Modeling maximum size-density relationships of loblolly pine (*Pinus taeda* L.) plantations

by

Curtis L. VanderSchaaf

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

Dr. Harold E. Burkhart, Chair

Dr. Richard G. Oderwald

Dr. Marion R. Reynolds, Jr.

Dr. Shepard M. Zedaker

October 30, 2006

Blacksburg, Virginia

Keywords: density management diagrams, mixed models, self-thinning, size-density trajectories, stand density index.

Modeling maximum size-density relationships of loblolly pine (*Pinus taeda* L.) plantations

by

Curtis L. VanderSchaaf

(ABSTRACT)

Self-thinning quantifies the reduction in tree numbers due to density-dependent mortality. Maximum size-density relationships (MSDRs) are a component of self-thinning that describe the maximum tree density per unit area obtainable for a given average tree size, often quadratic mean diameter ($\overline{D}$). An MSDR species boundary line has been defined as a static upper limit of maximum tree density – $\overline{D}$ relationships that applies to all stands of a certain species within a particular geographical area. MSDR dynamic thinning lines have been defined as the maximum tree density obtainable within an individual stand for a particular $\overline{D}$ which have been shown to vary relative to planting density. Results from this study show that differences in boundary levels of individual stands cause the MSDR species boundary line slope estimate to be sensitive to the range of planting densities within the model fitting dataset. Thus, a second MSDR species boundary line was defined whose slope is the average slope of all MSDR dynamic thinning lines. Mixed-models are presented as a statistical method to obtain an estimate of the population average MSDR dynamic thinning line slope.

A common problem when modeling self-thinning is to determine what observations are within generally accepted stages of stand development. Segmented regression is presented as a statistical and less subjective method to determine what observations are within various stages of stand development. Estimates of $\overline{D}$ and trees per acre (N) where MSDR dynamic thinning lines begin and end on the logarithmic scale were used as response variables and predicted as a function of planting density. Predictions of MSDR dynamic thinning line beginning and ending $\overline{D}$ and N are used in an alternative MSDR dynamic thinning line slope estimation method. These models show that the maximum value of Reineke's Stand Density Index (SDI) varies relative to planting density.

By relating planting density specific Zone of Imminent Competition Mortality boundaries to a MSDR species boundary line, self-thinning was found not to begin at a constant relative SDI. Thus, planting density specific Density Management Diagrams (DMD) showed that self-thinning began at 40 to 72% for planting densities of 605 and 2722 seedlings per acre, respectively.

ACKNOWLEDGEMENTS

There are many people who have helped to shape my career and more specifically made this dissertation better. Most notably, Dr. Harold E. Burkhart. I would like to sincerely thank him for his help in providing focus throughout this research and his encouragement and openness to my ideas about my dissertation and other research projects. All three other committee members have provided support, comments, and thoughts that have helped to make this dissertation better. Most especially, I would like to thank Drs. Marion R. Reynolds, Jr. and Shepard M. Zedaker for their challenges and Dr. Richard G. Oderwald for his encouragement. Dr. Philip J. Radtke has provided many valuable comments. Dr. Jeffrey B. Birch has been a great help in several instances when I had questions about statistics. Many informative and stimulating conversations were had with Dr. Boris Zeide about maximum size-density relationships (MSDRs) and self-thinning. Many useful comments were also received from Dr. Thomas B. Lynch about MSDRs. Dr. David B. South has been a constant force in shaping my career and has helped me to become a more well-rounded forest researcher. I would also like to thank Drs. A. Gordon Holley, J. David Lenhart, Young-Jin Lee, Kenneth L. McNabb, James A. Moore, and Michael G. Shelton for their encouragement throughout my career. Ralph L. Amateis has been very helpful in providing data and helping me measure the data used during this dissertation, not to mention his football trivia questions. Dr. Jungkee Choi has been a constant source of support and a great help in conducting field work. I would also like to thank my fellow forest biometric graduate students throughout my time at VPI. The help of Drs. Christine E. Blinn, Jason G. Henning, and Guillermo F. Trincado will be remembered. I would also like to thank Kevin Packard for his help and Nathan D. Herring and Matthew B. Russell. I sincerely appreciate the members of the Loblolly Pine Growth and Yield Research Cooperative for providing funding and encouragement. Many other friends and family members too numerous to mention have provided support and love.

Although many people have helped to shape my career, none more than my parents, Lee and Judith VanderSchaaf, and my brother, Brian, and his family Neva, Kevin, Jessica, and Nicholas. The love and encouragement they have provided will be eternally remembered. I would also like to thank Sts. Barbara, John Gualbert, Hubert of Liege, and Francis of Assissi, who are the patron saints of foresters, forest workers, ecology, mathematicians, and statistics and Our Mother for their help. Finally, I would like to thank the Holy Trinity for all they have done, may I always remain faithful.

ATTRIBUTION

This dissertation has been organized under what is generally termed the manuscript format. Dr. Harold E. Burkhart and I together have either submitted or plan to submit Chapters 3, 4, and 5 for publication in journals. For all three chapters, Dr. Burkhart has provided focus, help conceptually, and editorial comments. Entitled **Comparison of methods to estimate Reineke's maximum size-density relationship species boundary line slope,** Chapter 3 was submitted to Forest Science. Chapter 4, entitled **Using segmented regression to estimate stages of stand development,** will be submitted to Forest Science. Although acceptable for a dissertation chapter, Chapter 5, entitled **Impact of alternative methods to estimate maximum size-density relationships on density management diagrams for loblolly pine plantations,** will be modified prior to submission to the Southern Journal of Applied Forestry.

TABLE OF CONTENTS

List of Tables

Chapter 2

Chapter 3

Chapter 4

List of Figures

Chapter 1

Chapter 3

Chapter 4

Chapter 1

Introduction, Past Work on Maximum Size-Density Relationships, and Objectives

Self-thinning is the reduction in tree numbers due to density-dependent mortality. Maximum size-density relationships (MSDRs) are a component of self-thinning that quantify the maximum density that can occur for a given average tree size. Weller (1990) defined two types of MSDRs (*i*) individual stand MSDR boundaries referred to as MSDR dynamic thinning line boundaries and (*ii*) the MSDR species boundary line defined as a static upper limit of maximum tree density – average tree size relationships that applies to all stands of a certain species within a particular geographical area (Figure 1.1). Loblolly pine (*Pinus taeda* L.) is one of the most important commercial and widely planted tree species in the Southeastern US (McNabb and VanderSchaaf 2003). In the past, models describing self-thinning in loblolly pine plantations have been developed using data from either one site (Lloyd and Harms 1986, Cao 1994) or based on oversimplifications such as assuming all stands approach the same boundary level (Cao 1994, Zeide and Zhang 2006). Previous modeling of loblolly pine plantation MSDRs has concentrated on estimating the slope and boundary level of MSDR species boundary lines and has not concentrated on estimating MSDR dynamic thinning line slopes and boundary levels (Dean and Baldwin 1993, Cao 1994, Williams 1994, Zeide and Zhang 2006).

By quantifying MSDRs of individual stands relative to factors such as planting density and site quality, more meaningful MSDR models can be developed for constraining predicted stand density. For instance, Nilsson and Allen (2003) and VanderSchaaf and South (2004) define a Type C age-shift as a stand-level response to a particular treatment(s) that produces a short-term increase in growth but not an increase in the long-term yield or carrying capacity of a site. A Type C age-shift in MSDRs occurs when a treatment(s) reduces the time that the maximum tree density for particular average tree sizes of a site are reached (Figure 1.2). However, the maximum tree density for a particular average tree size will not be increased due to the treatment(s). As foresters strive to increase economic returns on investment, loblolly pine plantation rotations commonly range from 13 to 35 years, they need tools to assist them in determining whether treatments are economically viable as early in the rotation as possible. If a particular treatment(s) is generally thought to produce a Type C age-shift relative to independent data used in fitting MSDRs, MSDRs can be used to constrain stand development. Using this methodology, mortality equations are combined with height, diameter, or volume equations to estimate an approach to a linear MSDR constraint (Monserud et al. 2005). Once the projected stand density is equivalent to the linear constraint, self-thinning occurs such that stand density is maintained equivalent to the linear constraint for some period of time. The advantage of this method is that models can be fit using a limited range of ages for the treatments being tested to predict an approach to the constraint. Thus, economic analyses can be conducted to determine whether the treatment(s) produce(s) enough of an increase in growth to warrant investment.

