001. Thinning and growth: A full turnaround. Journal of Forestry 99(1):20.

Zeide, B. 2002. Density and the growth of even-aged stands. Forest Science 48(4):743-754.

Zeide, B. 2004. Optimal stand density: A solution. Canadian Journal of Forest Research 34(4):846-854.

Zeide, B. 2010. Comparison of self-thinning models: An exercise in reasoning. Trees 24(6):1117-1126.

Table 3.1: Descriptive statistics for datasets of thinned and unthinned loblolly pine.

Dataset	Stand Parameter	N	Mean	Std Dev	Minimum	Maximum
NIMP		874				
	Age (years after planting)		24.59	6.55	11.00	45.00
	Basal area (m^2 per ha)		32.95	7.57	5.51	55.12
	Trees per ha		1160.18	331.84	222.39	2520.47
	Site Index (m, base age 25 years)		18.40	2.30	12.80	24.69
IMP		652				
	Age (years after planting)		11.34	2.41	8.00	19.00
	Basal area (m^2 per ha)		26.07	6.96	4.47	44.77
	Trees per ha		1452.81	275.29	804.84	2158.27
	Site Index (m, base age 25 years)		22.45	2.38	16.11	28.71
Spacing Study		1606				
	Age (years after planting)		14.30	5.09	8.00	25.00
	Basal area (m^2 per ha)		32.06	9.42	7.84	59.18
	Trees per ha		2152.20	1266.28	549.18	6727.43
	Site Index (m, base age 25 years)		20.35	1.41	16.07	23.31
NIMP1t		1201				
	Age (years after planting)		25.55	5.90	14.00	43.00
	Basal area (m^2 per ha)		26.47	6.63	4.35	50.17
	Trees per ha		693.55	188.29	109.82	1563.17
	Site Index (m, base age 25 years)		18.46	2.34	11.58	25.60
IMP1t		206				
	Age		17.87	2.26	14.00	23.00
	Basal area (m^2 per ha)		23.78	7.11	3.30	43.00
	Trees per ha		525.29	224.18	67.62	1084.91
	Site Index (m, base age 25 years)		23.66	3.05	17.26	29.57
RW19		928				
	Age		17.31	2.44	13.00	22.00
	Basal area (m^2 per ha)		25.34	10.57	6.59	49.13
	Trees per ha		638.46	328.84	202.18	1284.95
	Site Index (m, base age 25 years)		22.41	1.94	18.29	27.13

Table 3.2: Approximate p-values for parameter α_2 from each fit of equation 12 to gross and net total, pulpwood, and sawtimber volume periodic annual increment (PAI, m^3/ha/yr) in relation to density measures stems per hectare (SPH), basal area per hectare (BPH, m^2), relative spacing based on diameter (RSD), relative spacing based on height (RSH), stand density index based on diameter (SDID), stand density index based on height (SDIH), and stand density index based on volume (SDIV) for datasets from unthinned loblolly pine. Values in bold indicate parameter is significantly different from zero.

PAI	Density	NIMP		IMP		Spacing Study	
		Gross	Net	Gross	Net	Gross	Net
Total	SPH	0.2646	0.7041	**0.0443**	**0.0405**	0.2040	0.2200
	BPH	0.8876	0.4139	0.2484	0.2098	**< 0.0001**	**< 0.0001**
	RSD	0.9187	0.4804	0.1758	0.1461	**< 0.0001**	**< 0.0001**
	RSH	0.1221	0.7578	**< 0.0001**	**< 0.0001**	**< 0.0001**	**< 0.0001**
	SDID	0.9070	**0.0325***	0.0778	0.0803	**< 0.0001**	**0.0104**
	SDIH	0.2860	0.2318	**< 0.0001**	**< 0.0001**	**< 0.0001**	**< 0.0001**
	SDIV	0.8237	0.0927	**0.0015**	**0.0017**	**< 0.0001**	**0.0025**
Pulpwood	SPH	0.7782	0.5058	0.1159	0.0954	**< 0.0001**	**< 0.0001**
	BPH	0.8922	0.5738	**< 0.0001**	**< 0.0001**	**0.0034**	**0.0006**
	RSD	0.8936	0.6599	**< 0.0001**	**< 0.0001**	**0.0007**	**0.0001**
	RSH	**0.0435***	0.9485	**< 0.0001**	**< 0.0001**	**0.0001**	**< 0.0001**
	SDID	0.7337	**0.0199***	**0.0001**	**0.0001**	**0.0094**	0.7439
	SDIH	0.1259	0.0562	**< 0.0001**	**< 0.0001**	**0.0010**	0.1372
	SDIV	0.6291	**0.0432***	**< 0.0001**	**< 0.0001**	**0.0008**	0.2824
Sawtimber	SPH	**< 0.0001**	**< 0.0001**	0.4491	0.4055		
	BPH	**0.0008**	**0.0026**	0.6003	0.5897	**0.0001**	**0.0005**
	RSD	**0.0010**	**0.0024**	0.5789	0.5703	**0.0002**	**0.0006**
	RSH	0.0996	0.0767	0.5619	0.5366	**< 0.0001**	**< 0.0001**
	SDID	0.4125	0.1757	**0.0159***	**0.0175***	**< 0.0001**	**< 0.0001**
	SDIH	0.2065	0.2810	0.8291	0.8635	**< 0.0001**	**< 0.0001**
	SDIV	0.3328	0.2376	0.0958	0.1075	**< 0.0001**	**< 0.0001**

* represents a significantly positive estimate for parameter α_2

Table 3.3: Stand density values where volume periodic annual increment is maximized as calculated from equation 12 fit to gross and net total, pulpwood, and sawtimber volume periodic annual increment (PAI, m^3/ha/yr) in relation to density measures stems per hectare (SPH), basal area per hectare (BPH, m^2), relative spacing based on diameter (RSD), relative spacing based on height (RSH), stand density index based on diameter (SDID), stand density index based on height (SDIH), and stand density index based on volume (SDIV) for datasets from unthinned loblolly pine.

PAI	Density	NIMP		IMP		Spacing Study	
		Gross	Net	Gross	Net	Gross	Net
Total	SPH			1475.8	1497.7		
	BPH					37.3	27.7
	RSD					6.8	5.9
	RSH			5.8	5.7	5.8	4.7
	SDID					1281.8	1108.3
	SDIH			560.5	553.8	764.7	491.4
	SDIV			908.6	896.2	1097.9	843.2
Pulpwood	SPH					2150.1	2440.5
	BPH			36.0	35.4	36.5	28.4
	RSD			6.8	6.7	6.7	5.9
	RSH			5.2	5.2	5.2	4.3
	SDID			952.8	949.1	1083.6	
	SDIH			503.8	501.7	569.9	
	SDIV			748.6	746.3	803.4	
Sawtimber	SPH	877.1	934.8				
	BPH	58.5	58.9			38.9	39.4
	RSD	9.0	8.9			7.0	7.1
	RSH					5.5	5.5
	SDID					772.7	776.1
	SDIH					461.7	456.9
	SDIV					633.6	632.8

Table 3.4: The coefficient of determination (R^2) and Akeike's Information Criterion (AIC) from each fit of equation 12 relating gross total, pulpwood, and sawtimber volume periodic annual increment (PAI, m^3/ha/yr) in relation to density measures stems per hectare (SPH), basal area per hectare (BPH, m^2), relative spacing based on diameter (RSD), relative spacing based on height (RSH), stand density index based on diameter (SDID), stand density index based on height (SDIH), and stand density index based on volume (SDIV) for datasets from unthinned loblolly pine. Values in bold indicate the three "best" fits.

PAI	Density	NIMP		IMP		Spacing Study	
		R^2	AIC	R^2	AIC	R^2	AIC
Total	SPH	0.0249	5390	0.0083	4308	0.0340	9803
	BPH	**0.1606**	**5259**	**0.3405**	**4042**	**0.1022**	**9685**
	RSD	**0.1606**	**5259**	**0.3411**	**4041**	**0.1066**	**9677**
	RSH	0.0589	5359	0.2217	4150	0.0864	9713
	SDID	**0.1683**	**5251**	**0.3037**	**4077**	**0.1018**	**9686**
	SDIH	0.0724	5346	0.1968	4170	0.0714	9739
	SDIV	0.1236	5296	0.2530	4123	0.0835	9718
Pulpwood	SPH	0.0359	5416	0.0085	4466	**0.0444**	**10798**
	BPH	**0.1266**	**5329**	**0.2446**	**4289**	**0.0210**	**10836**
	RSD	**0.1266**	**5329**	**0.2487**	**4285**	**0.0231**	**10833**
	RSH	0.0396	5412	0.1545	4362	0.0114	10852
	SDID	**0.1487**	**5307**	**0.2229**	**4307**	0.0139	10848
	SDIH	0.0560	5397	0.1306	4380	0.0078	10857
	SDIV	0.1052	5350	0.1756	4346	0.0103	10853
Sawtimber	SPH	0.0979	5456	0.0927	3607		
	BPH	**0.3499**	**5179**	**0.4253**	**3381**	0.0672	6063
	RSD	**0.3494**	**5180**	**0.4253**	**3381**	0.0666	6064
	RSH	**0.2117**	**5342**	0.1380	3582	0.0658	6065
	SDID	0.1727	5383	**0.2070**	**3540**	**0.1228**	**6011**
	SDIH	0.1291	5427	0.0691	3620	**0.1006**	**6032**
	SDIV	0.1625	5393	0.1389	3581	**0.1222**	**6011**

Table 3.5: Approximate p-values for parameter α2 from each fit of equation 12 to gross and net total, pulpwood, and sawtimber volume periodic annual increment (PAI, m^3/ha/yr) in relation to density measures stems per hectare (SPH), basal area per hectare (BPH, m^2), relative spacing based on diameter (RSD), relative spacing based on height (RSH), stand density index based on diameter (SDID), stand density index based on height (SDIH), and stand density index based on volume (SDIV) for datasets from thinned loblolly pine. Values in bold indicate parameter is significantly different from zero.

PAI	Density	NIMP1t		IMP1t		RW19	
		Gross	Net	Gross	Net	Gross	Net
Total	SPH	0.3121	0.8024	**0.0002**	**0.0006**	**0.0094**	**0.0171**
	BPH	**0.0142**	0.3045	0.2291	0.2001	**< 0.0001**	**< 0.0001**
	RSD	**0.0189**	0.2981	0.1883	0.1539	**< 0.0001**	**< 0.0001**
	RSH	0.5791	0.4190	**0.0187**	**0.0347**	**< 0.0001**	**< 0.0001**
	SDID	0.8790	0.2650	**0.0095**	**0.0100**	**0.0016**	**0.0002**
	SDIH	0.3442	0.8338	**0.0121**	**0.0245**	**0.0001**	**< 0.0001**
	SDIV	0.5803	0.5220	**0.0117**	**0.0154**	**0.0004**	**< 0.0001**
Pulpwood	SPH	0.4770	0.8579	**0.0002**	**0.0007**	**0.0096**	**0.0233**
	BPH	**0.0382**	0.4429	0.2237	0.1971	**< 0.0001**	**< 0.0001**
	RSD	0.0502	0.4413	0.1840	0.1519	**< 0.0001**	**< 0.0001**
	RSH	0.4755	0.5178	**< 0.0001**	**< 0.0001**	**< 0.0001**	**< 0.0001**
	SDID	0.7581	0.2118	**0.0095**	**0.0102**	**0.0014**	**0.0003**
	SDIH	0.3295	0.7272	**0.0114**	**0.0237**	**< 0.0001**	**< 0.0001**
	SDIV	0.5066	0.4258	**0.0115**	**0.0154**	**0.0003**	**< 0.0001**
Sawtimber	SPH	**< 0.0001**	**< 0.0001**	**< 0.0001**	**< 0.0001**	**0.0003**	**0.0004**
	BPH	**< 0.0001**	**0.0001**	0.5154	0.5658	**0.0002**	**0.0001**
	RSD	**< 0.0001**	**0.0001**	0.4334	0.4726	**0.0002**	**0.0001**
	RSH	0.0624	**0.0134**	0.0771	0.1186	**< 0.0001**	**< 0.0001**
	SDID	0.2618	0.6814	**0.0296**	**0.0384**	**0.0197**	**0.0121**
	SDIH	0.5006	0.4447	**0.0283**	**0.0464**	**< 0.0001**	**< 0.0001**
	SDIV	0.5480	0.7907	**0.0326**	**0.0452**	**0.0018**	**0.0011**

Table 3.6: Stand density values where volume periodic annual increment is maximized as calculated from equation 12 fit to gross and net total, pulpwood, and sawtimber volume periodic annual increment (PAI, m^3/ha/yr) in relation to density measures stems per hectare (SPH), basal area per hectare (BPH, m^2), relative spacing based on diameter (RSD), relative spacing based on height (RSH), stand density index based on diameter (SDID), stand density index based on height (SDIH), and stand density index based on volume (SDIV) for datasets from thinned loblolly pine.

PAI	Density	NIMP1t		IMP1t		RW19	
		Gross	Net	Gross	Net	Gross	Net
Total	SPH			732.8	731.1	1662.4	1627.0
	BPH	69.5				54.3	46.6
	RSD	10.6				8.9	8.0
	RSH			7.7	7.8	7.1	6.4
	SDID			791.0	765.6	1427.3	1187.6
	SDIH			585.1	590.0	736.7	615.8
	SDIV			710.7	693.4	1082.9	902.3
Pulpwood	SPH			736.5	735.5	1683.8	1713.4
	BPH	75.8				54.1	47.1
	RSD					8.9	8.1
	RSH			7.7	7.7	7.1	6.5
	SDID			792.4	768.1	1420.0	1211.7
	SDIH			584.3	590.4	733.2	633.0
	SDIV			711.3	695.4	1077.4	923.9
Sawtimber	SPH	701.4	727.4	684.2	688.8	1303.0	1317.5
	BPH	46.9	48.7			60.0	56.6
	RSD	8.0	8.1			9.6	9.2
	RSH		7.2			6.9	6.8
	SDID			804.0	803.8	1664.3	1548.5
	SDIH			586.3	601.2	694.2	678.9
	SDIV			720.3	724.7	1120.1	1064.9

Table 3.7: The coefficient of determination (R^2) and Akeike's Information Criterion (AIC) from each fit of equation 12 relating gross total, pulpwood, and sawtimber volume periodic annual increment (PAI, m^3/ha/yr) in relation to density measures stems per hectare (SPH), basal area per hectare (BPH, m^2), relative spacing based on diameter (RSD), relative spacing based on height (RSH), stand density index based on diameter (SDID), stand density index based on height (SDIH), and stand density index based on volume (SDIV) for datasets from thinned loblolly pine. Values in bold indicate the three "best" fits.

PAI	Density	NIMP1t		IMP1t		RW19	
		R^2	AIC	R^2	AIC	R^2	AIC
Total	SPH	0.0388	7262	0.2636	1373	0.2316	7501
	BPH	**0.3435**	**6804**	**0.4691**	**1306**	**0.4714**	**7106**
	RSD	**0.3432**	**6804**	**0.4700**	**1306**	**0.4713**	**7106**
	RSH	0.1538	7109	**0.4668**	**1307**	0.2591	7462
	SDID	**0.3165**	**6852**	0.4127	1327	**0.4095**	**7223**
	SDIH	0.1587	7102	0.4196	1324	0.2616	7459
	SDIV	0.2519	6961	0.4250	1323	0.3590	7309
Pulpwood	SPH	0.0444	7237	0.2665	1373	0.2374	7503
	BPH	**0.3251**	**6820**	**0.4684**	**1307**	**0.4730**	**7113**
	RSD	**0.3248**	**6820**	**0.4693**	**1307**	**0.4729**	**7113**
	RSH	0.1420	7108	**0.4681**	**1307**	0.2626	7467
	SDID	**0.3071**	**6851**	0.4142	1327	**0.4131**	**7226**
	SDIH	0.1505	7096	0.4220	1324	0.2660	7462
	SDIV	0.2415	6960	0.4269	1323	0.3631	7312
Sawtimber	SPH	0.0351	7599	0.2922	1404	0.2152	7722
	BPH	**0.3589**	**7109**	**0.3628**	**1383**	**0.4266**	**7394**
	RSD	**0.3590**	**7109**	**0.3635**	**1382**	**0.4265**	**7394**
	RSH	0.1562	7438	**0.3855**	**1375**	0.2395	7689
	SDID	**0.2639**	**7275**	0.3390	1390	**0.3713**	**7490**
	SDIH	0.1292	7476	0.3574	1384	0.2409	7687
	SDIV	0.2105	7359	0.3540	1385	0.3267	7562

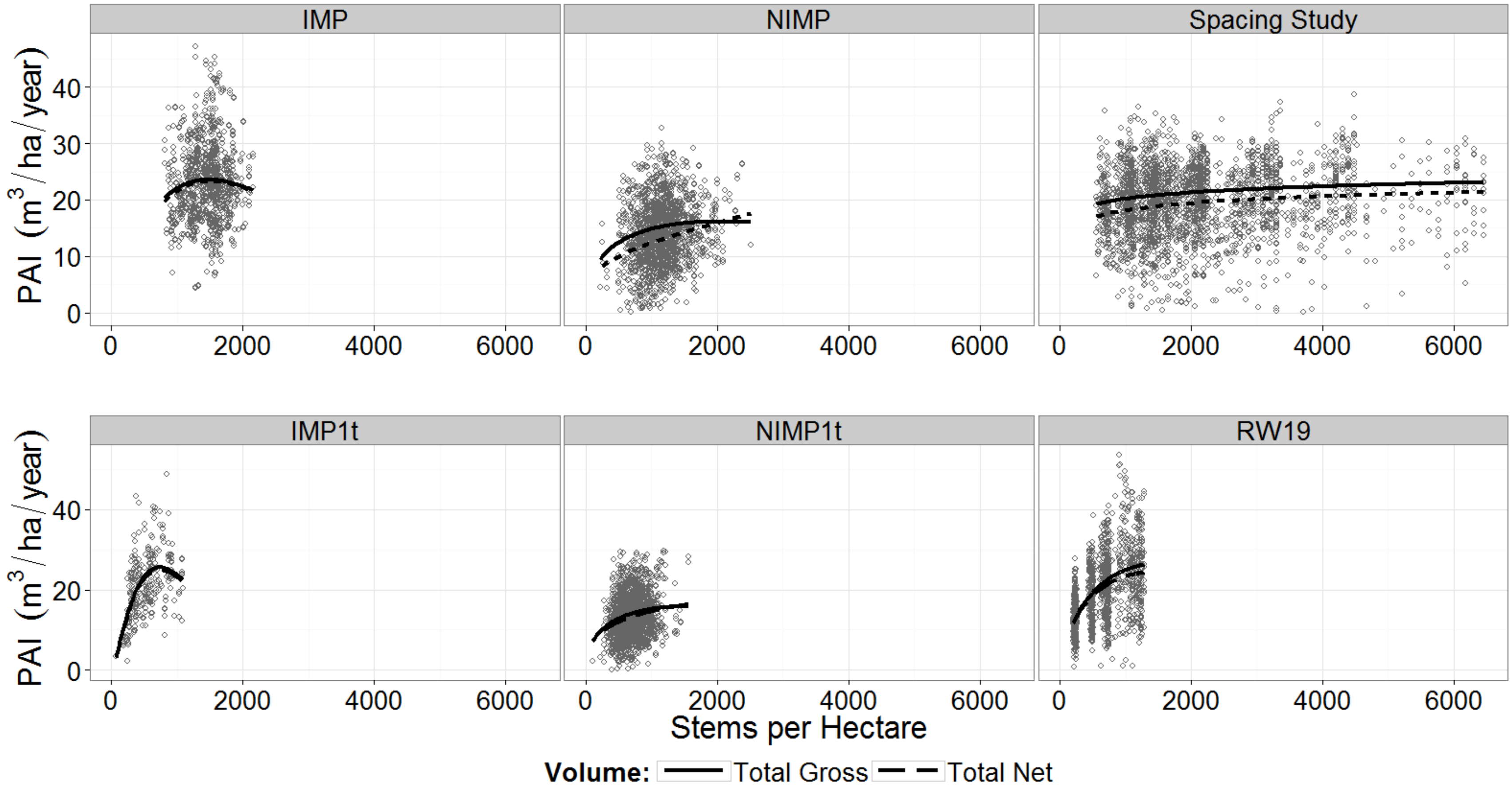


Figure 3.1: The relationship between total gross and net volume periodic annual increment (PAI) and the number of stems per hectare within unthinned and thinned datasets of loblolly pine.