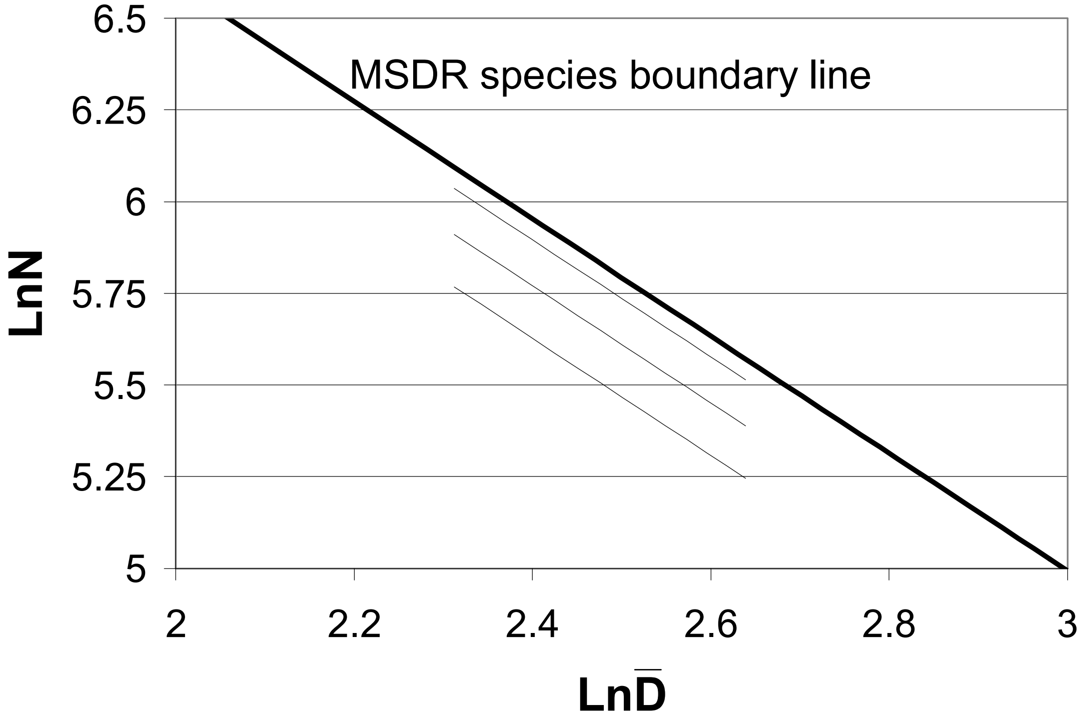


Figure 1.1. Depiction of a MSDR species boundary line and several MSDR dynamic thinning lines. MSDR dynamic thinning line boundary levels can differ relative to factors such as planting density and site quality, thus the greatest LnN that can occur for a particular Ln$\overline{D}$ can differ across stands. Boundary levels of individual stands can be equal to the MSDR species boundary line boundary level, but by definition, cannot exceed it. Although a constant slope is used in this figure, the slopes of MSDR dynamic thinning line boundary levels can also differ relative to factors such as planting density and site quality. Where Ln is the natural logarithm, N is trees per acre, and $\overline{D}$ is quadratic mean diameter (in.).

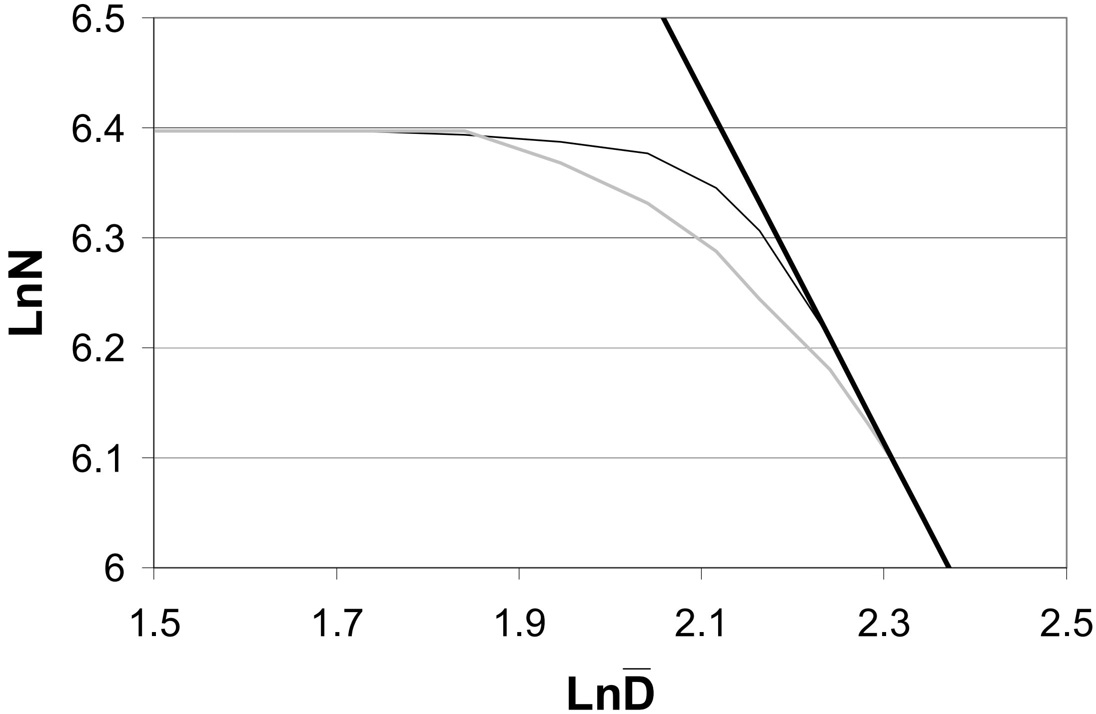


Figure 1.2. Depiction of one kind of a Type C age-shift for MSDRs. Both size-density trajectories have the same MSDR dynamic thinning line boundary level but have different approaches. A second kind of Type C age-shift for MSDRs is when stands have the same general size-density trajectory but move along the trajectory at different rates.

Estimating MSDR slopes

Several studies have estimated the slope on the natural logarithmic (Ln) scale between average tree volume (V) and tree density or quadratic mean diameter ($\overline{\mathrm{D}}$) and tree density. The simplest expression often takes the form of:

$$\mathrm{LnN} = b_0 + b_1 \mathrm{LnS} \qquad [1.1]$$

Where:

N -- trees per acre

S -- average tree size (e.g. V, or $\overline{\mathrm{D}}$)

b_0, b_1 – are parameters to be estimated

A variety of techniques have been used to estimate slopes of MSDR lines. Reineke (1933) hand fitted the slope for a variety of species but MacKinney and Chaiken (1935) reestimated the slope for loblolly pine stands using ordinary least squares, OLS. Several other studies have estimated slopes using OLS (e.g. Oliver and Powers 1978, Williams 1994, Wittwer et al. 1998) and ordinary nonlinear least squares (e.g. Smith and Hann 1984, Yang and Titus 2002). Since average tree size and tree density simultaneously impact one another, some authors have proposed using multivariate techniques such as principal components analysis (Mohler et al. 1978, Weller 1987) or the reduced major axis technique (Osawa and Allen 1993, Solomon and Zhang 2002). Thus, both average tree size and tree density were considered random variables when estimating parameters. However, after an initial fascination with multivariate techniques, for the sake of simplicity and since measurement error is negligible, subsequent studies have assumed that either average tree size or tree density is fixed (e.g. Yang and Titus 2002, Pretzsch and Biber 2005, Zeide 2005, Zhang et al. 2005).