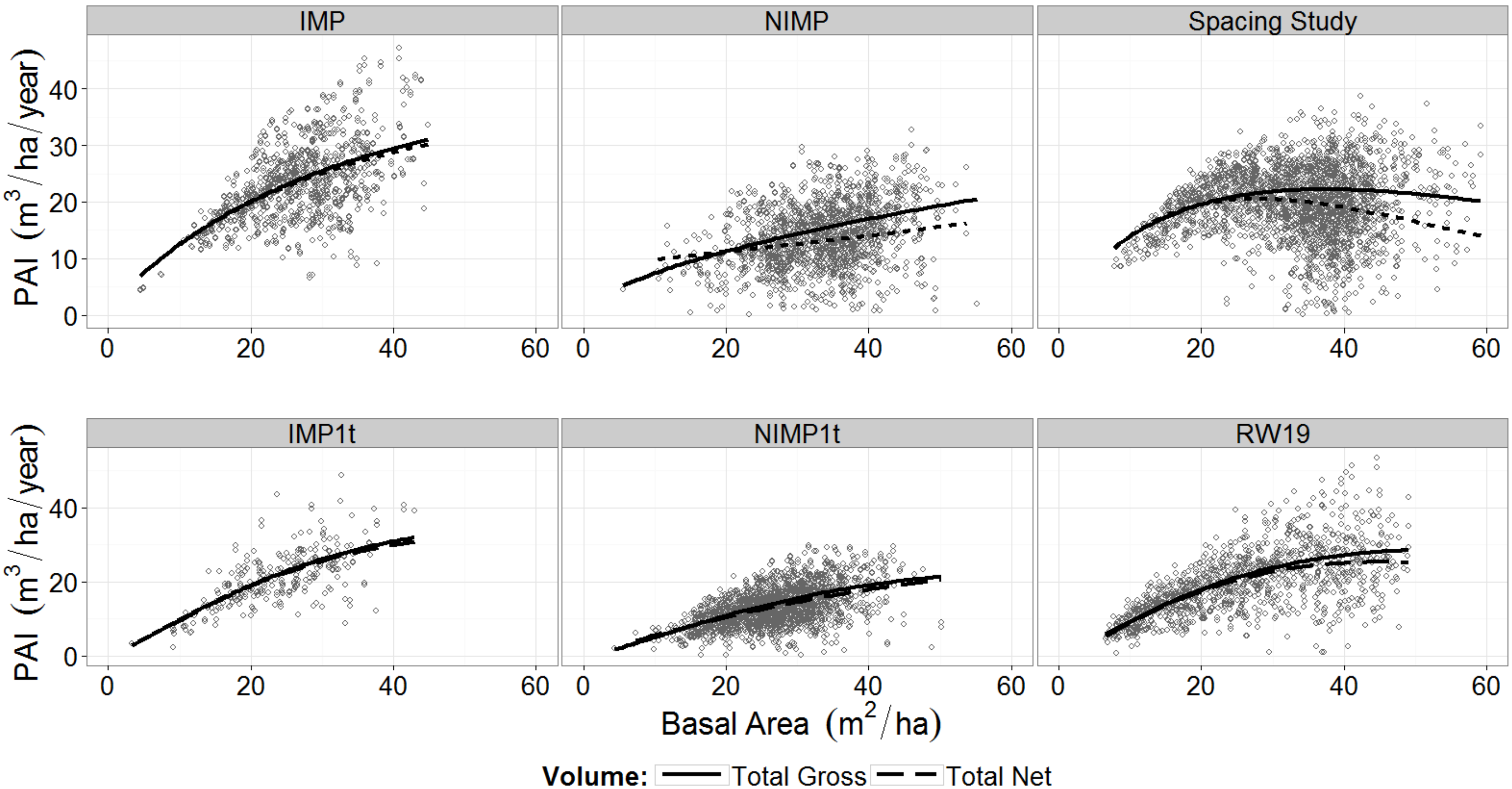


Figure 3.2: The relationship between total gross and net volume periodic annual increment (PAI) and basal area within unthinned and thinned datasets of loblolly pine.

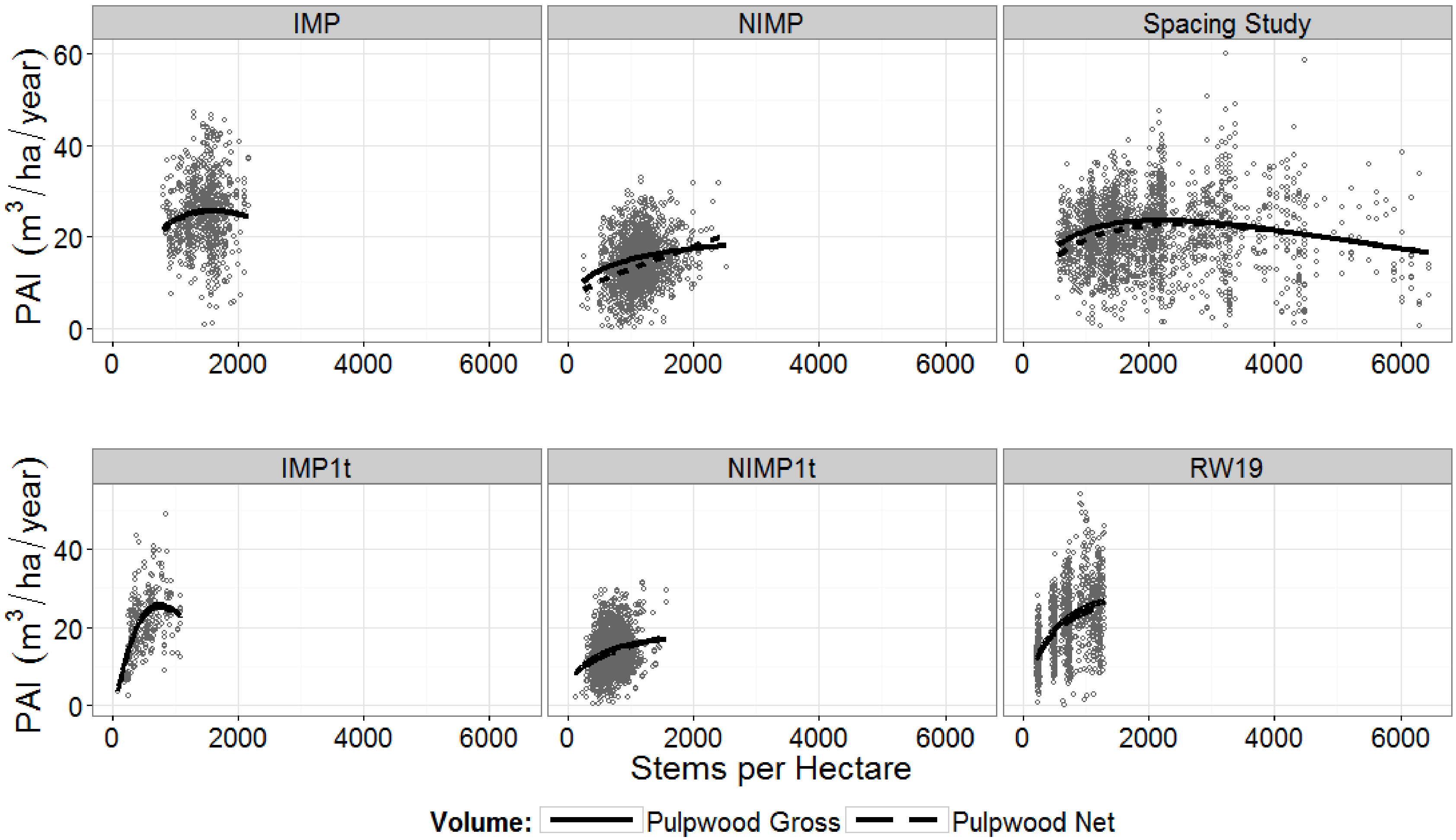


Figure 3.3: The relationship between pulpwood gross and net volume periodic annual increment (PAI) and the number of stems per hectare within unthinned and thinned datasets of loblolly pine.

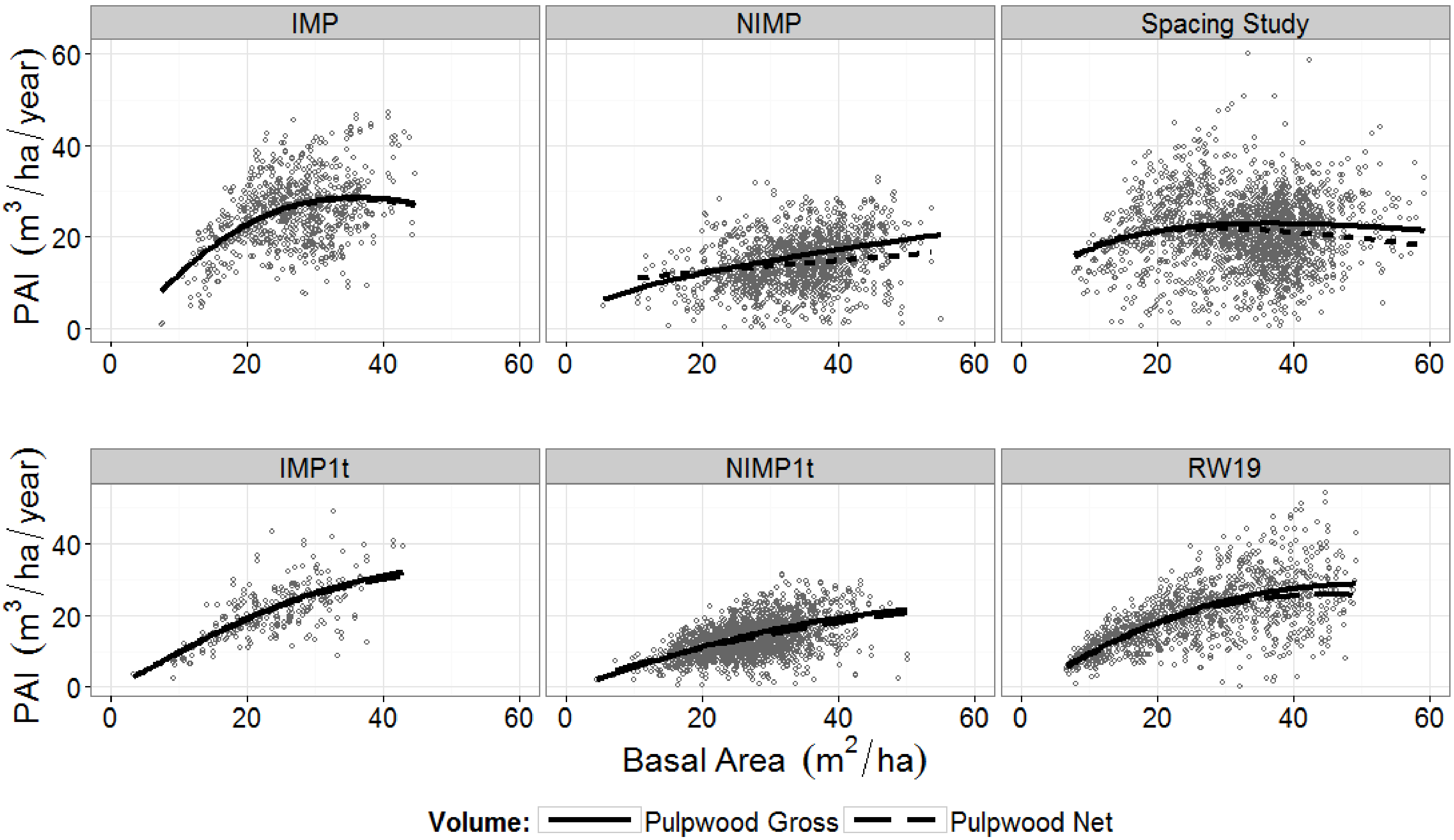


Figure 3.4: The relationship between pulpwood gross and net volume periodic annual increment (PAI) and basal area within unthinned and thinned datasets of loblolly pine.

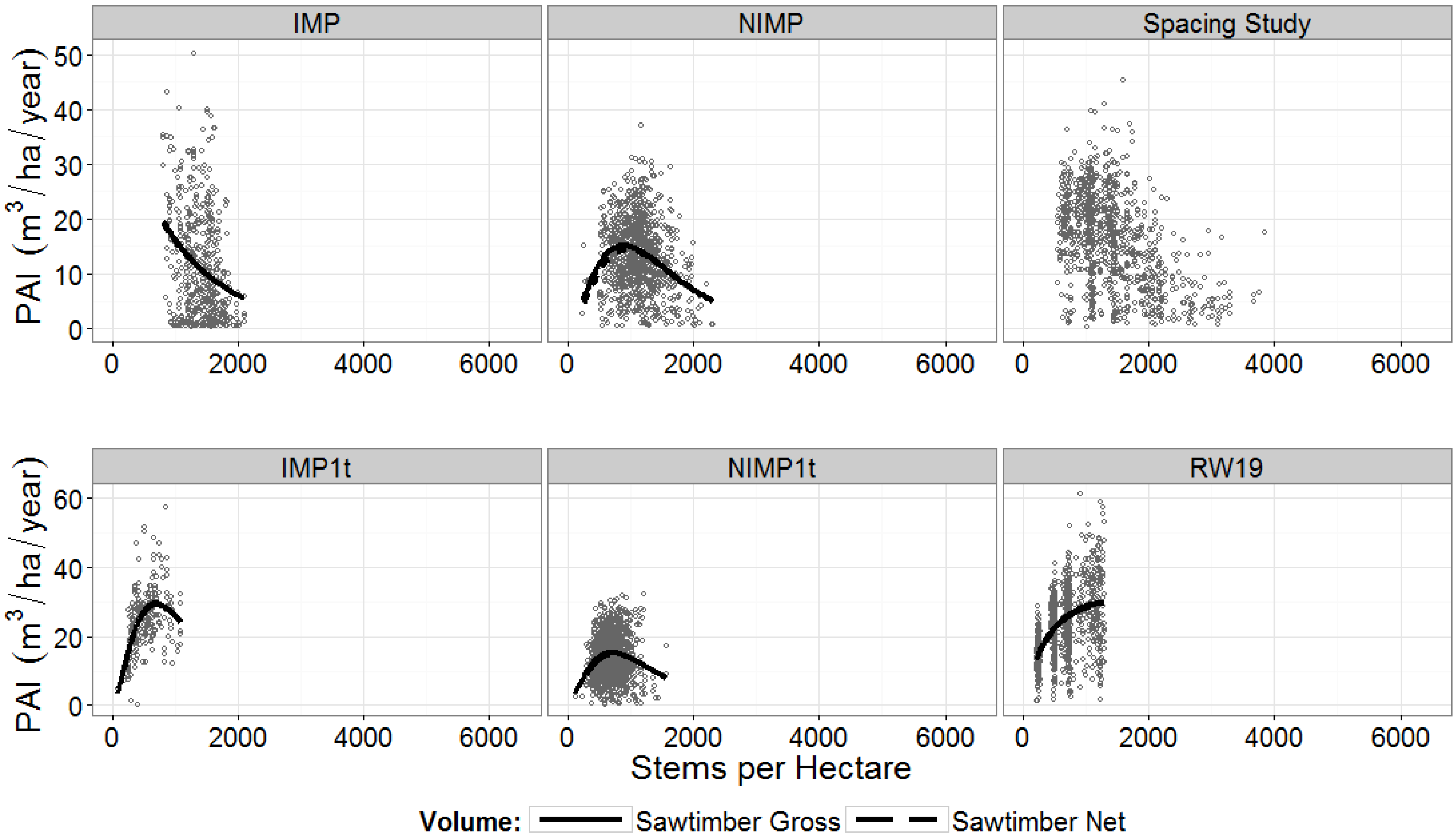


Figure 3.5: The relationship between sawtimber gross and net volume periodic annual increment (PAI) and the number of stems per hectare within unthinned and thinned datasets of loblolly pine.