Ordinary linear and non-linear least squares, principal components, and reduced major axis all suffer from the fact that the slope is fitted through the middle of the data, while interest is often in the upper limits. Thus, weighted least squares (Goelz 2006) and frontier production functions have been proposed to estimate MSDR slopes (Bi et al. 2000, Zhang et al. 2005). Goelz (2006) describes a somewhat involved procedure to estimate MSDR slopes using weighted least squares. The slope is estimated using a loss function that accounts for the weight assigned to individual observations. Weights of individual observations depend on the relative position of Reineke's stand density index for any observation to the maximum value of Reineke's stand density index observed in the dataset.

In economics, a frontier production function is defined as a function that gives the maximum possible output for a given input set (Bi et al. 2000, Bi 2004, Zhang et al. 2005). For MSDRs, a frontier production function would give the maximum possible tree density for a given average tree size. Production functions estimate slopes by generally positioning the boundary line above all observations and minimizing the one-sided sum of squares. Two general types of frontier production functions are recognized, deterministic and stochastic (Zhang et al. 2005). A deterministic frontier production function estimates the slope while forcing all observations to occur along or to be below the frontier, or MSDR in this case. Two parameter estimation methods have been used in the past, linear programming and quadratic programming (Zhang et al. 2005). When using linear programming, the sum of the absolute values of the residuals are minimized as:

$$\min_{\beta} \sum_{i} |\mathrm{y}_i - b_0 - b_1 x_i| \qquad [1.2]$$

$$\text{subject to } \varepsilon_i = \mathrm{y}_i - b_0 - b_1 x_i \le 0, \forall i$$

For the quadratic programming estimation method, the sum of squared residuals is minimized:

$$\min_{\beta} \sum_{i} (\mathrm{y}_i - b_0 - b_1 x_i)^2 \qquad [1.3]$$

$$\text{subject to } \varepsilon_i = \mathrm{y}_i - b_0 - b_1 x_i \le 0, \forall i$$

The negative residuals force all observations to be on or below the frontier production function. Deterministic frontier production functions have several problems associated with them 1) sensitivity to outliers, 2) due to the programming estimation methods, no standard errors are estimated, 3) obtaining statistics for inference is difficult.

Stochastic frontier production functions for MSDRs are expressed as:

$$\text{LnN} = b_0 + b_1 \text{ LnS} + (\varepsilon_i) = b_0 + b_1 \text{ LnS} + (v_i + u_i) \qquad [1.4]$$

Where:

$\varepsilon_i = (v_i + u_i)$

v_i -- is one of two error terms assumed to have a symmetric distribution, usually a normal distribution, $v_i \sim N(0, \sigma_v^2)$.

u_i -- is one of two error terms usually assumed to have a half-normal distribution, $u_i \sim \left|N(0, \sigma_u^2)\right|$, where $E(u_i) = (\sqrt{2} / \pi)\sigma_u$, and $\text{var}(u_i) = (1 - 2/\pi)\sigma_u^2$.

v_i and u_i are generally assumed to be independent and identically distributed (i.i.d.) across observations.

The random error term u_i in economic terminology represents technical inefficiency but in MSDR terminology represents an observation of a trajectory not occurring along the MSDR. When $u_i = 0$ a trajectory has reached the MSDR. The random error term v_i in economic terminology represents factors beyond a firms control. For MSDRs, v_i represents the fact that the true MSDR is seldom observed because of external factors such as fluctuations in soil and climatic conditions, insect attacks, and diseases across time that can influence observed MSDRs (Bi et al. 2000, Bi 2001, 2004, Zhang et al. 2005). Thus, unlike a deterministic frontier production function, observations can exceed the MSDR boundary level (Bi 2001, 2004, Zhang et al. 2005) and thus parameter estimates using a stochastic frontier production function are less sensitive to outliers. The concept of v_i is synonymous with the statement of Zeide (1991) that MSDRs are not directly observable from empirical data. The advantage of frontier production functions when estimating MSDR slopes is that subjective determination of what points are within the self-thinning stage of stand development is avoided (Bi et al. 2000, Bi 2004, Zhang et al. 2005).

Arisman et al. (2004) proposed using a geometric procedure to estimate MSDR slopes, what they called a minimum distance boundary method (Figure 1.3). An estimate of the MSDR species boundary line slope and level are found by minimizing the squared differences in both horizontal (x in Figure 1.3) and vertical (y in Figure 1.3) directions between observed average tree size - tree density values and the values estimated using the species boundary line:

$$\text{Dist} = x*y/(x^2 + y^2)^{1/2} \qquad [1.5]$$

Equation [1.5] calculates the Dist for any observation based on principles of right triangles. Estimates of the MSDR slope and boundary level are found by minimizing the sum of Dist for all observations. The method is somewhat similar to a deterministic frontier production function since the slope is estimated after forcing all observations to be below the boundary level.

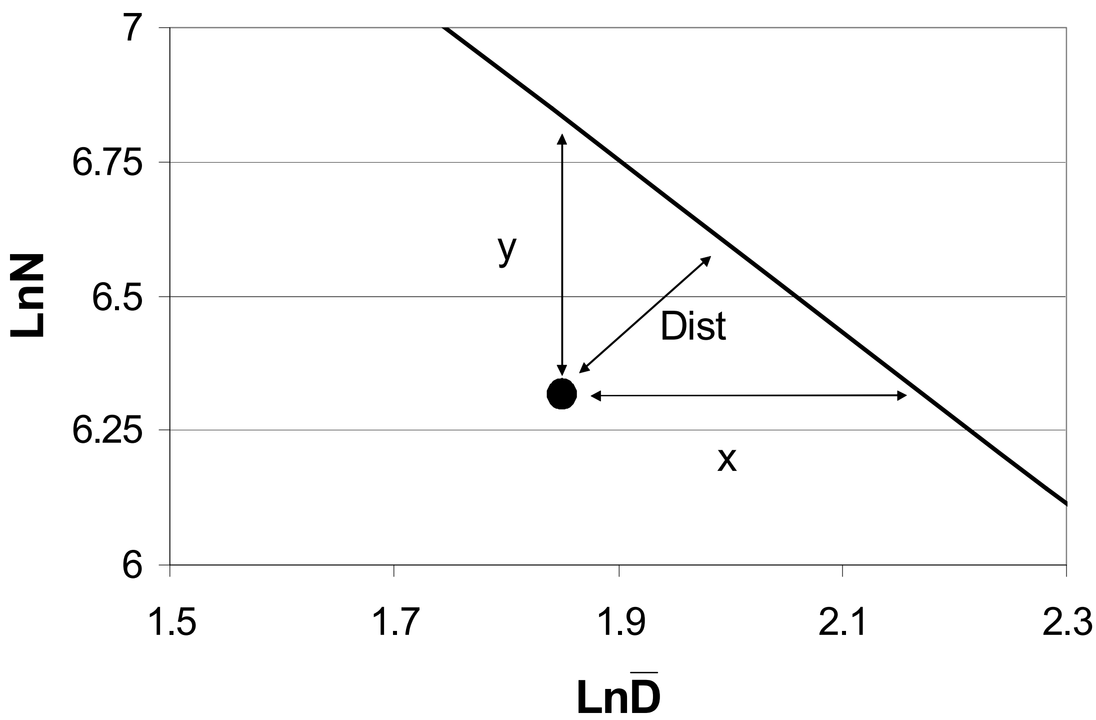


Figure 1.3. Minimum distance boundary method, adapted from Arisman et al. (2004).

All MSDR slope estimation methods previously discussed fail to account for the behavior of individual stands when estimating MSDR species boundary line slopes. Since MSDR boundary levels of individual stands can be impacted by genetics (Weller 1990), site quality (Westoby 1984, Strub and Bredenkamp 1985, Barreto 1989, Peterson and Hibbs 1989, Hynynen 1993, Pittman and Turnblom 2003, Bi 2004), and planting density (VanderSchaaf 2004), estimated MSDR species boundary line slopes may not, on average, be representative of how individual stands self-thin. A non-representative slope can be important when using MSDRs as constraints or in Density Management Diagrams (DMDs), an improperly estimated slope can produce large errors in predicted stand development and ultimately economic analyses. Wittwer et al. (1998) and Lynch et al. (2004) proposed using a first-difference model to estimate slopes:

$$\mathrm{Ln}N_2 - \mathrm{Ln}N_1 = b[\mathrm{Ln}\,\overline{D}_2 - \mathrm{Ln}\,\overline{D}_1] \qquad [1.6]$$

Where:

b is a parameter to be estimated and is equivalent to the b_1 from equation [1.1].