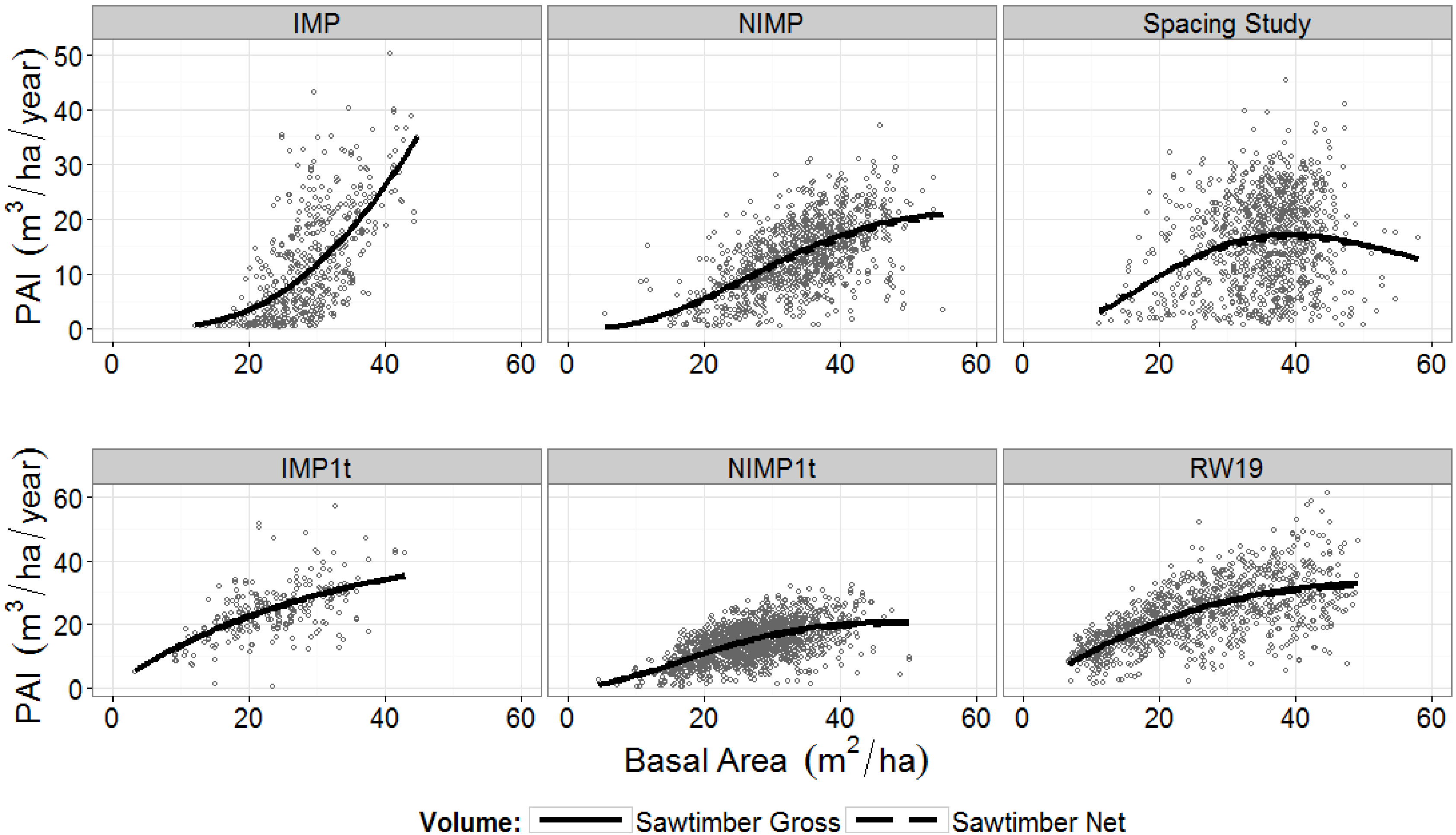


Figure 3.6: The relationship between sawtimber gross and net volume periodic annual increment (PAI) and basal area within unthinned and thinned datasets of loblolly pine.

Chapter 4: An Evaluation of Langsaeter's Hypothesis in Thinned and Unthinned Stands of Loblolly Pine

4.1. Abstract

The relationship between volume production and stocking has received much attention in the literature with the predominant theory that volume production is constant across a range of stocking. This relationship is typically summarized as Langsaeter's Hypothesis which states that "The total cubic-volume production of a stand is for all practical purposes constant and optimal for a wide range of stocking on a given site, age, and composition." Under this hypothesis volume production can be decreased, but not increased, by altering the level of stocking outside of this range. Recent studies have suggested that Lansaeter's Hypothesis is only accurate for young to middle aged stands while others indicate that it is not accurate at all. Data from a spacing trial with initial planting densities ranging from 750 to 6727 trees/ha along with data from a thinning experiment which includes thinning treatments which reduce the stocking from 247 to 1235 trees/ha were used to test Langsaeter's Hypothesis, and other alternate hypothesis, in loblolly pine. The relationship between volume production and stocking was found to be dependent on crown closure. An increasing pattern, whereby volume production increases with increasing stocking, was typically associated with the early stages of a rotation and immediately following thinning. Langsaeter's hypothesis held for stands in the middle to late stages of the roation.

4.2. Introduction

Defining the relationship between annual volume production and stocking has been and remains one of the most important and perplexing problems for forest managers. In order to meet the demands of wood and cellulose products, production forests are managed with the intent to increase either total or merchantable stem volume per unit area by maximizing volume growth. For the purposes of producing a desired product, forest stands can be managed through the initial number of trees planted per unit area and subsequently through thinning. While the determination of planting and thinning intensities are often guided by financial decisions, their effects on the general pattern between volume growth and stand density have not been established.

The search for a stand density where volume production is maximized has continued since the beginnings of forestry without producing a definite answer (Zeide 2004). Early beliefs were that undisturbed stands produced the highest maximum yields and that any decrease in the number of trees would result in a loss of volume growth (Zeide 2001). These beliefs were challenged in the late 18^{th} century most notably by one of the first "fathers of modern forestry" George Ludwig Hartig. Hartig (1795) advocated for the removal of dead and dying trees, when they could be sold profitably, in order to follow and support nature in its effects. Reventlow (1879) considered this view of thinning as too light and was convinced of an unimodal relationship whereby volume production is maximized when the number of trees is less than what is carried naturally in a stand. In contrast, Langsaeter (1941) hypothesized that cubic-volume production was constant and optimal across a wide range of density of stocking for a stand of a given age and composition on a given site. Under this hypothesis volume production can be decreased but not increased by altering levels of growing stock outside of this range. This pattern between volume production and stocking is often termed the 'Langsaeter Hypothesis'.

More recently, in an experiment designed to examine the effects of thinning on young Douglas-fir stands, Curtis et al. (1997) determined that the assumption of constant gross total cubic-volume production across a wide range of stocking levels is incorrect. Contradictory to the

Langsaeter Hypothesis, cubic-volume production increased with increasing numbers of stems per acre, though at a decreasing rate. Comparing the findings of Curtis et al. (1997) to the stagnation of lodgepole pine at unusually high densities, Zeide (2001) suggests that volume production must culminate, exhibiting a unimodal pattern, but at a higher density than is commonly observed and that the increasing pattern is simply the left portion of the entire relationship. From the conclusions of Curtis et al. (1997) which seemingly return the beliefs of the relationship between volume production and stand density to the beginning, Zeide (2001) fears an endless loop in the attempt to understand the relationship. Although, in a later paper Zeide concluded that volume production in loblolly pine increased with increasing stand density, measured as stand density index, up to the maximum densities that can be maintained on a given site (Zeide 2004).

The series of hypothesis concerning volume production were summarized by Smith et al. (1997) as: 1) volume production increases right up to the highest levels of density that can be maintained in nature, 2) production remains constant and optimum across a wide range of stand density from some lowest level at which there is full occupancy of growing space up to those levels at which excessive competition is postulated to restrict growth(i.e. Langsaeter's Hypothesis).; and 3) volume production follows a unimodal pattern with stand density. Similar to the findings of Curtis et al. (1997), in an evaluation of Langsaeter's Hypothesis in thinned plantations of Red Pine, Gilmore et al. (2005) concluded that the assumption of constant cubic-volume production was incorrect and that volume production increases with level of stocking. Although, confusingly, they mention in the discussion that their observed volume growth is consistent with Langsaeter's Hypothesis as well as hypothesis 3 of Smith et al. (1997).

The purpose of the research presented here was to analyze the relationship between volume production and stocking in loblolly pine using data from one Spacing Trial and from one experiment designed to examine the effects of thinning. The main objective was to test Langsaeter's Hypothesis, and other alternate hypotheses (Smith et al. 1997), to determine the relationship between volume production and stocking in loblolly pine stands. Additionally, multiple definitions of volume production were evaluated, included gross and net total and merchantable volume production to determine how the definition of growth affects the relationship between volume production and stocking.

4.3. Data

To evaluate the relationship between volume production and stocking in unthinned stands of loblolly pine, data from a spacing trial maintained by the Forest Modeling Research Cooperative (FMRC) at Virginia Polytechnic Institute and State University was used (Amateis and Burkhart 2012). The study design was nonsystematic, allowing the spacing to be varied in two dimensions on a factorial basis with a constant number of trees per plot. Data were available from four locations, two in the Coastal Plain and two in the Piedmont physiographic regions. At each location three replicates (blocks) were planted, and, in each replicate, 16 plots were planted allowing initial tree spacing to vary in all combinations of 1.2, 1.8, 2.4, and 3.6 meters. This design offered nine different initial tree spacings. Trees were measured annually for diameter and height until age 10 and annually for diameter and biannually for height thereafter. Diameter was measured at ground level from age 1 to age 5 and at breast height (4.5 ft, 1.37 m) from age 5 to age 25. Competing vegetation was chemically controlled up to age 3. To insure that most trees across all spacings and locations had achieved a diameter at breast height, and therefore volume, this analysis only used data from age eight to 25. Several plots were damaged at different ages by southern pine beetle, ice storms, or anthropogenic factors. A severe ice storm heavily damaged the plots at Pl at age 11; data from those plots after the ice storm were not be used. One of the plots at location P2, spacing 4.46 m^2 /tree (1.8X2.4 m), was abandoned at age 12 because of a southern pine beetle outbreak, and at age 19 the whole location was discarded because of thinning in the adjacent stand. At location C2 an ice storm after growing season 15 resulted in broken tops, which affected height. Data for age 16 was not used from that location for any analyses.

To examine the relationship between volume production and stocking in thinned stands an experimental study established jointly between the Forest Modeling Research Cooperative and the Forest Productivity Cooperative at Virginia Tech was used. This study was designed to examine the interaction of stand density and fertilization. Eight installations were established in the southern United States with each installation either a split-plot or randomized complete block design. Thinning treatments included four plots thinned to either 1235, 741, 494, or 247 stems per hectare. Fertilizer treatments included a non-treatment control for each thinning treatment and a one-time fertilization of 224 kg/ha N + 28 kg/ha P at the time of installation for each thinning treatment (5 plots). For this analysis only data from the thinned plots were used. At each installation these treatments were replicated four times. Planted trees were measured annually for diameter and either annually or biannually for total height. As this study was established over several years each installation had between two and seven measurements. Descriptive statistics for the two datasets are available in Table 4.1.

4.4. Methods

4.4.1. Defining Volume Production and Stand density

Volume production was defined as the periodic annual increment (PAI) based on: Net productivity: standing volume + volume removed in thinning; and Gross productivity: Net productivity + volume of mortality. Mortality volume was estimated as the volume of dead trees at the beginning of each growing period. Additionally, gross and net volume production was evaluated as total volume PAI, which uses all available trees, and merchantable volume PAI, which restricts the trees included in the volume production calculation based on diameter at breast height and upper stem diameter. Total gross and net volume were calculated using volume equations developed by Tasissa et al. (1997). They found that different coefficients were needed for thinned and unthinned stands. Therefore, total tree volumes for trees in unthinned (V_u) and thinned (V_t) plots were calculated as:

1) $V_u = 0.21949 + 0.00238D^2H$
2) $V_t = 0.25663 + 0.00239D^2H$

where D is tree diameter at breast height (in) and H is total tree height (ft). Using the volume ratio equations of Tasissa et al. (1997), merchantable volumes were calculated for unthinned (MV_u) and thinned (MV_t) plots as:

3) $MV_u = V_u exp\left(-0.78579 * (d^{4.9206}/D^{4.55878})\right)$
4) $MV_t = V_t exp\left(-1.04007 * (d^{5.25569}/D^{4.99639})\right)$

where *d* is the upper stem diameter limit and all other variables are defined as before. As these equations were fitted using English units, total and merchantable tree volumes were calculated in cubic feet and then converted to cubic meters.For the determination of merchantable volume diameter limits, two common merchantability specifications were used, pulpwood and sawtimber. Pulpwood was classified as any tree in the 13 cm (5 inch) diameter class or larger with an upper diameter limit of 7.6 cm (3 in). Sawtimber was classified as all trees in the 20 cm (8 inch) diameter class and greater with an upper diameter limit of 15.2 cm (6 in).

Within the Spacing Trial data volumes were calculated beginning at age six in order to insure that the majority of stems had obtained 1.3 meters in height and thus had a recorded D for calculating volume. As heights were in general measured biannually, PAI was calculated as the difference in volume, as defined above, over a two year period from age six to age 22 and then over a three year period from ages 22 to 25. Within the RW19 data, annual measurements were available resulting in PAI calculated as the annual difference in volume production. Thus, volume PAI (VPAI) can be calculated as:

5) $$VPAI = \frac{Volume_2 - Volume_1}{Age_2 - Age_1}$$

where, volume is calculate as defined above.

4.4.2. Evaluating Langsaeter's Hypothesis

The data used in this work were uniquely suited for evaluating Langsaeter's hypothesis. Where traditional growth and yield studies generally only include data from operational plantations and are subjected to a limited range in planting densities, the spacing trial data include a large range of initial planting densities. Additionally, traditional growth and yield studies examine thinning by reducing the density based on a percentage of basal area or reducing SDI to a designated value. As such, the residual stands from these thinning intensities can have largely different structures. Within the RW19 data, plots were selected based on strict criteria to reduce the variation in numbers of trees and average tree size. As the thinning treatments reduced the number of SPH to a common value (247, 494, 741, and 1247 SPH) the resulting residual stands had a similar stand structure across the eight locations.

In order to evaluate Langsaeter's hypothesis in unthinned stands a linear mixed-effects model approach was used to test the equality of volume production across planting densities within the Spacing Trial data for ages 8 to 25, testing at each age separately using the anova.lme and lme functions implemented in the nlme package (Pinheiro et al. 2014) within the open-source statistical environment R (R Core Team 2014). Random effects were included to account for the differences in location and block. Thus, the final models have the form:

6) $VPAI_{Amijk} = \mu_{Am} + a_i + a_{ij} + \varepsilon_{Amijk}$

Where, μ_{Am} is the average volume PAI for the *m*th planting density (*m* = 1, …, 9 planting densities) at age A(A = 8, 10, …, 22, 25 years of age); a_i and a_{ij} are the random effects at the location (*i* = 1, …, 4 locations) and block (*j* = 1, …, 3), respectively; *k* = 1, …, n_{Am} plots with spacing *m* at age A; and $\varepsilon_{Amijk} \sim N(0, \sigma^2)$.

Similarly, to evaluate Langsaeter's hypothesis in thinned stands a linear mixed-effects model approach was also used. However, because the eight locations were thinned at different ages, volume production was evaluated based on the number of years since treatment (yst). Random effects were also included to account for the differences in locations and blocks. Thus the final models for evaluating Langsaeter's hypothesis in thinned stands have the form:

7) $VPAI_{Ylijk} = \mu_{Yl} + a_i + a_{ij} + \varepsilon_{Ylijk}$

Where, μ_{Yl} is the average volume PAI for the *l*th thinning treatment (*l* = 1, …, 4 thinning treatments) at yst Y(Y = 1, …, 6 years since treatment); a_i and a_{ij} are the random effects at the location (*i* = 1, …, 8 locations) and block (*j* = 1, …, 4), respectively; *k* = 1, …, n_{Yl} plots with spacing *l* at yst Y; and $\varepsilon_{Ylijk} \sim N(0, \sigma^2)$.

When volume production was determined to be significantly different among the planting densities in the Spacing Trial data and among the thinning intensities in the RW19 data a

Tukey's multiple comparison test was used to determine where those differences occurred. This analysis was carried out using the glht function in the multcomp package in R (Torsten et al. 2008).

4.5. Results

4.5.1. Total Volume PAI in Unthinned Stands

The analysis of variance tests (Table 4.2) show that at $\alpha = 0.05$ there were several instances where volume production was not significantly different across all planting densities for a given age. Equality in mean volume production occurred at age 20 for pulpwood net PAI, and at age 25 for total gross, pulpwood gross and net, and sawtimber net PAI. These results directly contradict Langsaeter's hypothesis in that an excessive number of trees did not cause a reduction volume production, at least at those ages where volume production was not significantly different. Due to the large range in initial planting densities and the nature of maximum size-density relationships it is reasonable to believe that the number of trees per hectare in the largest planting density is close to the maximum that can be naturally sustained. As such, it is unlikely that a larger number of trees would result in a decrease in volume production.

Plotting the mean total gross and net volume PAI in relation to the mean number of SPH across all nine planting densities indicated a general pattern with age (Figure 4.1). From eight to 12 years of age total gross volume generally increased with increasing number of stems per hectare, although at a decreasing rate. After which total gross volume production was reduced in the larger densities resulting in a close to constant pattern across the range of densities in the data. From ages 18 to 20 volume production generally decreased withed an increasing number of stems per hectare. By age 25 total gross volume production was similar across all planting densities, although the range in mean numbers of SPH had been greatly reduced.

The results of a Tukey's multiple comparison test also indicated increasing volume production with increasing planting density from ages eight to 12. Although, there were several instances where gross and net PAI were not significantly different among planting densities (Table 4.3). Of particular interests is the equality in total gross and net volume production across planting densities 3363 to 6727 SPH. This is another indication that Langsaeter's plateau can extend out to the maximum densities that can be carried on a given site. Additionally, the Tukey test could not separate planting densities 1121 to 1494 SPH, 1494 to 1681 SPH, or 1681 to 2989 SPH within total gross volume PAI. This suggests that instead of a simple increasing pattern up to Langsaeter's plateau the relationship between volume production and stocking can be a stair stepping pattern with mini plateaus across a relatively smaller range of numbers of SPH. Within this pattern volume production gradually increases in steps up to the maximum. However, by age 10 this pattern was not as pronounced as volume production was not significantly different across planting densities 1121 to 2989 SPH or across planting densities 1681 to 6727 SP for total gross volume PAI. The pattern was even less distinct in total net PAI where volume production was not significantly different across planting densities 1121 to 2727 SPH with the exception of the 3363 SPH planting density. Additionally, at age 10 mean total gross and net volume PAI was maximized in planting densities 1681 to 6727 SPH. Total gross volume PAI would not reach this maximum again in planting densities 2989 SPH and larger out to age 25.

Total gross volume PAI began to decrease after age 10 in the larger planting densities while still increasing in the smaller planting densities. Although the analysis of variance indicated that volume production was slightly significantly different at age 14 (p-value = 0.45), the results of the Tukey test did not show any significant differences across all planting densities. After age 16 total gross PAI continued to increase in planting densities less than 1681 SPH while simultaneously decreasing in planting densities greater than 2989 SPH. This effect resulted in the general decreasing pattern seen in planting densities greater than 2242 SPH. However, by age 25 total gross PAI was reduced in the lower planting densities such that gross volume production was not significantly different across all planting densities.

After age 10 mortality began to noticeably affect total net volume production as seen in the divergence between the lines for total gross and net volume PAI in Figure 4.1. At age 12 total net PAI was significantly higher in the 2242 to 6727 SPH planting densities as compared to the 6727 SPH planting density. This was the first instance where Langsaeter's hypothesis would prove correct in that volume production increased up to a plateau and after which decreased due to an extreme amount of stocking. Similarly, at age 14 total net volume PAI was in general constant across planting densities 747 to 4484 SPH followed by a significant decrease in the 6727 planting density. After age 14 total net volume production followed a general decreasing pattern with increasing stocking out to age 25. Although, the relationship between total net PAI and stocking followed a stair stepping pattern. By age 25 total net volume production was not significantly different across planting densities 1121 to 6727 SPH. In general, Langsaeters hypothesis is accurate for these data at certain ages. However, the range of the constant portion of the relationship, where production is maximized, was dependent on age. The data indicated that maximum range of the constant portion generally decreased with age. Furthermore, a three segment pattern where volume production increases to the plateau and then decreases after the plateau does not hold for all ages in these data.

4.5.2. Merchantable Volume PAI in Unthinned Stands

Different results were seen when relating planting density to pulpwood volume PAI as compared to total volume PAI. Restricting the growth calculation to include only trees of 13 cm in diameter or greater resulted in smaller differences between pulpwood gross and net PAI (Figure 4.2). Due to planting density having a direct effect on average tree diameter, planting densities less than 2989 SPH initially had a larger number of trees growing into the pulpwood merchantability specifications at age eight. This resulted in planting densities 1121 to 2242 SPH have significantly larger pulpwood volume production than planting densities greater than or equal to 3363 SPH (Table 4.4). At age 10 an even larger proportion of trees grew into the pulpwood merchantability specifications resulting in the maximum pulpwood volume PAIs for planting densities 1681 to 3363 SPH. At this age pulpwood volume production was significantly larger in the 2242 SPH planting density as compared to the 747 to 1494 SPH and 4484 to 6727 SPH planting densities. However, pulpwood gross and net volume was not significantly different across plating densities 1681 to 3363 SPH. Again, the relationship between volume production and planting density seemed to follow a stair stepping pattern increasing up to a plateau where volume production was maximized across the range of planting densities 1681 to 3363 SPH followed by a decrease in volume production out to the 6727 planting density. The range in planting densities where pulpwood volume production was maximized then shifted to the right at age 12 with planting densities 2242 to 4484 SPH having significantly larger pulpwood gross and net PAIs than the 747, 1121, and 6727 SPH planting densities.

The differences in pulpwood volume production across planting densities became smaller beginning at age 14. From age 14 to 16 there were only slight, yet significant differences in pulpwood volume PAI across planting densities. However, by age 20 the results of the Tukey test did not show any significant differences in pulpwood gross or net PAI across all planting densities. At age 22 a general decreasing pattern in pulpwood volume production with increasing stocking was indicated in Figure 4.2. However, at age 25 there were again no significant differences in pulpwood gross PAI across all planting densities.

Similar results occurred within sawtimber gross and net volume PAI. Again, because planting density has a direct effect on average diameter, lower planting densities initially had higher sawtimber volume production (Figure 4.3). At age eight, there was only one observation of sawtimber volume PAI across all planting densities, which occurred in the 747 SPH planting density. Trees began to grow into the sawtimber merchantability specifications at age 10 within the 747 to 2242 SPH planting densities and by age 18 all planting densities had observations of sawtimber PAI. From ages 14 to 18 planting densities 747 to 1681 SPH were significantly producing more sawtimber gross and net volume than all other planting densities (Table 4.5). Additionally, sawtimber gross and net volume PAI was maximized for these densities at age 18. Sawtimber volume PAI was again maximized at age 22 for planting densities 747 to 2242 SPH. Although, at no age did planting densities greater than 2242 SPH achieve the maximum mean sawtimber gross and net PAI which was exhibited in planting densities less than or equal to 2242 SPH. By age 25 all planting densities were producing a similar amount of sawtimber volume annually. The only significant difference at age 25 was a larger sawtimber gross PAI in planting density 2242 SPH as compared to the 6727 SPH planting density.

Differences between sawtimber gross and net PAI were even less pronounced than in total and pulpwood volume PAI. This was due to a lower mortality rate in larger stems which was expected as larger trees are generally better competitors. The divergence between mean gross and net PAI began at age 20, as indicated in Figure 4.3, in the lower planting densities.

Because the effect of planting density on average tree diameter resulted in a larger proportion of trees in the sawtimber merchantability class in the lower planting densities, there was a higher probability of observing mortality in sawtimber class trees at those densities. However, the reduction in mean net production below that of the mean gross production appeared to be minimal.

Again, Langsaeter’s hypothesis is partly true for these data in that maximum sawtimber volume production at a given age is constant across a wide range of densities. However, the maximum range of the constant portion of the relationship increased with age, similar to total volume PAI. Additionally, a fourth segment occurred after the linear decreasing segment from ages 12 to 20. The results of the Tukey test indicate that there is a second plateau where sawtimber volume production is constant but significantly less than the maximum. This second plateau is indicated by the equality in sawtimber gross volume PAI among planting densities 2242 to 3363 SPH at age 12, planting densities 2989 to 4484 SPH at age 16, and planting densities 3363 to 6727 SPH at age 20.

4.5.3. Total and Merchantable Volume PAI in Thinned Stands.

The results of the analysis of variance tests show that at α=0.05 there were significant differences in total volume PAI among thinning treatments up to five years after thinning (Table 4.2). However, by six years after thinning a similar amount of total gross and net volume was being produced annually across all thinning treatments. Plotting the mean total gross and net volume PAI in relation to the mean number of stems per hectare across thinning treatments for each year after thinning indicated a strong linear relationship of increasing total volume production with increasing density in the first three years after treatment (Figure 4.4). The results of the Tukey test mirror this pattern, showing significant differences among all four thinning treatments from one to three years (Table 4.6). Figure 4.4 indicates that volume production in the larger residual density thinning treatments was reduced beginning at four years after thinning while volume production was increasing in the smallest residual density thinning treatments out to six years. This effect resulted in no significant differences in total volume production between thinning treatments 741 and 1235 SPH at four years after thinning or among thinning treatments 494 to 1235 SPH at five years after thinning.

Plotting the mean gross and net PAI for each thinning treatment in relation to the number of years since treatment shows a general increasing pattern with increasing age in the 247 and 494 SPH thinning treatments (Figure 4.5). As the mean number of trees was fairly constant within these thinning treatments, due to little mortality, it is reasonable to assume that the increase in production with an increase in age is due to an expansion in the canopy. Different patterns were exhibited in the 741 and 1235 SPH treatments. From four to six years after treatment volume production was fairly stable in the 741 SPH treatment, while over the same period volume production in the 1235 SPH treatment exhibited a decreasing pattern. Mortality began to affect total net PAI as early as two years after treatment in the 1235 SPH thinning treatment. However, there were no differences between mean total gross and net PAI in the 247 and 494 SPH thinning treatments for the entire six year period after thinning. The divergence of mean total gross and net growth is an indicator of the second stage of self-thinning, the distance-dependent stage, and suggests a nearly closed dominant canopy.

The results of the analysis of variance test were similar for both total and merchantable volume PAI. The p-values indicated significant differences among treatments up to five years after thinning and no significant differences at six years after thinning for both pulpwood and sawtimber PAI (Table 4.2). Results from the multiple comparison test also indicated that there were no differences in the conclusions between total or pulpwood volume PAI. Because the thinning treatments were from below only a small proportion of trees (generally less than 5%) did not meet the merchantability specifications for pulpwood. This resulted in large similarities between total and pulpwood volume PAI.

Slightly different results were indicated in the multiple comparison test for sawtimber volume PAI. In the first two years after thinning mean sawtimber volume PAI was not significantly different within the 494 and 741 SPH thinning treatments for both gross and net production (Table 4.6). However, at three years after treatment mean sawtimber volume production was significantly different for all thinning treatments with PAI increasing with increasing stocking. Similar to total and pulpwood volume PAI, sawtimber volume production began to slow in the 1235 SPH thinning treatment at four years after thinning and by five years after thinning there was no significant difference in mean sawtimber volume PAI within the 494 to 1235 SPH thinning treatment (Figure 4.6). However, unlike total and pulpwood volume PAI, significant differences were concluded from sawtimber gross PAI at six years after treatment. The results from the multiple comparison tests indicated that the mean sawtimber volume PAI was significantly larger within the 747 SPH thinning treatment than in the 247 SPH thinning treatment. Although, there were no significant differences for sawtimber net volume PAI at six years after treatment.

4.6. Discussion and Conclusions

Results from the spacing trial data indicate that at early ages, before the onset of distance-dependent mortality, total volume production is constant across a wide range of stocking.

Although, there seems to be no reduction in total volume PAI at higher levels of stocking. These results suggest that Langsaeter's hypothesis is partially true during the first stage of self-thinning. The relationship between total volume production and stocking became more complex after crown closure. Initially, mortality caused a decrease in total net volume PAI at larger levels of stocking resulting in the pattern hypothesized by Langsaeter. However, total gross volume PAI was relatively constant across a wide range of stocking during this initial period with no decrease exhibited at larger levels of stocking. Both patterns were fairly consistent for the middle ages of a traditional rotation (12 to 16 years) for both total gross and net volume PAI. Within ages approaching a general rotation age (18 to 25 years), mortality related suppression of stand growth led to a decrease in total gross volume PAI in the larger levels of stocking resulting in a decrease of the maximum range of the constant portion of the relationship. The overall results for total volume PAI indicate that the relationship between volume production and stocking is dynamic, changing with age from increasing to constant, without a decrease at larger levels of stocking, to the pattern hypothesized by Langsaeter.

The patterns exhibited between pulpwood volume PAI and stocking were different from those in total volume PAI at early ages. Particularly in ages eight to 12 where the pattern changed from unimodal to the typical pattern of Langsaeter. This is due to the effect of density on tree diameter resulting in more trees growing into the pulpwood merchantability class in relatively lower levels of stocking. However, due to the relatively small restrictions on diameters in the pulpwood merchantability class the patterns with stocking were highly similar between total gross volume PAI and pulpwood gross volume PAI by age 14 and thereafter. A similar effect of density on average diameter was seen when relating sawtimber volume PAI to stocking. At early ages sawtimber class trees occurred in the lowest levels of stocking resulting in a decreasing pattern in sawtimber volume PAI with increasing stocking. Sawtimber volume PAI became constant and optimal at age 16 and by age 20 the patterns with stocking were similar between all three measures of gross volume production (total, pulpwood, and sawtimber). Unlike total volume PAI, there was never a large divergence between mean sawtimber gross PAI and mean sawtimber net PAI due to larger trees being better competitors.

Overall, Langsaeter's hypothesis holds partially true for unthinned stands in that volume production can be constant and optimal across a wide range of stocking. However, the results show that the relationship between volume production and stocking is more complex and changes with age. Within their work *The Practice of Silviculture*, Smith et al. (1997) suggest that the optimal or unimodal pattern occurs at youth and middle ages while the increasing pattern best fits the final stages of the rotation. The patterns exhibited in both total and merchantable volume production in this work indicate the opposite, that the increasing pattern occurs in youth while the constant pattern is more accurate for middle ages up to the final stages of the rotation.

Collectively the results from thinned plots demonstrate that total volume production before canopy closure is highly related to stocking in the residual stand after thinning, increasing up to the highest levels. However, when the canopy is near full and density-dependent mortality has begun total gross volume PAI is constant across a range of stocking. This indicates that both an increasing pattern and a constant pattern between volume production and stocking in thinned stands can be exhibited and that the pattern depends on the stage of self-thinning. Curtis et al. (1997) concluded that volume production increased with increasing stocking, at a decreasing rate, and that the assumption of a constant pattern was incorrect. However, their data included thinning treatments whereby plots were thinned reducing basal area by a percentage of a control plot. The treatment plots were then maintained at a certain percentage of basal area less than the control by imposing subsequent thinnings after an initial 10 feet of height growth and at intervals of 10 feet thereafter. As such, each plot would have been subjected to a broken canopy due to gaps created from thinning. Aside from the differences in growing stock, one difference between the data used by Curtis et al. (1997) the RW19 data used in this work was that the plots only received on thinning. This resulted in the treatment plots recovering gaps in the canopy, with timing dependent on residual stocking, indicating both increasing and constant patterns. The results of this work do not contradict the conclusions of Curtis et al. (1997) but reinforce that volume production is negatively affected when stands are reduced below full occupancy by thinning, resulting in an increasing pattern. However, the results show that if full occupancy of the canopy is regained after thinning then a constant pattern between volume production and density can occur.

Literature Cited

Amateis, R.L., and H.E. Burkhart. 2012. Rotation-age results from a loblolly pine spacing trial. Southern Journal of Applied Forestry 36(1):11-18.

Curtis, R.O., D.D. Marshall, and J.F. Bell. 1997. LOGS: A pioneering example of silvicultural research in coast Douglas-Fir. Journal of Forestry 95(7):19-25.

Gilmore, D.W., T.C. O'Brien, and H.M. Hoganson. 2005. Thinning red pine plantations and the Langsaeter Hypothesis: A Northern Minnesota Case Study. Northern Journal of Applied Forestry 22(1):19-26.

Hartig, G.L. 1795. Anweisung zu taxation der forsten oder zur bestimmung des holzertrags der walder. In: KommiBion bei Buchhandler Heyer.

Langsaeter, A. 1941. Om tynning i enaldret gran-og furuskog. Medd. Nor. Skogforsosves 8:131-216.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarker, and R Core Team. 2014. _nlme: Linear and nonlinear mixed effects models_. R package version 3.1-117, <URL: http://CRAN.R-project.org/package=nlme>.

R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http:??www.R-project.org/.

Reventlow, C.D.F. 1879. Forslag til en forbedret Skovdrift grundet, paa Undersogelser over Traeernes Vegetation I Denmarks og Slesvigs Skove. In: Kjobenhavn, 1879, Ed. in English 1960: A treatise of forestry, Society of Forest History, Horsholm Denmark.

Smith, D.M., B.C. Larson, M.J. Kelty, and P.M. Ashton. 1997. The Practice of Silviculture. John Wiley & Sons, New York, NY.

Tasissa, G., H.E. Burkhart, and R.L. Amateis. 1997. Volume and taper equations for thinned and unthinned loblolly pine trees in cutover, site-prepared plantations. Southern Journal of Applied Forestry 21(3):146-152.

Torsten, H., B. Bretz, and P. Westfall. 2008. Simultaneous inference in general parametric models. Biometrical Journal 50(3):346-363.

Zeide, B. 2001. Thinning and growth: A full turnaround. Journal of Forestry 99(1):20.

Zeide, B. 2004. Optimal stand density: A solution. Canadian Journal of Forest Research

34(4):846-854.

Table 4.8: Descriptive statistics for datasets of thinned and unthinned loblolly pine.

Dataset	Stand Parameter	N	Mean	Std Dev	Minimum	Maximum
Spacing Trial		1606				
	Age (years after planting)		14.30	5.09	8.00	25.00
	Basal area (m^2 per ha)		32.06	9.42	7.84	59.18
	Trees per ha		2152.20	1266.28	549.18	6727.43
	Site Index (m, base age 25 years)		20.35	1.41	16.07	23.31
RW19		928				
	Age		17.31	2.44	13.00	22.00
	Basal area (m^2 per ha)		25.34	10.57	6.59	49.13
	Trees per ha		638.46	328.84	202.18	1284.95
	Site Index (m, base age 25 years)		22.41	1.94	18.29	27.13

Table 4.9: P-values for the significance of: 1) planting density effect in model 6 for gross and net total, pulpwood, and sawtimber periodic annual increment (m^3/ha/year) by age; and 2) thinning treatment effect in model 7 for gross and net total, pulpwood, and sawtimber periodic annual increment (m^3/ha/year) by the number of years since treatment (YST).

Spacing Trial - Unthinned						
	Total		Pulpwood		Sawtimber	
Age	Gross	Net	Gross	Net	Gross	Net
8	<0.001	<0.001	<0.001	<0.001	NA	NA
10	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
12	<0.001	<0.001	0.001	<0.001	<0.001	<0.001
14	0.045	<0.001	0.002	0.002	<0.001	<0.001
16	**0.012**	<0.001	0.0061	<0.001	<0.001	<0.001
18	<0.001	<0.001	<0.001	0.001	<0.001	<0.001
20	0.002	<0.001	0.042	**0.266**	<0.001	<0.001
22	<0.001	<0.001	<0.001	0.002	<0.001	<0.001
25	**0.586**	0.014	**0.668**	**0.053**	0.036	**0.216**
RW19 - Thinned						
	Total		Pulpwood		Sawtimber	
YST	Gross	Net	Gross	Net	Gross	Net
1	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
2	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
3	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
4	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
5	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
6	**0.067**	**0.232**	**0.069**	**0.204**	**0.05**	**0.239**

Table 4.10: Results of a Tukey's multiple comparison test for differences in mean gross and net total periodic annual increment (PAI, m^3/ha/year) among nine different planting densities by age.