This method takes into account that observations from the same stand within the overall fitting dataset are correlated, or in terms of MSDRs, that MSDR dynamic thinning line boundary levels vary. Thus, Wittwer et al. (1998) and Lynch et al. (2004) were among the first to account for MSDR dynamic thinning lines when estimating MSDR species boundary line slopes. When using OLS to estimate a MSDR species boundary line slope, a value of –1.7686 was obtained while the first-difference model produced a slope estimate of –1.6863 for shortleaf pine (*Pinus echinata* Mill.) stands located in Southeastern Oklahoma. However, the first-difference model only accounts for the first-order correlation and fails to account for the dependency among all observations from the MSDR dynamic thinning line of a particular stand.

Three techniques that can account for dependencies among several observations from individual stands when estimating a species boundary line slope are 1) what is referred to as the "two-step" approach (Schabenberger and Pierce 2001), 2) generalized estimating equations (GEE), and 3) a mixed-models analysis. Johnson (2000) used the "two-step" approach of accounting for autocorrelation when estimating a MSDR species boundary line slope for western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) stands in the Pacific Northwest. By estimating slopes for all individual stands within the dataset, and then taking the average of the intercepts and slopes, an estimate of the MSDR species boundary line intercept and slope were obtained while accounting for cluster specific behavior (a cluster is an individual experimental unit and in this particular case a MSDR dynamic thinning line). When simply using OLS which assumes no correlation among observations, an estimate of –1.9020 was obtained for the MSDR species boundary line slope while the "two-step" approach produced an estimate of –1.5159.

Generalized estimating equations allow for a variety of within cluster error term structures to be modeled when estimating population average parameters. Thus, a GEE is more parsimonious than the "two-step" approach and produces more efficient estimates of the MSDR species boundary line intercept and slope. However, conceptually, a mixed-models analysis is superior to a GEE if a modeler wants to account for cluster specific behavior when estimating MSDR species boundary line slopes. In concept, the population average parameters are estimated based on a sample of all loblolly pine plantations across the Southeastern US (or some physiographic region within the Southeastern US). Across repeated random sampling, different plantations would be selected within a sample that would have different cluster specific behavior than clusters in other random samples. Thus, LnN contains an additional source of variability due to random sampling that GEEs don't conceptually account for. Cluster specific random effects account for the variability in LnN due to cluster specific behavior when estimating population average parameters. Parameter estimation methods such as OLS, principal components, and reduced major axis fail to account for cluster specific behavior within the overall dataset and thus may produce population average parameter estimates that are not representative of the general trends of clusters in the current sample. Similar to GEEs, since cluster specific random effects induce autocorrelation among observations from the same cluster, mixed-models are more parsimonious than the "two-step" approach and produce more efficient parameter estimates.

Based on the conceptual reasoning for using mixed-models, this dissertation examined using mixed-models to estimate MSDR species boundary line slopes relative to other slope estimation methods. Due to the ability of mixed-models to account for cluster specific behavior when estimating MSDR species boundary line slopes, vastly different slope estimates may be obtained relative to other methods. Hynynen (1993) used linear mixed-models to estimate slopes of stands located in Finland. However, he did not compare parameter estimates to other slope estimation procedures and failed to explain the conceptual reason for using mixed-models when estimating MSDR species boundary line slopes. This research accounts for entire cluster specific behaviors when estimating a MSDR species boundary line slope.

Assumptions when using MSDR constraints

MSDR species boundary lines have often been used as constraints in growth and yield models. Equations that predict volume, height, diameter, etc. are used to predict stand development until size-density trajectories reach the boundary level and stands are then assumed to self-thin along this constraint (Monserud et al. 2005). For example, MSDR species boundary lines have been used to constrain predicted stand development for ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) stands in California (Oliver and Powers 1978), acacia (*Acacia nilotica*) in Pakistan (Maguire et al. 1990), western hemlock in the Pacific Northwest (Johnson 2000), mixed species stands in Alberta (Yang and Titus 2002), and a variety of species in the Southern US (Donnelly et al. 2001). MSDR constraints have also been used in more process based models (Landsberg and Waring 1997). Dynamic size-density models have been developed relative to MSDR species boundary lines for a variety of species, including red alder (*Alnus rubra* Bong.) and red pine (*Pinus resinosa* Ait.) (Smith and Hann 1984), red pine (Tang et al. 1994), red alder and Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) (Puettmann et al. 1993), and loblolly pine (Cao 1994, Zeide and Zhang 2006). All of these models assume a constant MSDR species boundary line and slope regardless of planting density, site quality, genetics, etc. More amenable dynamic size-density models have been developed for a variety of species that produce different MSDR boundary levels relative to planting density, site quality, etc., including slash pine (*Pinus elliottii* var. *elliottii* Engelm.) in Louisiana (Cao et al. 2000) and red pine in the Lake States (Turnblom and Burk 2000). Hara (1984) developed a model for several species. However, all of these models assume the slope is constant across all stands.

The only size-density model found which allows the slope and boundary level to vary relative to site and genetic factors and silvicultural practices was developed by Pittman and Turnblom (2003) for Douglas-fir stands in the Pacific Northwest. Consistent with Pittman and Turnblom, several studies have shown that individual stand MSDR boundary levels vary with site quality (Westoby 1984, Barreto 1989, Peterson and Hibbs 1989, Hynynen 1993, Bi 2004) including loblolly pine in South Africa (Strub and Bredenkamp 1985), genetics (Weller 1990), and planting density (VanderSchaaf 2004). These studies imply that the maximum tree density that can be obtained for a given average tree size varies among stands for a particular species. Thus, in order to provide more meaningful MSDR constraints in growth and yield models and perhaps to produce more precise DMDs, models to estimate loblolly pine plantation MSDRs need to be developed that account for the impacts of factors such as site quality and planting density on boundary levels and slopes.

Determining what observations are within the self-thinning stage of stand development

Size-density trajectories are generally thought to be composed of two major stages of stand development, density-independent and density-dependent mortality stages (Drew and Flewelling 1979, McCarter and Long 1986, Williams 1994). For conventional planting densities, stand development is initially composed of a density-independent stage where any mortality is considered independent of stand density. Within early stages of monospecific plantations, stand density does not impact mortality because intraspecific competition is not occurring for limited site resources such as moisture, nutrients, and light. However, due to limited site resources, as trees continue to increase in size eventually some trees must die so that others can grow. Therefore, stands will be in the density-dependent mortality stage sometimes referred to as self-thinning. The self-thinning stage of stand development is often referred to as the Zone of Imminent Competition Mortality in DMDs.

Size-density trajectories are said to be within the Zone of Imminent Competition Mortality when the probability of mortality is related to stand density due to intraspecific competition. For stands of any age and depending on the average tree size, continual increases in N will eventually cause the probability of mortality to be related to stand density and thus self-thinning will occur. Conversely, during the self-thinning stage of stand development, decreases in N will reduce the probability of mortality occurring. However, at some point, decreases in tree density will not further reduce the probability of mortality occurring since intraspecific competition will not occur.

Within the overall self-thinning stage of stand development, when density-dependent mortality is occurring, there is generally considered to be three stages of stand development:

1. The self-thinning stage of stand development is initially composed of a curved approach to the MSDR dynamic thinning line. During this initial component of self-thinning, mortality is less than the mortality at maximum competition and thus the trajectory has a concave shape (del Rio et al. 2001).
2. With increases in individual tree growth and the death of other trees, eventually the size-density trajectory approximates linear where an increase in $\overline{D}$ is a function of the maximum value of Reineke's SDI (1933), the change in N, and the MSDR dynamic thinning line slope. This stage is known as the MSDR dynamic thinning line stage of stand development (Weller 1990), or when a stand is fully-stocked (del Rio et al. 2001) and Reineke's SDI remains relatively constant.
3. Eventually, as trees die, the residual trees cannot maintain full canopy closure and the trajectory diverges from the MSDR dynamic thinning line (Bredenkamp and Burkhart 1990, Zeide 1995, Cao et al. 2000).