	Planting Density								
	747	1121	1494	1681	2242	2989	3363	4484	6727
Age	Total Gross PAI								
8	a	b	bc	cd	de	df	efg	fg	g
10	a	b	bc	bd	bd	bd	d	cd	d
12	a	ab	bc	bd	cd	cd	d	d	cd
14	a	a	a	a	a	a	a	a	a
16	ab	b	b	b	b	a	b	ab	ab
18	bd	d	cd	bd	cd	abc	ab	ab	a
20	ab	b	b	ab	ab	ab	ab	ab	a
22	bc	c	c	ac	c	ac	ac	ab	a
25	a	a	a	a	a	a	a	a	a
Age	Total Net PAI								
8	a	b	bc	cd	d	de	de	e	de
10	a	b	bc	bc	bc	bc	c	bc	bc
12	a	abc	bd	ad	d	cd	d	d	ab
14	bc	bc	bc	bc	c	bc	bc	b	a
16	cd	d	cd	bd	bc	a	bd	ab	a
18	cd	d	d	cd	cd	bc	ab	ab	a
20	bc	c	c	ac	ac	ab	ab	a	ab
22	c	ac	ac	bc	ab	bc	b	b	ab
25	b	ab	ab	ab	ab	a	ab	ab	ab

Table 4.11: Results of a Tukey's multiple comparison test for differences in mean gross and net pulpwood periodic annual increment (PAI, m^3/ha/year) among nine different planting densities by age.

	Planting Density								
	747	1121	1494	1681	2242	2989	3363	4484	6727
Age	Pulpwood Gross PAI								
8	bc	c	c	c	c	bc	b	a	ab
10	ab	bcd	bcd	ce	e	ce	de	bc	a
12	ab	ab	bc	bd	cd	cd	d	cd	a
14	a	ab	ab	ab	b	ab	b	ab	ab
16	ab	ab	ab	ab	ab	a	ab	ab	b
18	ab	b	b	ab	ab	ab	a	ab	a
20	a	a	a	a	a	a	a	a	a
22	bc	c	c	bc	c	ac	ac	ab	a
25	a	a	a	a	a	a	a	a	a
Age	Pulpwood Net PAI								
8	bc	c	c	c	c	bc	b	a	ab
10	ab	bcd	bcd	ce	e	ce	de	bc	a
12	ab	ab	bc	ac	c	c	c	c	a
14	a	ab	ab	ab	b	ab	b	ab	ab
16	ab	ab	ab	ab	a	a	b	b	b
18	ac	c	c	ac	bc	ac	ab	ac	a
20	a	a	a	a	a	a	a	a	a
22	c	bc	ac	ac	ac	ac	ab	a	ab
25	b	ab	ab	ab	ab	a	ab	ab	b

Table 4.12: Results of a Tukey's multiple comparison test for differences in mean gross and net sawtimber periodic annual increment (PAI, m^3/ha/year) among nine different planting densities by age.

	Planting Density								
	747	1121	1494	1681	2242	2989	3363	4484	6727
Age	Sawtimber Gross PAI								
8									
10	b	a	a	a	b				
12	c	c	b	b	a	a	a		
14	c	c	c	c	b	a	a		
16	c	c	c	c	b	a	a	ab	
18	c	c	c	c	b	a	a	a	a
20	b	b	b	b	b	ab	a	a	a
22	cd	cd	cd	cd	d	bd	bc	a	a
25	ab	ab	ab	ab	b	ab	ab	a	ab
Age	Sawtimber Net PAI								
8									
10	b	a	a	a	b				
12	c	c	b	b	a	a	a		
14	c	c	c	c	b	a	a		
16	c	c	c	c	a	ab	b	ab	
18	c	c	c	c	b	a	a	a	a
20	b	b	b	b	b	ab	a	a	a
22	b	b	b	b	b	b	b	a	a
25	a	a	a	a	a	a	a	a	a

Table 13: Results of a Tukey's multiple comparison test for differences in mean gross and net total, pulpwood, and sawtimber periodic annual increment (PAI, m^3/ha/year) among four different thinning treatments by the number of years since treatment (YST).

	Thinning Treatment											
	247	494	741	1235	247	494	741	1235	247	494	741	1235
YST	Total Gross PAI				Pulpwood Gross PAI				Sawtimber Gross PAI			
1	a	b	c	d	a	b	c	d	a	b	b	c
2	a	b	c	d	a	b	c	d	a	b	b	c
3	a	b	c	d	a	b	c	d	a	b	c	d
4	a	b	c	c	a	b	c	c	a	b	c	c
5	a	b	b	b	a	b	b	b	a	b	b	b
6	a	a	a	a	a	a	a	a	a	a	a	a
YST	Total Net PAI				Pulpwood Net PAI				Sawtimber Net PAI			
1	a	b	c	d	a	b	c	d	a	b	b	c
2	a	b	c	d	a	b	c	d	a	b	b	c
3	a	b	c	d	a	b	c	d	a	b	c	c
4	a	b	bc	c	a	b	bc	c	a	b	c	c
5	a	b	b	b	a	b	b	b	a	b	b	b
6	a	a	a	a	a	a	a	a	a	a	a	a

Figure 4.7: Mean total gross and net volume periodic annual increment (m^3/ha/year) in relation to the mean number of stems per hectare across nine planting densities from stand ages 8 to 25.

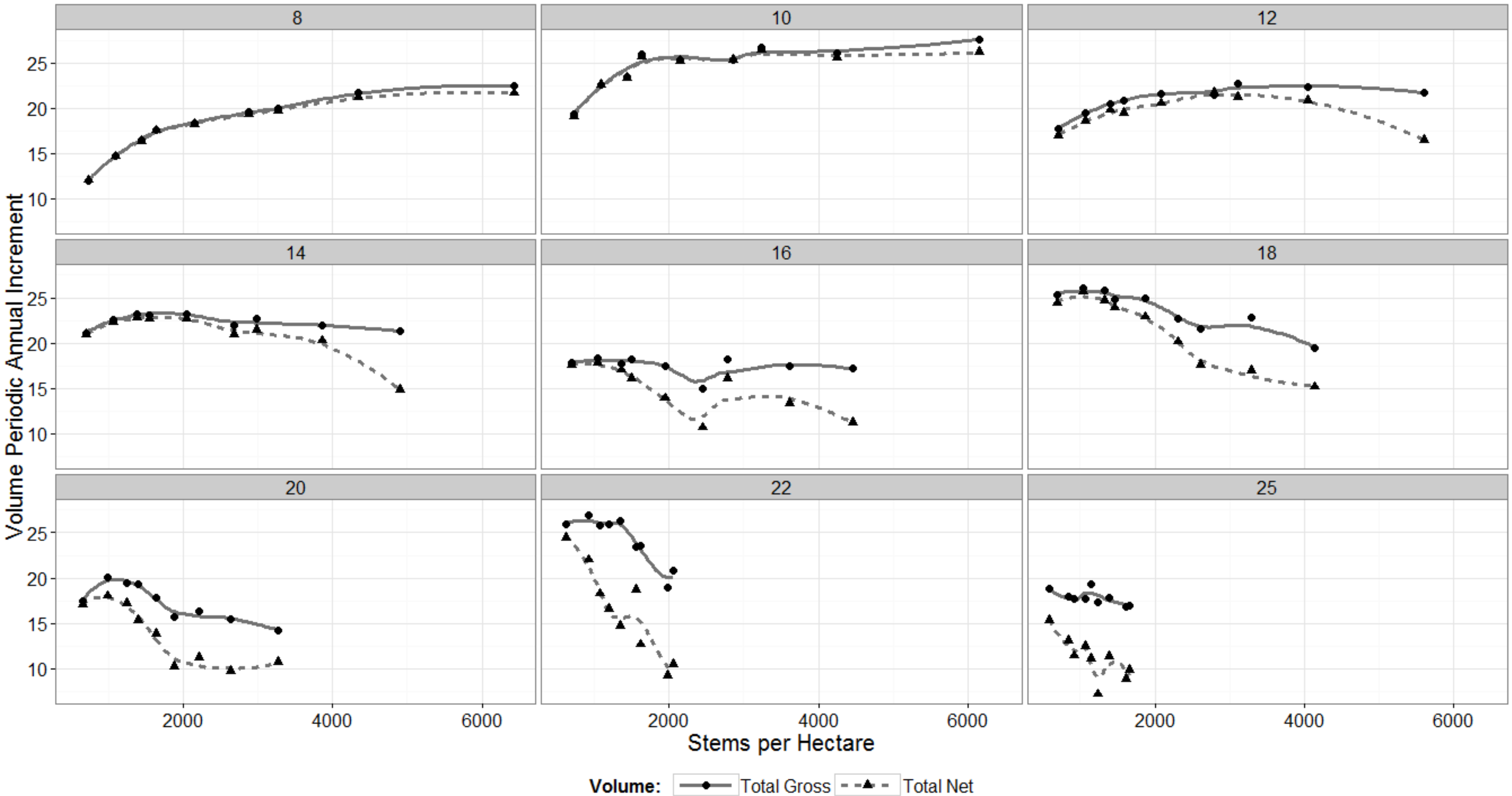


Figure 4.8: Mean pulpwood gross and net volume periodic annual increment (m^3/ha/year) in relation to the mean number of stems per hectare across nine planting densities from stand ages 8 to 25.

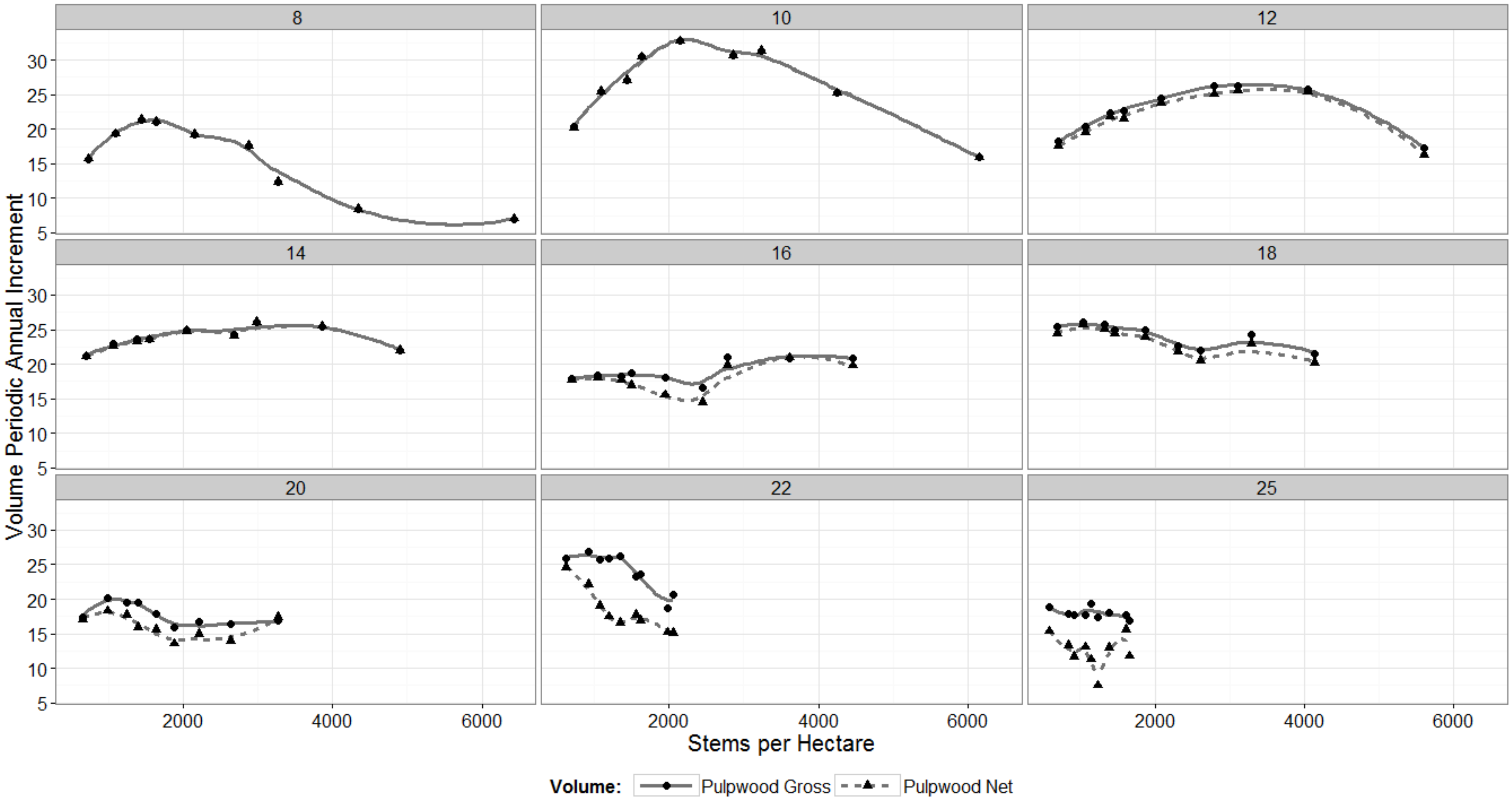


Figure 4.9: Mean sawtimber gross and net volume periodic annual increment (m^3/ha/year) in relation to the mean number of stems per hectare across nine planting densities from stand ages 8 to 25.

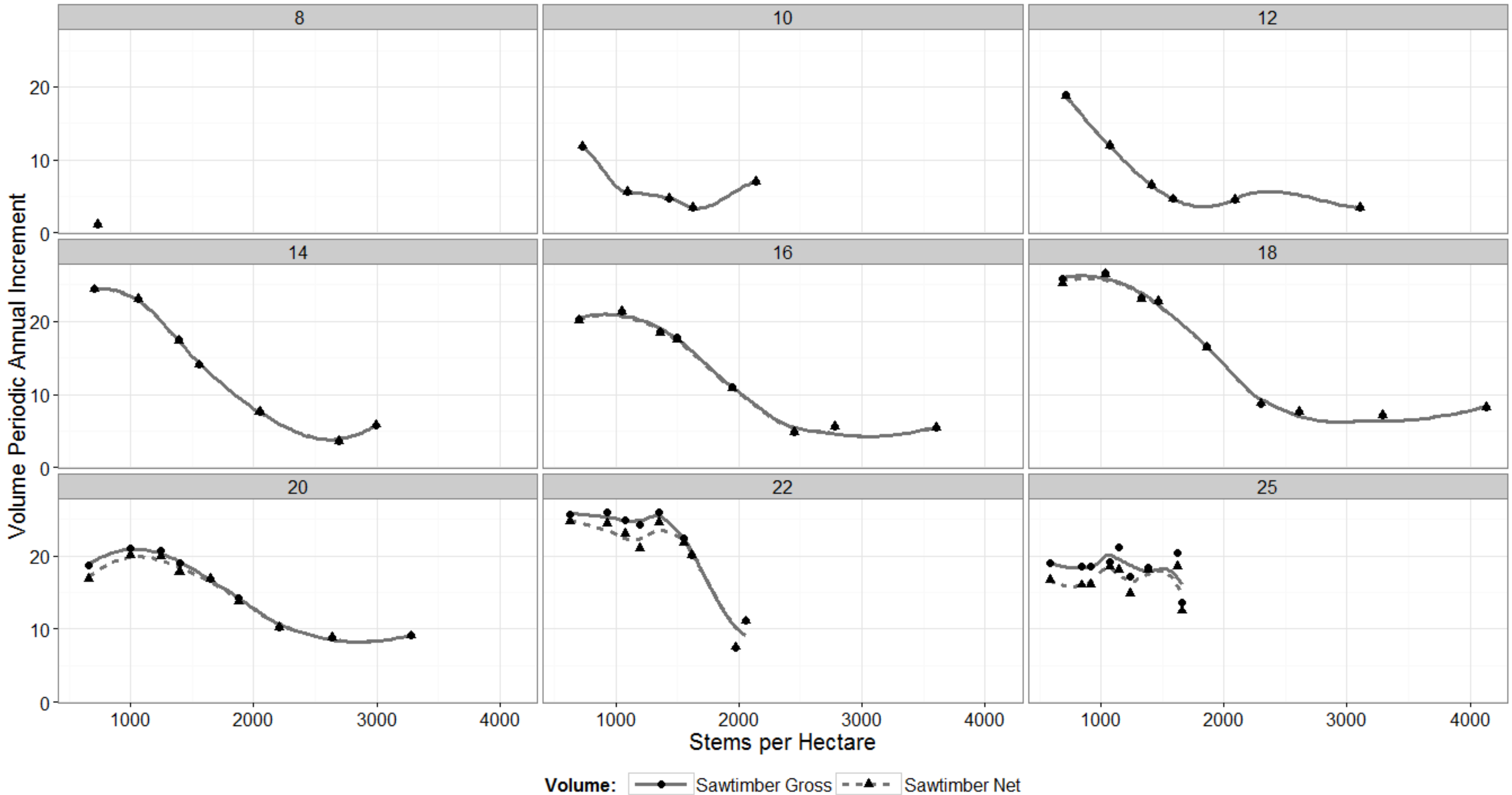


Figure 4.10: Mean total gross and net volume periodic annual increment (m^3/ha/year) in relation to the mean number of stems per hectare across four thinning treatments from one to six years after thinning.

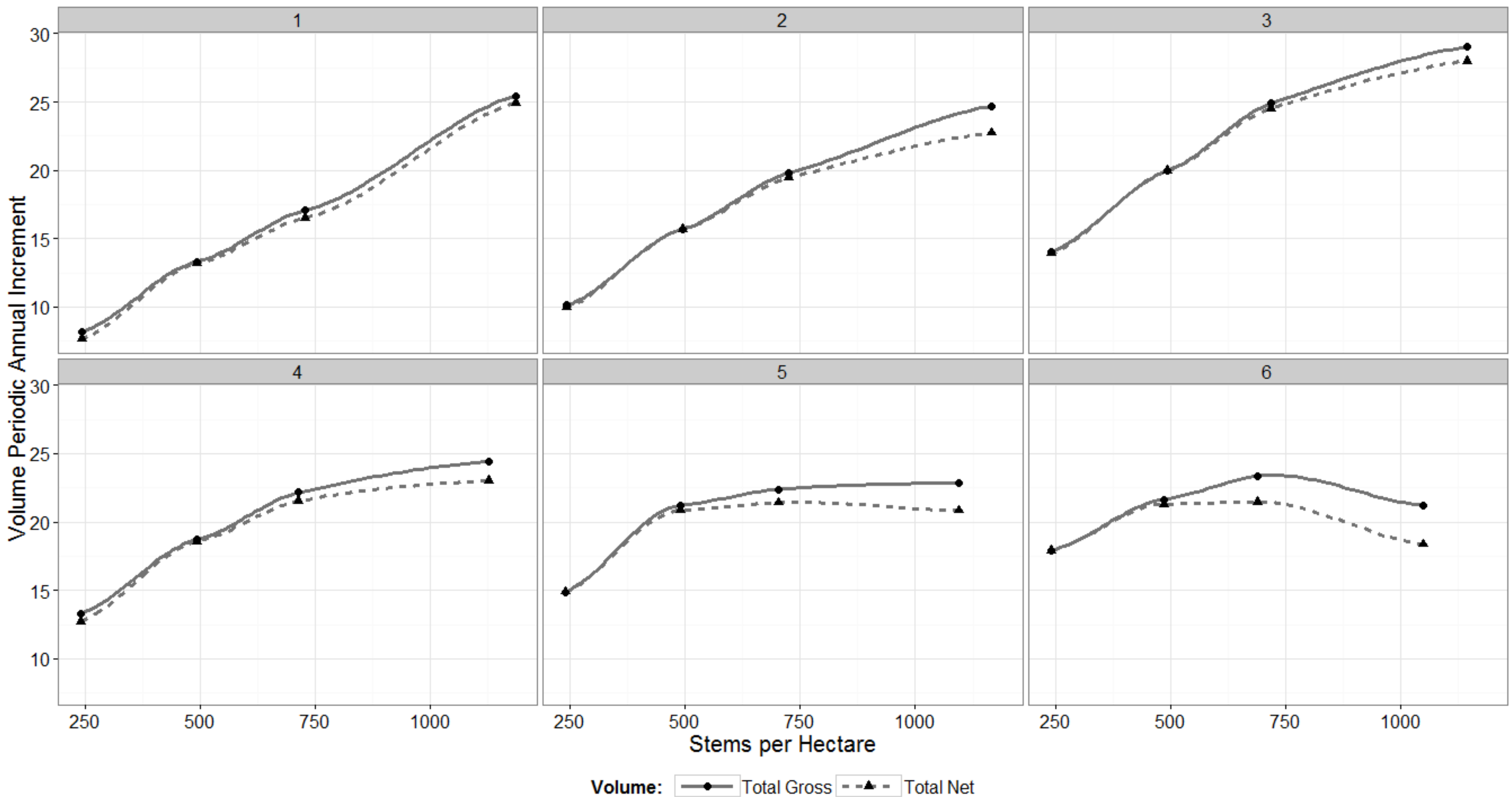


Figure 4.11: Mean sawtimber gross and net volume periodic annual increment (m^3/ha/year) in relation to the mean number of years since treatment across four levels of thinning whereby the residual stand was reduced to 247, 494, 741, and 1235 stems per hectare.

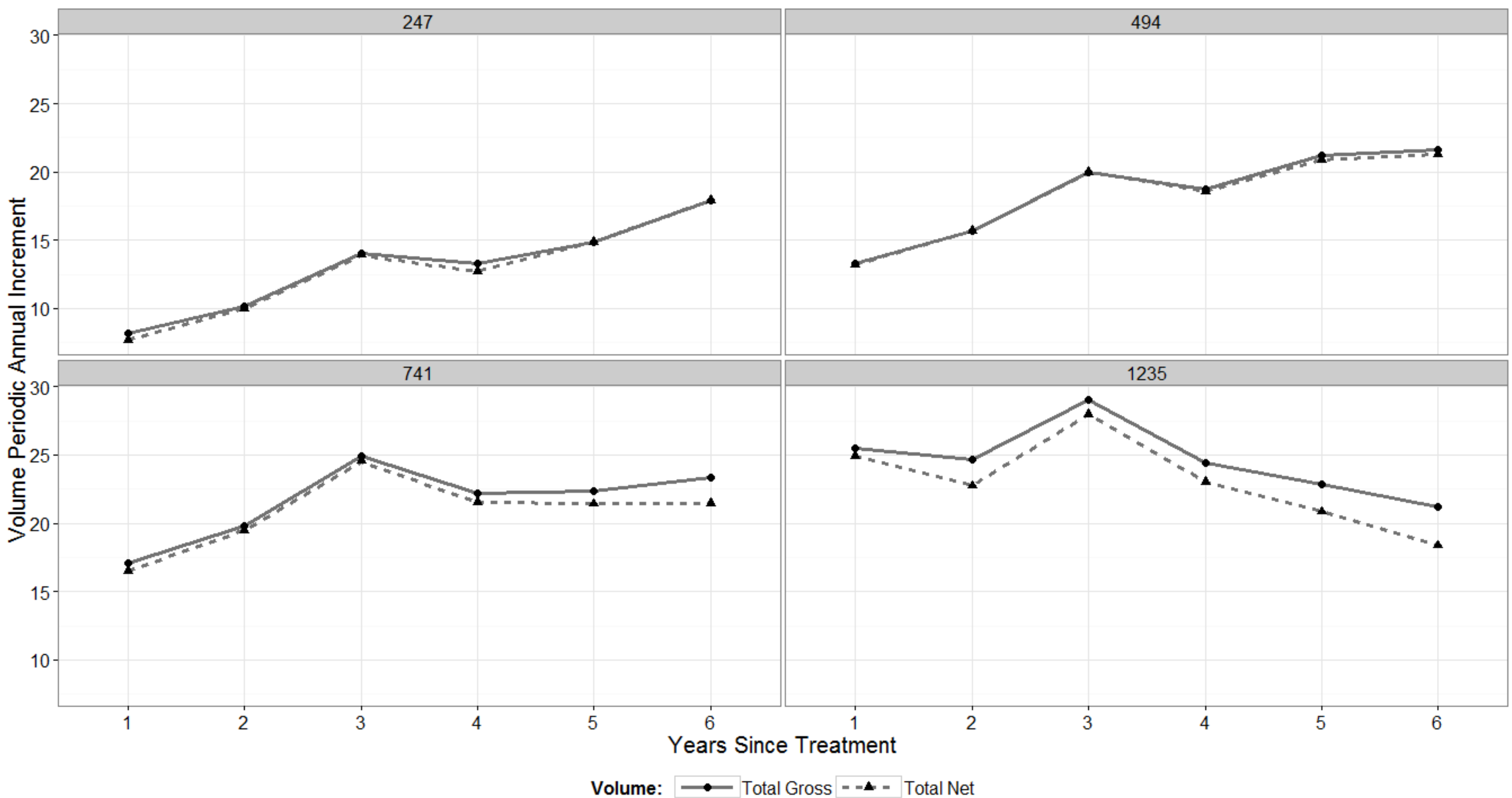
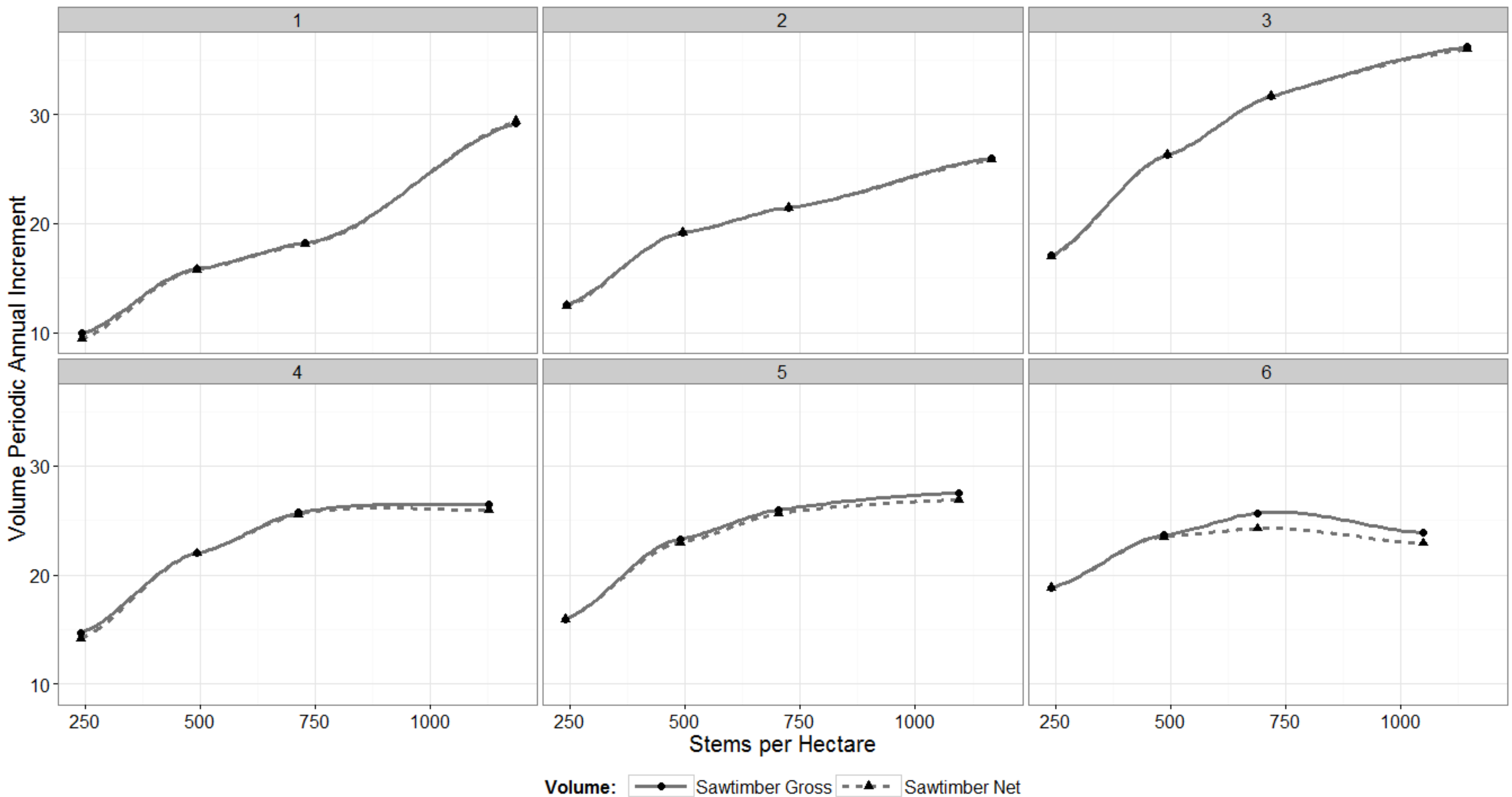


Figure 4.12: Mean sawtimber gross and net volume periodic annual increment (m^3/ha/year) in relation to the mean number of stems per hectare across four thinning treatments from on to six years after thinning.



Chapter 5: Modeling Volume Production in Loblolly Pine Stands

5.1. Abstract

The relationship between volume production and stand density has been studied since the beginnings of forest management and yet no conclusive evidence on a general relationship has been established. Using data from a spacing trial and a thinning experiment in loblolly pine a system of equations were developed to explain 1) individual tree volume production and 2) stand level volume periodic annual increment (PAI) as a function of stand density, and other variables, for thinned and unthinned stands of loblolly pine. A comparison of different stand density measures indicated that stand density index (SDI) was the most appropriate measure of density for modeling PAI in these data. The models for individual tree and stand volume production were an improvement over other models developed for loblolly pine and proved adequately flexible for representing growth of both thinned and unthinned stands. Based on the new model, an increasing and unimodal pattern were tested for both gross and net volume PAI. Significance of the parameters indicated that a unimodal pattern held for both gross and net PAI, although, the density at which PAI was maximized was well outside the maximum range of SDI in loblolly pine. This indicates that PAI increases at a decreasing rate up to the maximum densities that can be maintained on a given site.

5.2. Introduction

The relationship between volume production and stand density, often termed the "growth-density relationship," has received much attention throughout the literature. It is not overly difficult to ascertain the importance of fully understanding the growth-density relationship as many modern management practices are implemented to increase forest productivity. While increasing the availability of limiting resources through fertilization and decreasing competitive vegetation through herbicide application aid in increased volume production, manipulating stand density through varying initial planting density and thinning has been and remains the most common management tool used in forestry. However, the relationship between volume production and stand density is still highly debated.

Zeide (2001) provides a comprehensive review of the history of beliefs concerning the growth-density relationship since the beginnings of forest management and how views have changed over the years. In short, initial beliefs were that volume production increased right up to the largest densities that can be carried on a given site naturally. This belief was challenged by Hartig (1795) who advocated for the removal of dead and dying trees, when they could be sold profitably, in order to follow and support nature in its effects. Reventlow (1879) considered this view of thinning as too light and was convinced of an unimodal relationship whereby volume production is maximized when the number of trees is less than what is carried naturally in a stand. Although, volume production has been demonstrated to be independent of thinning intensity over a wide range of densities (Langsaeter 1941; Mar:Moller 1954). More recently, in a study of young Douglas-fir plantations, Curtis et al. (1997) concluded that volume production was not independent of thinning intensity and that volume production increases with increasing stand density. Seemingly returning the views on the growth-density relationship to the beginning, Zeide (2001) fears an endless loop in our ability to understand the relationship.

The conflicting claims and counter claims dealing with the effect of stand density on volume production have been attributed to data inadequacies, differences in site quality, and the diverse definitions of stand density and volume (Assmann 1970; Smith et al. 1997; Zeide

2001).However, even when these pitfalls are accounted for the specific approach at determining the growth-density relationship often falls short. In many cases the pattern between volume production and stand density is depicted as a two-dimensional relationship. As such, a series of hypothesis concerning the growth-density relationship have been put forth (Smith et al. 1997). However, each hypothesis is generally associated with the caveat "applicable to a specific species, site, and age." So when comparing the growth-density relationship across species at different sites and ages it is no surprise that many different claims and counter-claims can be found in the literature. The confusion that has arisen can be summarized from one paragraph in *Forest Stand Dynamics*, where Oliver and Larson (1996) state that stand density is somewhat related to growth, approximately related to growth, or simply gives misleading results. In order to avoid going in circles forever Zeide (2001) advocates for the development of a quantitative, not graphical, relationship that subsumes all patterns.

The purpose of this work was to develop a model to describe volume production in thinned and unthinned stands as a function of density and stand age. Using data from a spacing trial and a thinning experiment a system of equations were developed to: 1) model individual tree periodic annual volume production from stand level components and 2) model periodic annual stand level volume production. One of the controversial issues with past approaches is the choice of the stand density measure used to model the growth-density relationship. In this work an objective approach was used to compare different stand density measures. The model for stand level volume production was then used to test if stand level volume production follows either an increasing or unimodal pattern with stand density.

5.3. Data

To develop a model for volume production, data from one spacing trial and one thinning experiment in loblolly pine were used. A full description of the spacing trial maintained by the Forest Modeling Research Cooperative (FMRC) at Virginia Polytechnic Institute and State University is available in (Amateis and Burkhart 2012). The study design was nonsystematic, allowing the spacing to be varied in two dimensions on a factorial basis with a constant number of trees per plot. Data were available from four locations, two in the Coastal Plain and two in the Piedmont physiographic regions. At each location three replicates (blocks) were planted, and, in each replicate, 16 plots were planted allowing initial tree spacing to vary in all combinations of 1.2, 1.8, 2.4, and 3.6 meters. This design offered nine different initial tree spacings. Trees were measured annually for diameter and height until age 10 and annually for diameter and biannually for height thereafter. Diameter was measured at ground level from age 1 to age 5 and at breast height (4.5 ft, 1.37 m) from age 5 to age 25. Competing vegetation was chemically controlled up to age 3. To insure that most trees across all spacings and locations had achieved a diameter at breast height, and therefore volume, this analysis only used data from age eight to 25. Several plots were damaged at different ages by southern pine beetle, ice storms, or anthropogenic factors. A severe ice storm heavily damaged the plots at Pl at age 11; data from those plots after the ice storm were not be used. One of the plots at location P2, spacing 4.46 m^2 /tree (1.8X2.4 m), was abandoned at age 12 because of a southern pine beetle outbreak, and at age 19 the whole location was discarded because of thinning in the adjacent stand. At location C2 an ice storm after growing season 15 resulted in broken tops, which affected height. Data for age 16 was not used from that location for any analyses.

To thinning data come from an experimental study established jointly between the Forest Modeling Research Cooperative and the Forest Productivity Cooperative at Virginia Tech. This study was designed to examine the interaction of stand density and fertilization. Eight installations were established in the southern United States with each installation either a split-plot or randomized complete block design. Thinning treatments included four plots thinned to either 1235, 741, 494, or 247 stems per hectare. Fertilizer treatments included a non-treatment control for each thinning treatment and a one-time fertilization of 224 kg/ha N + 28 kg/ha P at the time of installation for each thinning treatment (5 plots). For this analysis only data from the thinned plots were used. At each installation these treatments were replicated four times. Planted trees were measured annually for diameter and either annually or biannually for total height. As this study was established over several years each installation had between two and seven measurements.Descriptive statistics for the two datasets are presented in Table 5.1.

5.4. Defining Volume Production

Stand volume production was defined as the periodic annual increment (PAI) based on: Gross productivity: standing volume + volume removed in thinning + volume of mortality; and Net productivity: standing volume + volume removed in thinning. Mortality volume was estimated as the volume of dead trees at the beginning of each growing period. Individual tree volume was calculated using the volume equations developed by Tasissa et al. (1997). They found that different coefficients were needed for thinned and unthinned stands. Therefore, total tree volumes for trees in unthinned (V_u) and thinned (V_t) plots were calculated as:

1) $V_u = 0.21949 + 0.00238D^2H$
2) $V_t = 0.25663 + 0.00239D^2H$

where D is tree diameter at breast height (in) and H is total tree height (ft). As these equation were fit using English units, total tree volumes were calculated in cubic feet and then converted to cubic meters.

Within the Spacing Trial data volumes were calculated beginning at age six in order to insure that the majority of stems had obtained 1.3 meters in height and thus had a recorded D for calculating volume. As heights were in general measured biannually, PAI was calculated as the difference in volume, as defined above, over a two year period from age six to age 22 and then over a three year period from ages 22 to 25. Within the RW19 data, annual measurements were available resulting in PAI calculated as the annual difference in volume production. Thus, volume PAI (VPAI) can be calculated as:

3) $VPAI = \frac{Volume_2 - Volume_1}{Age_2 - Age_1}$

where, volume is calculate as defined above.