Over the entire range of self-thinning the relationship between Ln$\overline{D}$ and LnN is curvilinear; however, it is commonly assumed there is a linear portion during self-thinning (Cao et al. 2000, del Rio et al. 2001, Yang and Titus 2002, Monserud et al. 2005). The three stages of self-thinning can be seen in Figure 1.4 (adapted from

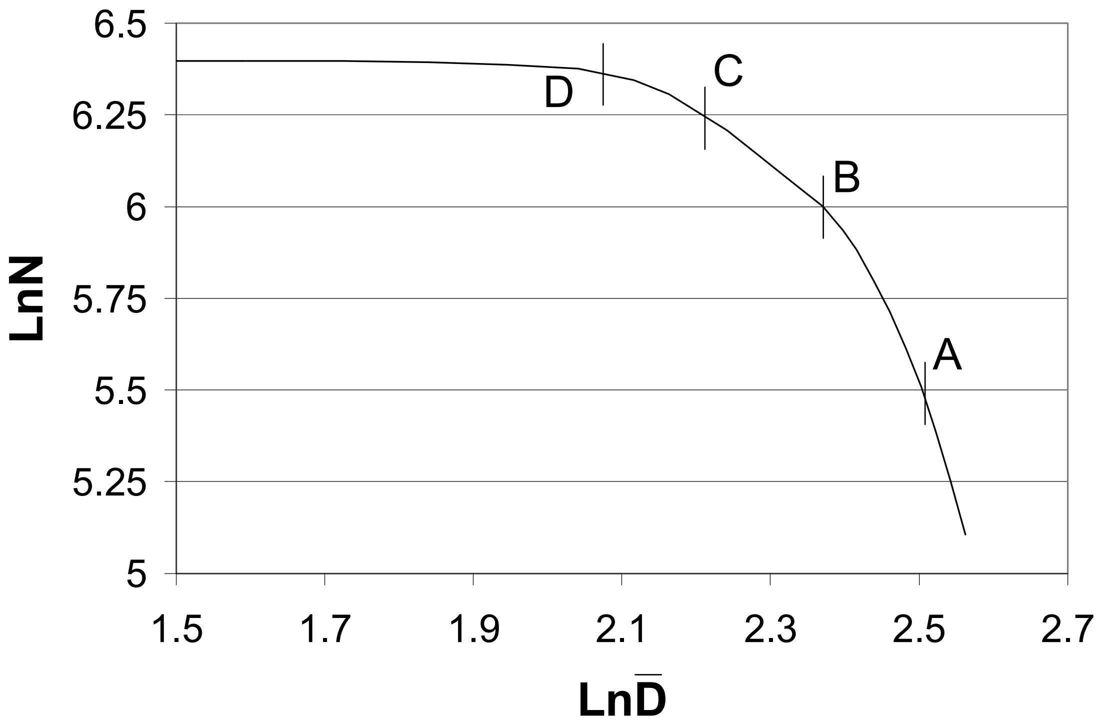


Figure 1.4. Depiction of a size-density trajectory that includes markers to indicate different stages of stand development and what observations to select when modeling maximum size-density relationships (adapted from Weller 1991).

Weller 1991). Within Figure 1.4, the CD component is part of the approach to the MSDR dynamic thinning line stage of self-thinning, BC is the MSDR dynamic thinning line, and AB is part of the divergence from the MSDR dynamic thinning line stage of self-thinning.

Past studies have simply used older unthinned stands without catastrophic mortality to estimate MSDR boundary levels and slopes (Hynynen 1993, Williams 1994, 1996, Wittwer et al. 1998, Zeide 2005), thus, although observations were not selected, specific stands were selected. Many studies have visually determined what observations are within the MSDR dynamic thinning line stage of stand development (Harms 1981, Zeide 1985, Weller 1991, Johnson 2000). Weller (1991) provides a visual aid to determine what observations to select (Figure 1.4). The problem associated with visually selecting observations is that selections can be subjective and may vary among modelers.

Several studies have used some form of quantifiable selection criteria to determine what observations are within the self-thinning stage, or more specifically, within the MSDR dynamic thinning line stage of stand development. For example, del Rio et al. (2001) used a combination of three criteria to determine what observations occurred within the MSDR dynamic thinning line stage of stand development 1) observations must have had at least 1% mortality from the previous measurement, 2) data from the first inventory period were eliminated since it could not be determined if mortality had occurred, and 3) stands with catastrophic mortality were not included. Yang and Titus (2002) used different criteria to determine what observations occurred along MSDR dynamic thinning lines. Stands were grouped into density classes of 240 N and if more than five data points occurred within a density class, observations with the five largest $\overline{D}$s were selected to model the MSDR species boundary line. Bi and Turvey (1997) used a methodology similar to Yang and Titus (2002) when determining what observations occurred along MSDR dynamic thinning lines. They divided the range of tree densities into distinct groups and selected those observations with the greatest biomass within a particular group for estimating the slope of a MSDR species boundary line. Solomon and Zhang (2002) used a different procedure to select what observations occurred along MSDR dynamic thinning lines:

> "…assuming the theoretical value of the slope for the Ln(V) – Ln(N) relationship [Ln(V) = a – 1.5Ln(N)] is –1.5, the intercept coefficient was determined by a = Ln(V) + 1.5Ln(N) using the plot with the largest combination of Ln(V) and Ln(N). The determined equation was then used to compute the maximum stand density (N_{max}) for the V of a given plot. The relative density index (RD) (Drew and Flewelling 1979) was calculated by N/N_{max}. The RD was computed for each plot, and we expected the plot with the largest combination of Ln(V) and Ln(N) to have RD = 1.0. Next, all plots with RD > 0.7 were selected as the most fully-stocked plots for developing the maximum size-density relationship. Although this threshold (RD > 0.7) was arbitrary, we chose this for two reasons: 1) any stands with the relative density index higher than 0.7 should have been undergoing the self-thinning process and experiencing density-related mortality of

late successional species, and 2) a sufficient number of plots would be obtained for fitting the maximum size-density relationship."

Although the criteria given above are reproducible, similar to visually selecting observations, subjectivity can be introduced and often the selection criteria are difficult to follow. Other selection methods that include a combination of subjective and well-defined criteria have also been used (Westoby 1984, Osawa and Allen 1993, Zhang et al. 2005).

Several foresters have proposed using frontier production functions to avoid having to determine what observations to select when modeling MSDRs (Bi et al. 2000, Zhang et al. 2005). However, frontier production functions provide no information about determining when self-thinning begins or what factors cause a divergence from MSDR dynamic thinning lines. By determining what observations are within the density-independent stage of stand development and the three stages of self-thinning, models can be developed to not only determine what factors impact MSDRs but also to determine what factors influence the beginning of self-thinning and what factors cause a divergence from MSDRs. By examining what factors influence the onset of self-thinning, more stand specific DMDs can be developed.

Other modelers have tried to avoid selecting what observations are within the self-thinning stage by developing dynamic size-density trajectories (Smith and Hann 1984, Puettmann et al. 1993, Cao et al. 2000, Pittman and Turnblom 2003). Thus, the entire trajectory is modeled and all observations, whether in the density-independent or density-dependent mortality stages, are included when estimating parameters. However, these models are usually developed based on oversimplications of self-thinning, e.g. assuming a constant boundary level and/or slope (Smith and Hann 1984, Puettmann et al. 1993, Cao 1994, Tang et al. 1994, Cao et al. 2000, Turnblom and Burk 2000, Zeide and Zhang 2006). Additionally, although predicted trajectories can be visually examined to generally determine when self-thinning begins, they don't provide a means to develop regression models that explicitly estimate the expectation of self-thinning as a function of regressors.