5.5. Formulating a model

5.5.1. Volume increment of the average tree size

In order to develop a model that describes the growth-density relationship a methodology similar to that of Zeide (2004) was used. Instead of beginning at the stand level this methodology begins with describing the volume increment of the average size tree. After which, this volume increment can be multiplied by the number of stems per hectare to obtain total volume production on a per hectare basis. Herein the average tree size is defined as quadratic mean diameter (D_q, cm) which can be written:

4) $D_q = \sqrt{\frac{BPH}{0.0000785 * SPH}}$

where, BPH is the basal area per hectare (m^2) and SPH is the number of stems per hectare. Because the foundation of this methodology depends on the underlying average tree volume increment equation, it is imperative that the most appropriate equation be chosen. The volume increment of an average tree can be determined by taking the derivative of a total stem volume equation. In single stem species, such as spruce, pine, and fir, the most commonly-used volume equations express total stem volume as a function of diameter or as a function of diameter and height. The simplest form of this relationship expresses total stem volume (*v*) as a function of diameter alone:

5) $v = \alpha {D_q}^{\beta}$

where α and β are parameters to be estimated from tree data. Total stem volume equations such as this one are used in areas where heights for a given diameter are fairly uniform and are often termed "local volume equations" because of their limited applicability (Burkhart and Tomé 2012). In order to improve accuracy and increase applicability, total stem volume can be expressed as both a function of height and diameter:

6) $v = \alpha_1 D_q^2 H_d$

where H_d is the average tree height (m). Equation (6), termed a "combined variable" equation, is one of the most effective total stem volume equations. This equation can be augmented with an intercept to account for form factor and/or the exponents can be allowed to vary but is sufficient in its current form for the purpose of defining a volume increment equation. The implied volume increment equations derived from equations (5) and (6) are, respectively:

7) $\frac{dv}{dt} = \alpha\beta D_q^{\beta-1} \frac{dD_q}{dt}$, and

8) $\frac{dv}{dt} = \alpha_1 \left(2D_q H_d \frac{dD_q}{dt} + D_q^2 \frac{dH_d}{dt}\right)$

where, $\frac{dv}{dt}$, $\frac{dD_q}{dt}$, and $\frac{dH_d}{dt}$ are average tree volume, diameter, and height increments over time (t), respectively. Equations (5) and (6) can be fit using ordinary non-linear regression techniques and then the parameter estimates can be applied to equations (7) and (8) in order to determine volume increment. However, this procedure does not produce the best fitting volume increment equations. The parameter estimates can be improved by fitting equations (7) and (8) directly to volume increment. Additionally, equation (7) can be improved by grouping constants and fitting in the form:

9) $\frac{dv}{dt} = \alpha D_q^{\beta} \frac{dD_q}{dt}$

Comparing the fit of equations (8) and (9) provides a method for determining if average tree height and its increment are needed in addition to average tree diameter and its increment for describing total stem volume increment. To evaluate model performance, the sum of squared error (SSE), standard error of the estimate (SEE), and R^2 were used for model comparison. Both equations, and all equations hereafter, were fit using the nls method in the open source statistical software R (R Core Team 2014). The additional information from height and its increment reduced the SEE between equation (8) and equation (9) by 2.7% and 4.5 % while increasing the explained variation in volume increment by 22.6% and 13.2% for the Spacing Trial and RW19 data, respectively (Table 2). For both datasets equation (8) explained about 96% of the variation in volume increment indicating that including height and its increment in addition to diameter and its increment works well for predicting volume increment.

To further explain volume increment, equations (8) and (9) can be augmented to account for other changes which may better explain the relationship, particularly stand age and stand density. With increasing age the change in height and the change in diameter of the average tree declines. Similarly, when age is held constant both the changes in height and in diameter decline with increasing density ((Antón-Fernández et al. 2012; Antón-Fernández et al. 2011). One of many different growth equations could be used to describe these effects, or lack thereof, but all can be expressed in the basic forms of either exponential decline or power decline (Zeide 1993). This greatly reduces the amount of comparisons needed in order to determine the most appropriate function to account for the effects of age and density. Analysis indicated no improvement between the power decline and exponential decline forms so the exponential decline form was chosen for convenience. Thus, equations (8) and (9) can be modified by including the following components for stand age and density, respectively:

10) $exp(t/\gamma)$, and

11) $\exp(DENS/\delta)$

where, DENS is a measure of density, and γ, δ are parameters to be estimated. Several measures of density where compared including basal area per hectare (m^2), relative spacing, and the stand density index of Reineke (1933). All produced comparable sum of squared errors that where not different to the ten thousandths place. For brevity only the results of fitting with stand density index are shown for the remainder of developing an individual tree volume increment model. Thus, equations (8) and (9) can be reformulated as:

12) $\frac{dv}{dt} = \alpha_1 \left(2D_q H_d \frac{dD_q}{dt} + D_q^2 \frac{dH_d}{dt}\right) exp(t/\gamma)$

13) $\frac{dv}{dt} = \alpha D_q^{\beta} \frac{dD_q}{dt} exp(t/\gamma)$

14) $\frac{dv}{dt} = \alpha_1 \left(2D_q H_d \frac{dD_q}{dt} + D_q^2 \frac{dH_d}{dt}\right) \exp(DENS/\delta)$

15) $\frac{dv}{dt} = \alpha D_q^{\beta} \frac{dD_q}{dt} \exp(DENS/\delta)$

where all variables are defined as previously. By fitting the volume increment equations with the stand age and density components separately a comparison of their effects on the equations can be made.

Including components for stand age and stand density did little to improve equation (8). In general SEE was reduced less than 1% while the explained variation was increased by 1% or less (Table 5.2). Intuitively, these results seem reasonable because the effects of stand age and density on the change in height and diameter are directly accounted for by including height and diameter increments in the model. Alternatively, including components for stand age and stand density improved equation (9). Within the Spacing Trial data the explained variation in volume increment was increased by 8% in equation (13) and by 12% in equation (15). Less improvement was seen in the RW19 with increases of 3 and 4% in the explained variation in equation (13) and (15), respectively. To test the combined effect of stand density and age on volume increment in equation (9) both components for stand age and stand density were included resulting in the following formulation:

$$16)\frac{dv}{dt} = \alpha D_q^{\beta} \frac{dD_q}{dt} exp(t/\gamma)\exp(DENS/\delta)$$

where all variables are as before.

Including both age and density components in equation (9) resulted in further improvements to the predictability of volume increment in unhinned stands but did not greatly improve the predictability in unthinned stands The explained variation in volume increment increased in equation (16) above that of equation (9) by 12% and 6% in the Spacing Trial and RW19 datasets, respectively. However, equation (8) was still superior to equation (16) with only one estimated parameter. These results suggest that, in absence of height and its increment, age and density can improve the fit of the model and increase its predictability. However, when height and its increment are included in a model for volume increment, the effects of age and density are accounted for.

5.5.2. Stand level volume increment

The simplest model for stand volume increment can be constructed by multiplying the volume increment of the average tree, $\frac{dv}{dt}$, by the number of stems per hectare. Such a model makes the assumption that stand level volume production is directly proportional to the volume production of the average tree. However, volume production at the stand level also depends on the degree of crown closure. When gaps are created in the canopy due to mortality and/or thinning a reduction in stand level volume production can occur due to a less than optimum interception of light. In stands of pre-crown closure, volume production increases with an increasing number trees. Due to maximum size-density relationships, after crown closure stands are generally in a constant fluctuation of losing trees to mortality and increasing crown widths to recover those gaps in the canopy. When the size of the gaps created in the canopy are relatively small, the recovery period is shorter. However, as the size of the crowns increase, gaps created in the canopy become larger resulting in an increasingly longer recovery period. Eventually the gaps become so large that the residual stand is unable to recover a full canopy. A similar situation occurs after thinning where trees expand their crowns to recover gaps in the canopy while also increasing their diameters to support the larger crowns. As the intensity of thinning increases, the recovery period to a full canopy also becomes increasingly longer. The result is that with age, stand level volume production increases to a point where volume production remains fairly stable but somewhat less than optimum due to mortality. After which, when gaps in the canopy become so large that they are unrecoverable by the residual stand, volume production declines with age. This indicates that volume production at the stand level is also dependent on age as well as a particular stage of stand development.

To account for these effects a model for stand level volume production can be augmented to include components for age and stand development as well as the number of stems per hectare and volume increment of the average tree size. While age is easily measured, the determination of a point of stand development can be more complicated. However, maximum size-density relationships indicate that as stands of a similar density relative to a maximum are in similar stages of stand development. Therefore, the stage of stand development can be accounted for by including some measure of density. Thus, a model for stand level volume production can be formulated as:

$$17)\ \frac{dV}{dt} = \alpha\left(\frac{dv}{dt}\ SPH\right) exp(-age/\beta)\exp(-DENS/C)$$

where, $\frac{dV}{dt}$ is stand level volume increment and all other variables are defined as previously.

The complexity of a choosing a measure of stand density has been noted in the literature, although, the most commonly used measure is basal area (Burkhart and Tomé 2012). However, Zeide (2005) highlights that depending on tree size, basal area varies in equally dense stands and suggests that the stand density index of Reineke (1933) is a more reasonable measure of density. Presumable, stand density index, which is a function of SPH multiplied by D_q raised to some power, provides an unbiased measure of density which remains constant in equally dense stands, regardless of their average diameter. Reineke (1933) determined the power to be 1.6, although, published values for loblolly pine range from 1.3 to 2.2 (VanderSchaaf and Burkhart 2007). Typically, the power is determined by subjectively choosing stands at “normal” density and fitting a model that describes the linear relationship between SPH and D_q on the log-log scale.

For the purposes of determining that power in this work a different approach was taken. It is important to note that Reineke's SDI can written in the form:

$$18)\ SDI = SPH * D_q^r * 25^{-r}$$

where, r defines the power of the maximum size-density relationship. As such, SDI is a function of SPH, D_q raised to the power r, and a constant. Fitting equation (17) with Reineke's SDI as the measure of density with and without the constant, $25^{-1.6}$, proved that the constant only affected parameter C by a factor of exactly $25^{-1.6}$. Basal area per hectare can similarly be written as a function of SPH, D_q raised to the power of 2, and a constant. Since the constant itself has no effect on the model, other than decreasing parameter C, it can be removed from equation (18). This result suggest that a comparison of density measures can be made by changing the power of r.

For the determination of an appropriate power a modeling approached was used. Specifically, equation (17) was fit separately using $SDI = SPH * D_q^r$, allowing the power, r, to vary from 1.3 to 2.2 in steps of 0.1 for both the Spacing Trial and RW19 datasets. Each model was then evaluated using Akeike's Information Criterion (AIC). In both datasets a power of r = 1.6 resulted in the minimum value of AIC. While this approach is different than those used for determining maximum-size density relationships, from a pure modeling standpoint it appears that original SDI developed by Reineke is the best choice for modeling volume production in these data. As such the final model for stand level volume production can be formulated as:

$$19)\ \frac{dV}{dt} = \alpha\left(\frac{dv}{dt}\ SPH\right) exp(-age/\beta)\exp(-SDI/C)$$

Where all variables are as before.

Through a similar process, Zeide (2004) developed a model for stand level volume production beginning at the individual tree level. However, by the final model formulation the most important component, the volume increment of the average sized tree, had been conditioned away. For the purposes of evaluating the performance equation (19) a comparison of the model of Zeide (2004) was made. This particular model can be formulated as:

$$20)\ \frac{dV}{dt} = \alpha\ D_q^{\gamma}\ SPH\ exp(-age/\beta)\exp(-SDI/C)$$

where all variables are defined as previously.

Both equations (19) and (20) were fit with total gross and net volume PAI to the Spacing Trial and RW19 datasets using the nls function in R. In all cases the results from fitting to net volume PAI were similar to those from gross volume PAI so were not shown. Within the Spacing trial data, which is representative of unthinned stands, the explained variation in total gross volume PAI from equation (19) was increased by 55% above that of equation (20), with R^2 values of 81 and 26, respectively. Similarly, within the RW19 data, which is representative of thinned stands, the explained variation was increased in equation (19) above that of equation (20) by 37% with R^2 values of 94 and 57 for the two equations, respectfully. Plotting the residuals from equation (19) indicated no obvious pattern within the Spacing Trial and RW19 datasets (Figure 5.1). However, the residuals showed that in both datasets the model had a tendency to overpredict. An inspection of the observations which were overpredicted by greater than 5 m^3/ha/year indicated those data points were from plots that had incurred unusually high mortality rates. Even though those data points represented less than 2% of the observations in both the Spacing Trial and RW19 datasets, the relatively high overprediction is an indication that the equation does not work well in stands with high mortality. The residual plots from the fit of equation (20) to both the Spacing Trial and RW19 data indicate an obvious bias in the model.

Particularly, the model had a tendency to overpredict total gross volume PAI at values less than 25 m^3/ha/year and underpredict thereafter. Plotting the observed PAIs in relation to the predicted values further indicated an obvious bias in equation (20) (Figure 5.2). The model did not predict any values greater than 27 or 31 m^3/ha/year in the Spacing Trial and RW19 datasets, respectfully. These results are an indication that equation (20) is not well conditioned for describing volume PAI in loblolly pine.

5.6 Growth and Density

Even though the relationship between stand volume production and stand density has been studied for a long time, no conclusive evidence about a general pattern has been established (Trincado et al. 2004). The determination of a stand density where volume production is maximized, often referred to as the "optimal" stand density, is generally hypothesized to follow one of three patterns. The first is an increasing pattern where volume PAI increases with increasing stand density, although there has been some debate about whether stand volume production linearly increases or increases at a decreasing rate. The second says that volume production is constant and optimal for a wide range of densities. While this has been shown true for stocking, due to the number of stems not defining a unique stand structure, it is less certain for stand density measures such as SDI which determine a particular point of stand development. The last is the unimodal or optimum pattern which says that volume production is maximized at a density somewhat less than the maximum that can be carried in nature. This final hypothesis is often derived from species, such as ponderosa pine, that have been shown to stagnate at "excessive" densities.

Within the literature many claims and counterclaims concerning the hypothesized pattern have been made. For instance Curtis et al. (1997) determined that volume production follows an increasing pattern while Pretzsch (2005) concluded the unimodal or optimum pattern. Zeide (2004) suggested that too often the effects of stand density on volume production are not separated from the effects of age and average tree size and developed equation (20) for determining the general pattern between volume production and stand density. Equation (19) was also constructed to account for the effects age and average tree size but proved superior to equation (20) for modeling stand level volume production. Similarities between equations (19) and (20) indicate that both are describe a similar process. However, the difference is that the age and stand density components of equation (20) have to describe two process: 1) the slowing of stand level volume production with age and the stage of stand development and 2) the effects of age and density on the individual tree volume increment. Since the equation has to model two processes, individual tree and stand level volume production, it does not fully separate the effects of the individual tree and the stand. Equation (19) does however fully separate the two by including individual tree volume increment in the formulation. Based on these properties it seems reasonable that equation (19) is more suited for determining the general pattern between stand level volume production and density.

Under the current parameterization of equation (19) volume production increases with increasing density. However, equation (19) can be re-written so that PAI culminates at some maximum SDI by using the identity in equation (20), solving for SPH and substituting back into equation (19). This newly formulated model has the form:

21) $\frac{dV}{dt} = \alpha\ \frac{dv}{dt}\ D_q^{-1.6}\ SDI\ exp(-age/\beta)\exp(-SDI/C)$

Note that equations (19) and (20) are equivalent and the constant $25^{-1.6}$ has been absorbed into the parameter α. The SDI where PAI is maximized (SDI^*) can be found by calculating the first derivative of equation (21) with respect to SDI, setting equal to zero, and solving for SDI: It follows that $SDI^* = C$.

Equation (21) was fit with gross and net PAI to the Spacing Trial and RW19 datasets in all cases the parameters were significantly different from zero. For the Spacing trial data parameter C was estimated to be 3773 and 2613 for gross and net growth, respectively, while the estimated values were 5636 and 3536 for the RW19 data. Reineke (1933) determine that the maximum SDI for Loblolly Pine in the southeastern U.S. is 1112 which is less than the estimated values of C in equation (21) for all cases. These results indicate that when age and individual tree growth is held constant, both gross and net volume PAI increases with increasing SDI, although at a decreasing rate, in both thinned and unthinned stands of loblolly pine.

Past work has often attributed different growth-density patterns to differences in site and age. For example, Smith et al. (1997) suggests that when PAI is related to basal area an increasing pattern occurs on sites of excellent, nonrestrictive soils, or on sites of more ordinary and common soils in the final stages of the rotation. Furthermore, the constant or unimodal pattern was linked to common and ordinary soils during the early to mid-stages of a rotation. As Zeide (2004) highlights, when analyses of the growth-density relationship do not take into account the effects of the individual tree, then those effects are confounded in the relationship between stand volume production and density. The results from equation (21) suggest that regardless of site and age, stand volume production increases with increasing stand density when all other factors are held constant. These results do not deny that volume production increases with better site quality as those effects are accounted for by including the volume increment of the average sized tree in the model. As such, the formulation of equation (21) is suited for describing only the effects of stand density on stand level volume production.

From these results, the first hypothesis on the growth-density relationship, an increasing pattern, holds true. Equation (21) can also be used to explain why the second and third hypotheses, the constant and optimum patterns, have been concluded in the past. The constant pattern indicates that PAI is constant and optimal across a wide range of stocking for a given age. As the number of SPH does not define a unique stand structure, stands of similar SDI values can have a wide range of SPH depending on the average tree size. So a constant pattern between PAI and SPH is not contradicted in equation (21) as stands in a similar stage of stand development will have a similar SDI but can also have widely different numbers of SPH. The third pattern, which indicates volume production is optimal at densities somewhat less than the maximum density that can be carried on a given site, could also occur if the effects of individual tree growth are not accounted for. For instance, the individual tree has an increased growth response to reduced competition and increased growing space. If a stand is experiencing increased individual tree growth after a wave of mortality then it is possible that the volume production in another stand of larger density is somewhat reduced below that of the first stand. Such a scenario would result in the unimodal or constant pattern of hypothesis three.

5.7. Conclusions

The two models proposed in this study (equations 9 and 21) proved flexible for describing individual tree and stand level volume production of thinned and unthinned stands of loblolly pine. Furthermore, they were an improvement over existing models. While volume PAI is not often predicted, the developed models can be useful for providing constraints on yield predictions. Both are particularly suited for incorporation into a forest growth and yield simulator where estimates of future average tree diameter and height are available.

One of the noted reasons for contradictory conclusions on the relationship between volume production and stand density is the large diversity of definitions of density. Within this work a modeling approach was taken for the determination of the best measure of stand density to use. By noting that density measures such as basal area and stand density index can be written as a function of stems per hectare and quadratic mean diameter raised to a power, different density measures could be compared. In all cases the stand density index of Reineke (1933) resulted in the lowest AIC for equation (19). A result which indicates that SDI with a power of 1.6 was the best measure of density for modeling volume production.

Past work which indicated different patterns in the relationship between volume production and stand density generally did not take into account the effects of average trees size. As such, the effects of stand density on stand level volume production were confounded due to differences in average tree size. The conclusion of an increasing pattern whereby stand level volume production increases with increasing stand density provides an important result. The determination of a truly "optimal" stand density will come from combination of maximizing individual tree growth at maximal stand densities.

Literature Cited

Amateis, R.L., and H.E. Burkhart. 2012. Rotation-age results from a loblolly pine spacing trial. Southern Journal of Applied Forestry 36(1):11-18.

Antón-Fernández, C., H.E. Burkhart, and R.L. Amateis. 2012. Modeling the effects of initial spacing on stand basal area development of loblolly pine. Forest Science 58(2):95-105.

Antón-Fernández, C., H.E. Burkhart, M. Strub, and R.L. Amateis. 2011. Effects of initial spacing on height development of loblolly pine. Forest Science 57(3):201-211.

Assmann, E. 1970. The principles of forest yield study. Pergamon, Press Inc., New York. 489 p.

Burkhart, H.E., and M. Tomé. 2012. Modeling forest trees and stands. Springer, Dordrecht. 457 p.

Curtis, R.O., D.D. Marshall, and J.F. Bell. 1997. LOGS: A pioneering example of silvicultural research in coast Douglas-Fir. Journal of Forestry 95(7):19-25.

Hartig, G.L. 1795. Anweisung zu taxation der forsten oder zur bestimmung des holzertrags der walder. In: KommiBion bei Buchhandler Heyer.

Langsaeter, A. 1941. Om tynning i enaldret gran-og furuskog. Medd. Nor. Skogforsosves 8:131-216.

Mar:Moller, C. 1954. The influence of thinning on volume Increment. I. Results of investigations. In Thinning problems and practices in Denmark, eds. C. Mar:moller, J. Abell, T.Jadg, and F.Junker, 5 - 32. Technical Publication 76. Syracuse: State University of New York College of Forestry.

Oliver, C.D., and B.C. Larson. 1996. Forest stand dynamics. Wiley, New York.

Pretzsch, H. 2005. Stand density and growth of Norway spruce (Picea abies (L.) Karst.) and European beech (Fagus sylvatica L.): evidence from long-term experimental plots. Eur J Forest Res 124(3):193-205.

R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http:www.R-project.org/.

Reineke, L.H. 1933. Perfecting a stand-density index for even-aged forests. Journal of Agricultural Research 46:627-638.

Reventlow, C.D.F. 1879. Forslag til en forbedret Skovdrift grundet, paa Undersogelser over Traeernes Vegetation I Denmarks og Slesvigs Skove. In: Kjobenhavn, 1879, Ed. in English 1960: A treatise of forestry, Society of Forest History, Horsholm Denmark.

Smith, D.M., B.C. Larson, M.J. Kelty, and P.M. Ashton. 1997. The practice of silviculture. John Wiley & Sons, New York, NY.

Tasissa, G., H.E. Burkhart, and R.L. Amateis. 1997. Volume and taper equations for thinned and unthinned loblolly pine trees in cutover, site-prepared plantations. Southern Journal of Applied Forestry 21(3):146-152.

Trincado, G., H.E. Burkhart, and R.L. Amateis. 2004. Volume increment and stand density relationship: Hypothesis testing of patterns and modeling approach. Department of Forestry, Virginia Polytechnic Institute and State University, Blacksburg, VA., Loblolly Pine Growth and Yield Research Cooperative, Report No. 137.

VanderSchaaf, C.L., and H.E. Burkhart. 2007. Comparison of methods to estimate reineke's maximum size-density relationship species boundary line slope. Forest Science 53(3):435-442.

Zeide, B. 1993. Analysis of growth equations. Forest Science 39(3):594-616.

Zeide, B. 2001. Thinning and growth: A full turnaround. Journal of Forestry 99(1):20.

Zeide, B. 2004. Optimal stand density: A solution. Canadian Journal of Forest Research 34(4):846-854.

Zeide, B. 2005. How to measure stand density. Trees 19(1):1-14.

Table 5.14: Descriptive statistics for datasets of thinned and unthinned loblolly pine.

Dataset	Stand Parameter	N	Mean	Std Dev	Minimum	Maximum
Spacing Trial		1606				
	Age (years after planting)		14.30	5.09	8.00	25.00
	Basal area (m^2 per ha)		32.06	9.42	7.84	59.18
	Trees per hectare		2152.20	1266.28	549.18	6727.43
	Site Index (m, base age 25 years)		20.35	1.41	16.07	23.31
RW19		928				
	Age		17.31	2.44	13.00	22.00
	Basal area (m^2 per ha)		25.34	10.57	6.59	49.13
	Trees per hectare		638.46	328.84	202.18	1284.95
	Site Index (m, base age 25 years)		22.41	1.94	18.29	27.13

Table 5.15: Fit statistics sum of squared error (SSE), standard error of the estimate (SSE) and the coefficient of variation (R^2) for equations 8 – 16 fit to the Spacing Trial and RW19 datasets.

	Spacing Trial			RW19		
Equation	SSE	SEE	R^2	SSE	SEE	R^2
8	0.37	0.02	0.97	0.93	0.04	0.96
9	2.87	0.04	0.74	3.97	0.09	0.83
12	0.36	0.01	0.97	0.89	0.04	0.96
13	1.92	0.03	0.83	3.21	0.08	0.86
14	0.34	0.01	0.97	0.65	0.04	0.97
15	1.54	0.03	0.86	2.94	0.07	0.87
16	1.49	0.03	0.87	2.53	0.07	0.89

Figure 5.13: Observed total gross volume periodic annual increment (PAI, m^3/ha/year) from the Spacing Trial and RW19 datasets in relation to the residuals (observed – predicted) from equations (19) and (20).

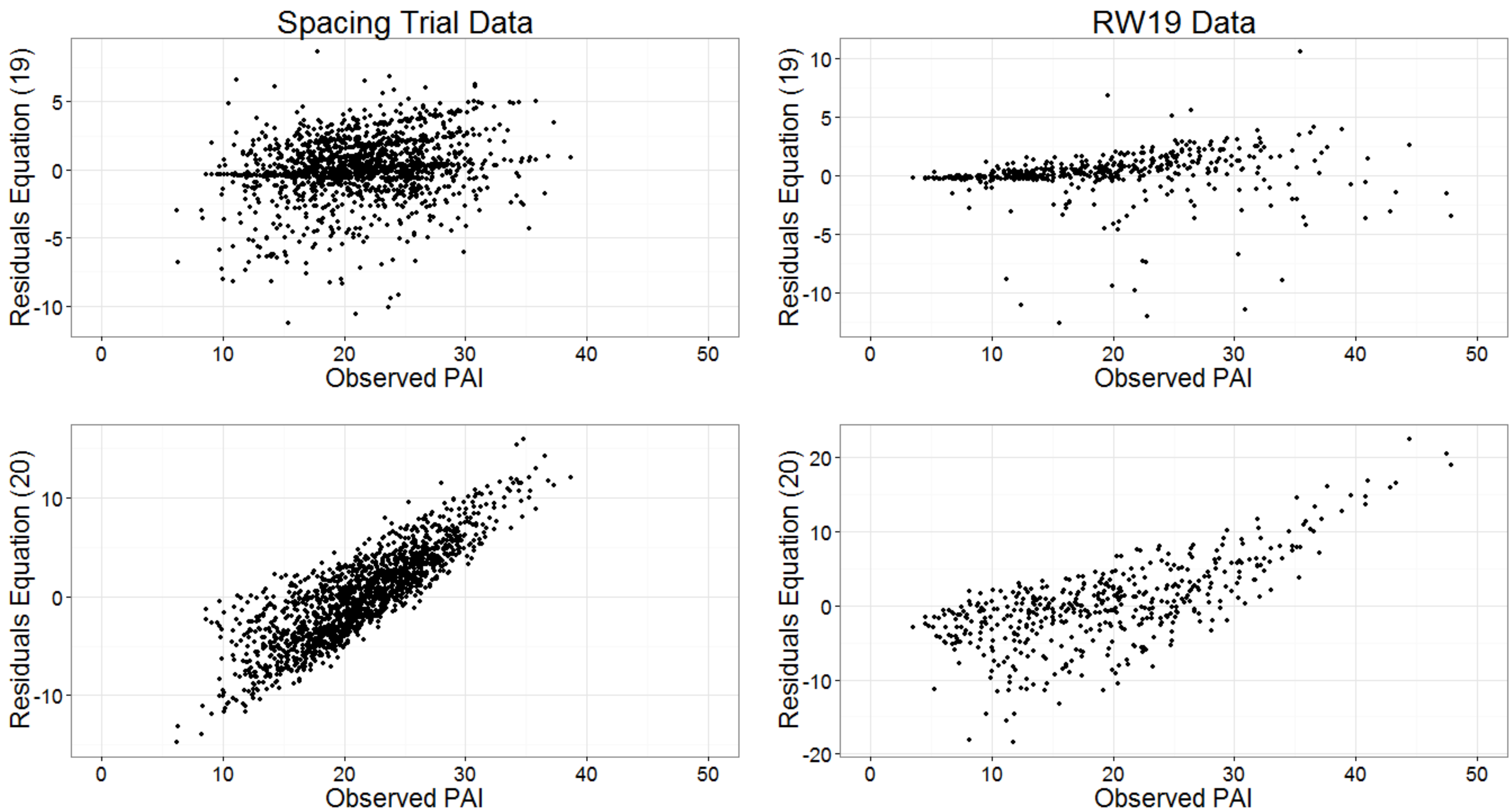
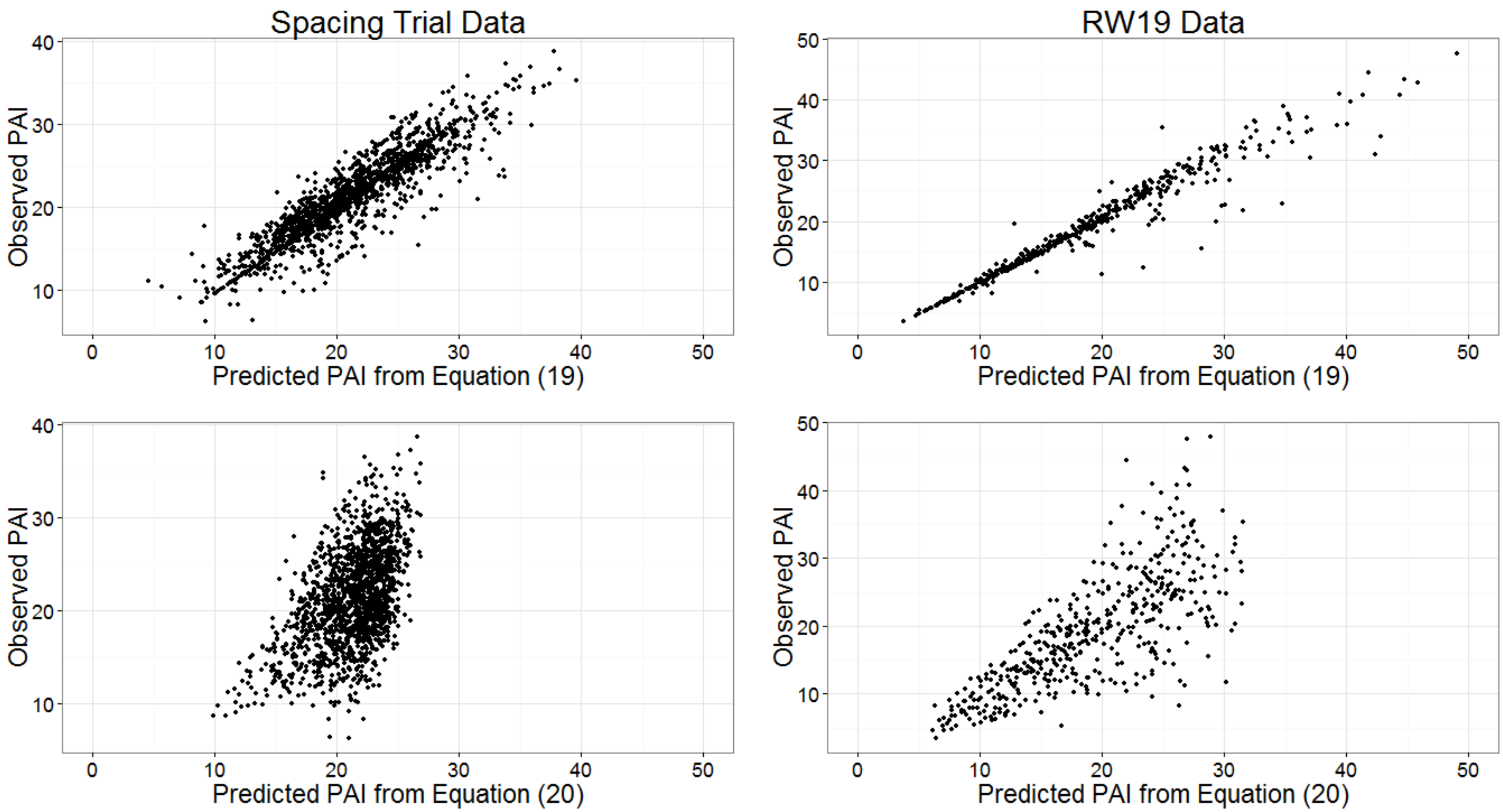


Figure 5.14: Observed total gross volume periodic annual increment (PAI, m^3/ha/year) from the Spacing Trial and RW19 datasets in relation to predicted total gross volume PAI from equations (19) and (20).



Chapter 6: Summary

The relationship between volume production and stand density, often termed the growth-density relationship, is an important concept in stand density management, yet many contradictory conclusions on general pattern exist. The overall goal of this dissertation was to comprehensively examine the relationship between volume production and stand density in thinned and unthinned stands of loblolly pine. This dissertation explored different methods for determining the growth-density relationship while additionally comparing different measures of volume production and stand density. Forest management of southern pine plantations is often performed with the goal to increase volume production. While improved management techniques are available, controlling stand density is still the oldest and most commonly used management tool. Understanding the relationship between volume production and stand density will help in making better density management decisions as well as aiding in the proper formulation of growth and yield models.

The series of hypothesis concerning the relationship between volume production and stand density can be summarized as: 1) volume production increases right up to the highest levels of density that can be maintained in nature, 2) production remains constant and optimum across a wide range of stand density from some lowest level at which there is full occupancy of growing space up to those levels at which excessive competition is postulated to restrict growth ; and 3) volume production follows a unimodal or optimal pattern with stand density. The first hypothesis is sometimes attributed to either good soils or the later stages of a rotation while hypotheses two and three are attributed to early to mid-stages of a rotation on common soils. Recent research has indicated that volume production purely follows an increasing pattern with stand density while others have indicated that volume production is unimodal and at times is optimal at densities less than the maximum that can be carried on a given site. AS such, there has been some con

The study presented in this dissertation was designed to test the three hypothesis concerning the relationship for thinned and unthinned stands of loblolly pine. The data used for analysis of the growth-density relationship came from two growth and yield thinning studies, one spacing trial, and one thinning experiment. The two growth and yield studies were established by the Forest Modeling Research Cooperative (FMRC) at Virginia Tech. The first is representative on non-intensively managed plantations (NIMP) and was designed to examine two levels of thinning (either a 30% or 50% basal area removal) across a range of ages from 8 to 25 years. The second is representative of intensively managed plantations (IMP) and was also designed to examine two levels of thinning (30% or 50% basal area removal) but stands were thinned at a common point in height development, when the height of the dominants and codominant was about 45 feet tall. The Spacing Trial, also established by the FMRC, was designed to test the effects of planting density on growth and yield. The trial was established at four locations (2 in Virginia and 2 in North Carolina) and included nine initial planting densities, ranging from 247 to 6727 trees per hectare. The thinning experiment was established jointly by the FMRC and the Forest Productivity Cooperative to examine the interaction between stand density and fertilization. Data were available from eight locations located throughout the southern US. Within this dissertation only the data from thinned plots were used.

The objectives of this research were to examine the growth-density relationship in thinned and unthinned stands of loblolly pine. In the three previous chapters the major objectives were to:

1) Use a generalized power and exponential model to test the hypothesis that volume production and stand density follows either an increasing or unimodal pattern with stand density (see chapter 3)
2) Test the equality in mean volume production separately at different ages for different planting densities and thinning intensities to determine if volume production follows a constant pattern with stocking (see chapter 4)
3) Model the individual tree and stand level volume production for thinned and unthinned stands of loblolly pine (see chapter 5)

Collectively, the findings from the research in this dissertation provide reasoning why some of the contradictory conclusions concerning the growth-density relationship have been made, illustrate the general pattern of the growth-density relationship, and provide a framework for modeling volume production in plantations. From this research the following conclusions were determined:

1) Stand density alone, while having a generally positive relationship, is not highly correlated with volume production. Although, if volume production is described as purely a function of stand density:
    a. Stand density measures which use quadratic mean diameter as a measure of average tree size are more correlated with volume production than measures which use mean tree height or volume.
    b. In general, nonintensively managed plantations follow an increasing pattern while intensively managed plantations follow a unimodal pattern for both thinned and unthinned stands.

2) When volume production is related to stocking, the general pattern depends on if volume production is defines either total or merchantable.
    a. For total volume production, the general pattern is initially increasing (hypothesis 1) in pre-crown closure stands but becomes constant (hypothesis 2) after crown closure. In the later stages of a typical rotation volume production can highly decline in stands planted at higher densities potentially due to weak formation of crowns. This results in the maximum range of the constant portion decreasing with age.
    b. The pattern in merchantable volume production for a given age depends on the constraints of diameters used in the merchantability class but a general pattern was noted. At early to mid-rotation ages the lightest planting densities had the highest merchantable volume production. As constraint on diameters goes from none (total volume production) to the most strict (sawtimber volume production) the pattern changes from increasing to unimodal or constant to decreasing. As the proportion of trees growing into the merchantability limits approach 1 the patterns converge to those in total volume production.
3) To evaluate the relationship between stand level volume production and stand density the effects stand density on individual tree volume production must be accounted for. From the developed model, which accounts for the both age and mean tree volume production, it was determined that volume production follows an increasing pattern with stand density.

A better understanding of the growth-density relationship gives the potential for making better management decisions. Different conclusions concerning the growth density relationship are the result of different approaches used to determine the relationship. As such, all three hypothesis can be true and it is not necessary for them to be mutually exclusive. However, when all other factors are accounted for, volume production increases with increasing stand density, although at a decreasing rate. This result indicates that the true "optimal" density will be a balance between decreased growth from a reduction in density and increased individual tree growth. The models developed in this study, when incorporated into a forest growth and yield simulator, will be useful for determining where that balance occurs.