Segmented regression has been used in forestry applications such as fitting taper equations (Max and Burkhart 1976, Leites and Robinson 2004) and estimating critical foliar nutrient concentrations (Jokela and Martin 2000). Since segmented regression provides a rather flexible technique to describe several components of a particular dependent variable, this tool can be used to model size-density trajectories on the Ln-Ln scale. When modeling MSDRs it is necessary to determine what observations should be included because not all self-thinning stands are within the MSDR dynamic thinning line stage of stand development (e.g. Figure 1.4). Segmented regression may provide a more standardized methodology when determining what observations are within particular stages of stand development and thus provide a more objective and reproducible methodology. Based on the density-independent stage and the three self-thinning stages of stand development, a variety of segmented regression models can be developed to describe size-density trajectories. Unlike frontier production functions or dynamic size-density models, segmented regression analyses provide a means to explicitly estimate when stages of stand development begin and end. The estimates of when stages begin and end can be used as response variables in regression analyses and predicted as a function of variables such as planting density or site quality.

Determining the existence and duration of a linear stage during self-thinning

Reineke (1933) proposed self-thinning was linear on the Ln-Ln scale for individual stands. Whether Reineke thought the entire self-thinning trajectory was linear or not for individual stands cannot be deduced from his paper. It is commonly thought a portion of self-thinning on the Ln-Ln scale can be assumed linear, the MSDR dynamic thinning line. Several authors have directly stated that a portion of their data can be assumed linear during self-thinning on the Ln-Ln scale (Zeide 1985, Hynynen 1993, Cao et al. 2000, Johnson 2000, Pretzsch and Biber 2005, Zhang et al. 2005) while many authors have assumed a portion of self-thinning can be represented as linear since equation [1.1] is fit (e.g. Williams 1996, Arisman et al. 2004, Bi 2004, Lynch et al. 2004, Goelz 2006). Many dynamic size-density models have also implied a linear component can be assumed during self-thinning since predicted trajectories approach or self-thin along a line (e.g. Smith and Hann 1984, Puettmann et al. 1993, Tang et al. 1994, Turnblom and Burk 2000, Mack and Burk 2005, Zeide and Zhang 2006).

Zeide (1987) was one of the first to claim trajectories of self-thinning stands on the Ln-Ln scale have no linear portion for the LnV-LnN relationship. However, Zeide (1987) states LnV-LnN trajectories have a portion that can be roughly approximated by linear regression and the LnN-Ln$\overline{D}$ relationship is less sensitive to canopy gaps. More recently though, Zeide (2005) states the LnN-Ln$\overline{D}$ relationship is entirely non-linear. Zeide (2005) modified Reineke's original equation by adding a component allowing for divergence from the MSDR dynamic thinning line, resulting in:

$$\mathrm{LnN} = b_0 + b_1 \mathrm{Ln}\left[\frac{\overline{D}}{10}\right] - c(\overline{D}-10) \qquad [1.7]$$

Where:

b_0, b_1, c are parameters to be estimated where b_1 = MSDR dynamic thinning line slope.

Equation [1.7] was developed because the number of trees decreases faster than predicted by Reineke's original equation during the divergence stage of self-thinning suggesting an exponential modification of Reineke's SDI untransformed scale equation.

The use of linear MSDRs makes using them as constraints in growth and yield models rather simple and straightforward (Jack and Long 1996). However, the use of non-linear constraints would make the situation more complicated. For instance, when using linear constraints, the point at which a size-density trajectory first reaches the asymptotic constraint is irrelevant, for any change in Ln$\overline{D}$, LnN changes at a constant rate -- the MSDR dynamic thinning line slope. For non-linear constraints, the slope is not constant and thus the MSDR boundary level is never constant. The point at which a size-density trajectory first reaches the asymptotic constraint would need to be correctly estimated such that a proper upper boundary was used to change LnN given any change in Ln$\overline{D}$ --

this could be problematic (Figure 1.5). For example, depending on the size-density trajectory path, a particular trajectory may not reach the predicted maximum stand density. Somewhat related, if one assumed that various treatments produced a Type C age-shift, when using nonlinear boundaries to constrain stand development the treatments may not all obtain the same maximum stand density.

The argument of entirely non-linear self-thinning trajectories may very well be trivial. Due to the effects of measurement errors and environmental variation among years, strictly concluding that self-thinning is entirely non-linear or strictly concluding that self-thinning consists of a linear portion may not possible. For example, assuming a size-density trajectory was within the MSDR dynamic thinning line portion of self-thinning, a few mediocre environmental years followed by a few superior environmental years followed by a few mediocre environmental years could make the trajectory appear non-linear. If in fact self-thinning is entirely non-linear, the argument may then be the degree of non-linearity (e.g. Zeide 1987). Slight non-linearity would be very difficult to detect and model. Additionally, non-linearity may be related to the time interval between measurements -- over a period of one month residual trees may not be able to respond fast enough to canopy gaps such that a linear LnN-Ln $\overline{\mathrm{D}}$ relationship is maintained but over a three year period a linear LnN-Ln $\overline{\mathrm{D}}$ relationship may be maintained. Most foresters would certainly agree that a divergence from a MSDR dynamic thinning line would occur (Cao et al. 2000, del Rio et al. 2001, Yang and Titus 2002, Monserud et al. 2005) and thus the need for a divergence when using linear constraints is certainly not trivial. Using the segmented regression model methodology discussed earlier,

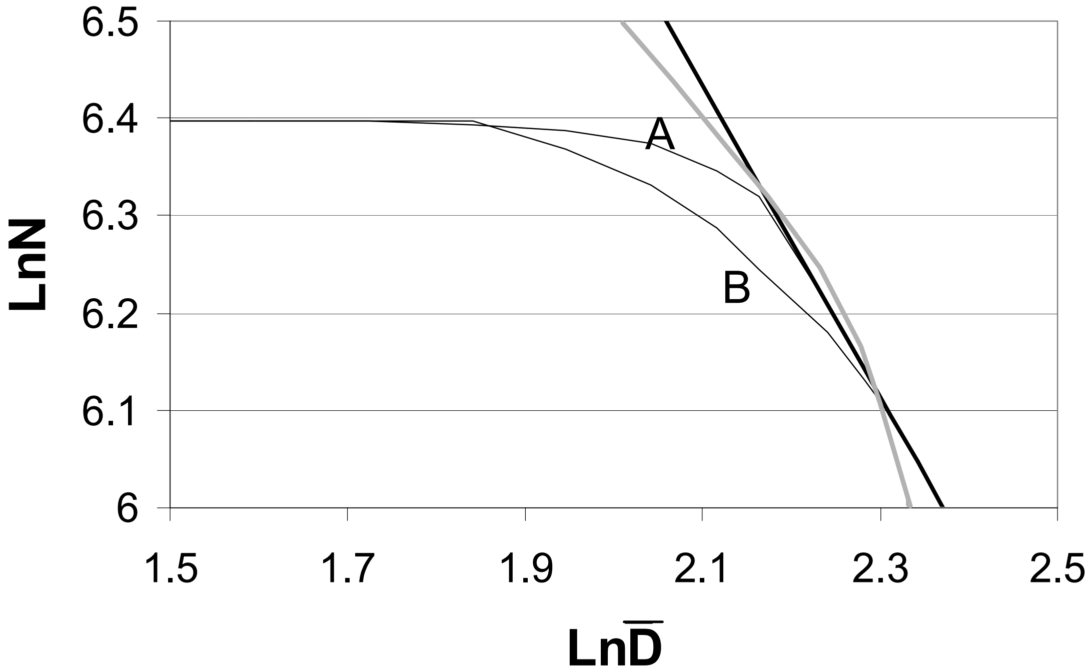


Figure 1.5. Depiction of a MSDR dynamic thinning line and a nonlinear MSDR dynamic boundary. Two size-density trajectories are also shown that attain the same linear MSDR dynamic thinning line boundary level but do not have the same nonlinear MSDR dynamic boundary. When using the nonlinear MSDR dynamic boundary as a constraint, Trajectory A will attain a higher maximum stand density, since it converges to the boundary line prior to the predicted maximum stand density occurring, relative to Trajectory B.

statistics can be used to determine if a portion of self-thinning on the Ln-Ln scale can be represented as linear.

Objectives

Given the work that has been done to quantify maximum size-density relationships and the need to further refine understanding of this aspect of forest stand dynamics, the objectives of this study were to:

1. Provide alternative methods, under the assumption that self-thinning contains a linear portion, to estimate the slope of maximum size-density relationships on the Ln-Ln scale.
2. Demonstrate that an estimate of the MSDR species boundary line slope can be sensitive to the range of planting densities contained in the model fitting dataset.
3. Define a third type of maximum size-density relationship, the MSDR species boundary line **II**, which accounts for MSDR dynamic thinning line boundary levels and slopes when estimating a MSDR species boundary line slope.
4. Demonstrate that segmented regression is a new, less subjective and statistically based, criterion to determine what observations are within the self-thinning stage of stand development, and more specifically, what observations are within the MSDR dynamic thinning line stage of stand development.
5. Determine statistically if a portion of self-thinning on the Ln-Ln scale can be represented as linear.

6. Develop a model system to determine when MSDR dynamic thinning lines begin and end, the slope of that line, and the boundary level of that line all relative to planting density.
7. Show that more stand-specific DMDs need to be developed and present planting density specific DMDs for stands located in the Piedmont and Atlantic Coastal Plain physiographic regions.

Literature cited

Arisman, H., S. Kurinobu, and E. Hardiyanto. 2004. Minimum distance boundary method: maximum size-density lines for unthinned *Acacia mangium* plantations in South Sumatra, Indonesia. J. For. Res. 9: 233-237.

Barreto, L.S. 1989. The '3/2 power law': A comment on the specific constancy of K. Ecol. Model. 45: 237-242.

Bi, H. 2001. The self-thinning surface. For. Sci. 47: 361-370.

Bi, H. 2004. Stochastic frontier analysis of a classic self-thinning experiment. Austral Ecology 29: 408-417.

Bi, H., and N.D. Turvey. 1997. A method of selecting data points for fitting the maximum biomass-density line for stands undergoing self-thinning. Australian J. Ecol. 22: 356-359.

Bi, H., G. Wan, and N.D. Turvey. 2000. Estimating the self-thinning boundary line as a density-dependent stochastic biomass frontier. Ecology 81: 1477-1483.

Bredenkamp, B.V., and H.E. Burkhart. 1990. An examination of spacing indices for *Eucalyptus grandis*. Can. J. For. Res. 20: 1909-1916.

Cao, Q.V. 1994. A tree survival equation and diameter growth model for loblolly pine based on the self-thinning rule. J. Appl. Ecol. 31: 693-698.

Cao, Q.V., T.J. Dean, and V.C. Baldwin. 2000. Modeling the size-density relationship in direct-seeded slash pine stands. For. Sci. 46: 317-321.

Dean, T.J., and V.C. Baldwin. 1993. Using a stand density-management diagram to develop thinning schedules for loblolly pine plantations. USDA For. Serv. Res. Pap. SO-275. 7 p.

del Rio, M., G. Montero, and F. Bravo. 2001. Analysis of diameter-density relationships and self-thinning in non-thinned even-aged Scots pine stands. For. Ecol. Manage. 142: 79-87.

Donnelly, D., B. Lilly, and E. Smith. 2001. The Southern variant of the Forest Vegetation Simulator. Forest Management Service Center, Fort Collins, CO.

Drew, T.J., and J.W. Flewelling. 1979. Stand density management: an alternative approach and its application to Douglas-fir plantations. For. Sci. 25: 518-532.

Goelz, J.C.G. 2006. Dynamics of dense direct-seeded stands of southern pines. P. 310-316 *in* Proc. of the Thirteenth biennial southern silvicultural research conference, Connor, K.F., (ed). USDA For. Serv. Gen. Tech. Rep. SRS-GTR-92.

Hara, T. 1984. Modelling the time course of self-thinning in crowded plant populations. Ann. Bot. 53: 181-188.

Harms, W.R. 1981. A competition function for tree and stand growth models. P. 179-183 *in* Proc. of the First biennial southern silvicultural research conference, Barnett, J.P., (ed). USDA For. Serv. Gen. Tech. Rep. SO-GTR-34.

Hynynen, J. 1993. Self-thinning models for even-aged stands of *Pinus sylvestris, Picea abies*, and *Betula penula*. Scand. J. For. Res. 8: 326-336.

Jack, S.B., and J.N. Long. 1996. Linkages between silviculture and ecology: an analysis of density management diagrams. For. Ecol. Manage. 86: 205-220.

Johnson, G. 2000. ORGANON calibration for western hemlock project: Maximum size-density relationships. Willamette Industries, Inc. Internal Research Report. 8 p. Can obtain a pdf file at http://www.cof.orst.edu/cof/fr/research/organon/orgpubdl.htm

Jokela, E.J., and T.A. Martin. 2000. Effects of ontogeny and soil nutrient supply on production, allocation, and leaf area efficiency in loblolly and slash pine stands. Can. J. For. Res. 30: 1511 - 1524.

Landsberg, J.J., and R.H. Waring. 1997. A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. For. Ecol. Manage. 95: 209-228.

Leites, L.P., and A.P. Robinson. 2004. Improving taper equations of loblolly pine with crown dimensions in a mixed-effects modeling framework. For. Sci. 50: 204-212.

Lloyd, F.T., and W.R. Harms. 1986. An individual stand growth model for mean plant size based on the rule of self-thinning. Ann. Bot. 57: 681-688.

Lynch, T.B., R.F. Wittwer, and D.J. Stevenson. 2004. Estimation of Reineke and volume-based maximum size-density lines for shortleaf pine. P. 226 *in* Proc. of the Twelfth biennial southern silvicultural research conference, Connor, K.F., (ed). USDA For. Serv. Gen. Tech. Rep. SRS-GTR-71.

MacKinney, A.L., and L.E. Chaiken. 1935. A method of determining density of loblolly pine stands. USDA For. Serv., Appalachian Forest Experiment Station, Tech. Note 15. 3 p.

McCarter, J.B., and J.N. Long. 1986. A lodgepole pine density management diagram. West. J. Appl. For. 1: 6-11.

McNabb, K., and C. VanderSchaaf. 2003. A survey of forest tree seedling production in the South for the 2002 – 2003 planting season. Auburn University Southern Forest Nursery Management Cooperative. Tech. Note 03-02. 10 p.

Mack, T.J., and T.E. Burk. 2005. A model-based approach to developing density management diagrams illustrated with Lake States red pine. North. J. Appl. For. 22: 117-123.

Maguire, D.A., G.F. Schreuder, and M. Shaikh. 1990. A biomass/yield model for high-density *Acacia nilotica* plantations in Sind, Pakistan. For. Ecol. Manage. 37: 285-302.

Max, T.A., and H.E. Burkhart. 1976. Segmented polynomial regression applied to taper equations. For. Sci. 22: 283-289.

Mohler, C.L., P.L. Marks, and D.G. Sprugel. 1978. Stand structure and allometry of trees during self-thinning of pure stands. J. Ecol. 66: 599-614.

Monserud, R.A., T. Ledermann, and H. Sterba. 2005. Are self-thinning constraints needed in a tree-specific mortality model? For. Sci. 50: 848-858.

Nilsson, U., and H.L. Allen. 2003. Short- and long-term effects of site preparation, fertilization and vegetation control on growth and stand development of planted loblolly pine. For. Ecol. Manage. 175: 367-377.

Oliver, W.W., and R.F. Powers. 1978. Growth models for ponderosa pine: I. Yield of unthinned plantations in northern California. USDA For. Serv. Res. Pap. PSW-RP-133. 21 p.

Osawa, A., and R.B. Allen. 1993. Allometric theory explains self-thinning relationships of mountain beech and red pine. Ecology 74: 1020-1032.

Peterson, W.C., and D.E. Hibbs. 1989. Adjusting stand density management guides for sites with low stocking potential. West. J. Appl. For. 4: 62-65.

Pittman, S.D., and E.C. Turnblom. 2003. A study of self-thinning using coupled allometric equations: implications for coastal Douglas-fir stand dynamics. Can. J. For. Res. 33: 1661-1669.

Pretzsch, H., and P. Biber. 2005. A re-evaluation of Reineke’s rule and stand density index. For. Sci. 51: 304-320.

Puettmann, K.J., D.W. Hann, and D.E. Hibbs. 1993. Evaluation of the size-density relationships for pure red alder and Douglas-fir stands. For. Sci. 39: 7-27.

Reineke, L.H. 1933. Perfecting a stand-density index for even-age forests. J. Agri. Res. 46: 627-638.

Schabenberger, O., and F.J. Pierce. 2001. Contemporary statistical models for the plant and soil sciences. CRC Press, Boca Raton, FL. 738 p.

Smith, N.J., and D.W. Hann. 1984. A new analytical model based on the -3/2 power rule of self-thinning. Can. J. For. Res. 14: 605-609.

Solomon, D.S., and L. Zhang. 2002. Maximum size-density relationships for mixed softwoods in the northeastern USA. For. Ecol. Manage. 155: 163-170.

Strub, M.R., and B.V. Bredenkamp. 1985. Carrying capacity and thinning response of *Pinus taeda* in the CCT experiments. South African For. J. 2: 6-11.

Tang, S., C.H. Meng, F. Meng, and Y.H. Wang. 1994. A growth and self-thinning model for pure even-age stands: theory and applications. For. Ecol. Manage. 70: 67-73.

Turnblom, E.C., and T.E. Burk. 2000. Modeling self-thinning of unthinned Lake States red pine stands using nonlinear simultaneous differential equations. Can. J. For. Res. 30: 1410-1418.

VanderSchaaf, C.L. 2004. Can planting density have an effect on the maximum size-density line of loblolly and slash pine? P. 115-126 *in* Proc. of the Northeastern Mensurationist Organization and Southern Mensurationists Joint Conference, Doruska, P.F., and Radtke, P. (comps.). Department of Forestry, Virginia Polytechnic Institute and State University, Blacksburg, VA. Can obtain a pdf file at http://filebox.vt.edu/users/cvanders/

VanderSchaaf, C.L., and D.B. South. 2004. Early growth response of slash pine to double-bedding on a flatwoods site in Georgia. P. 363-367 *in* Proc. of the Twelfth biennial southern silvicultural research conference, Connor, K.F., (ed). USDA For. Serv. Gen. Tech. Rep. SRS-GTR-71.

Weller, D.E. 1987. A reevaluation of the -3/2 power rule of plant self-thinning. Ecol. Monogr. 57: 23-43.

Weller, D.E. 1990. Will the real self-thinning rule please stand up? – A reply to Osawa and Sugita. Ecology 71: 1204-1207.

Weller, D.E. 1991. The self-thinning rule: Dead or unsupported? – A reply to Lonsdale. Ecology 72: 747-750.

Westoby, M. 1984. The self-thinning rule. Adv. Ecol. Res. 14: 167- 225.

Williams, R.A. 1994. Stand density management diagram for loblolly pine plantations in north Louisiana. South. J. Appl. For. 18: 40-45.

Williams, R.A. 1996. Stand density index for loblolly pine plantations in north Louisiana. South. J. Appl. For. 20: 110-113.

Wittwer, R.F., T.B. Lynch, and M.M. Huebschmann. 1998. Stand density index for shortleaf pine (*Pinus echinata* Mill.) natural stands. P. 590-596 *in* Proc. of the Ninth biennial southern silvicultural research conference, Waldrop, T.A., (ed). USDA For. Serv. Gen. Tech. Rep. SRS-GTR-20.

Yang, Y. and S.J. Titus. 2002. Maximum-size density relationship for constraining individual tree mortality functions. For. Ecol. Manage. 168; 259-273.

Zeide, B. 1985. Tolerance and self-tolerance of trees. For. Ecol. Manage. 13: 149-166.

Zeide, B. 1987. Analysis of the 3/2 power law of self-thinning. For. Sci. 33: 517-537.

Zeide, B. 1991. Self-thinning and stand density. For. Sci. 37: 517-523.

Zeide, B. 1995. A relationship between size of trees and their number. For. Ecol. Manage. 72: 265-272.

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

Zeide, B, and Y. Zhang. 2006. Mortality of trees in loblolly pine plantations. P. 305-309 *in* Proc. of the Thirteenth biennial southern silvicultural research conference, Connor, K.F., (ed). USDA For. Serv. Gen. Tech. Rep. SRS-GTR-92.

Zhang, L., H. Bi, J.H. Gove, and L.S. Heath. 2005. A comparison of alternative methods for estimating the self-thinning boundary line. Can. J. For. Res. 35: 1-8.

Chapter 2

Data

For this dissertation, two sets of data were used to fit and validate presented models. All datasets are from loblolly pine plantations established on cutover sites in the Southeastern US.

Model fitting dataset

Tree and stand measurements were obtained from a spacing trial maintained by the Loblolly Pine Growth and Yield Research Cooperative at Virginia Polytechnic Institute and State University. The spacing trial was established on four sites; two in the Upper Atlantic Coastal Plain and two in the Piedmont. There is one Coastal plain site in both North Carolina and Virginia while both Piedmont sites are in Virginia. Three replicates of a compact factorial block design were established at each location in either 1983 or 1984. Sixteen initial planting densities were established in each replicate ranging from 2722 to 302 seedlings per acre (Table 2.1). Thus, a total of 192 research plot replicates were established when combining all four sites (4 sites x 3 replications x 16 planting densities). A variety of planting distances between and within rows were used (not all spacings were square). For the planting densities of 2722, 1210, 680, and 302 there was one plot established for a particular site and replication combination, for the planting densities of 1815, 1361, 605, and 453 there were two plots established, and for the planting density of 907 there were four plots established. Seed sources were of genetically improved stock considered superior for a particular physiographic region, for both sites within a particular physiographic region the same genetic stock were used. All seedlings planted at each location were lifted from the same nursery and were 1-0 stock. See Amateis et al. (1988) or Sharma et al. (2002) for a more comprehensive description of the studies.

Measurements of quadratic mean diameter and trees per acre have been conducted annually beginning at age 5 to age 21 on one of the Coastal plain sites and to age 22 on the other site. On the Piedmont sites, measurement ages are to 18 and 21 years of age. At the latter Piedmont site, one replication had measurements to 22 years of age.

Model validation datasets

Validation data were obtained from a long-term loblolly pine plantation thinning study established on cutover sites throughout the Southeastern United States (Burkhart et al. 1985, Burkhart et al. 2004). Study plots were established in 1980-1982 at 186 locations. At each study location, three plots were established; one was left unthinned and the two other plots were thinned; a lightly thinned plot and a heavily thinned plot. Thinnings were generally from below and the light thinning removed approximately one-third of the plot basal area per acre while the heavy thinning removed approximately one-half of the plot basal area per acre. The three experimental plots were located so as to minimize variation among the plots due to microsite differences.

Measurement ages ranged from 8 to 45 years and inventories were conducted every three years following initial plot establishment. For sites where planting density is known, it ranged from 570 to 1223 seedlings per acre. Genetic seed are of unimproved sources. Most likely, seedlings are of local seed sources near the particular plot location and were 1-0 at time of planting.

Literature Cited

Amateis, R.L., H.E. Burkhart, and S.M. Zedaker. 1988. Experimental design and early analyses for a set of loblolly pine spacing trials. P. 1058-1065 *in* Forest Growth Modelling and Prediction, Vol. 2, Ek, A.R., S.R. Shifley, and T.E. Burk, (eds.). USDA For. Serv. Gen. Tech. Rep. NC-GTR-120.

Burkhart, H.E., D.C. Cloeren, and R.L. Amateis. 1985. Yield relationships in unthinned loblolly pine plantations on cutover, site-prepared lands. South. J. Appl. For. 9: 84-91.

Burkhart, H.E., R.L. Amateis, J.A. Westfall, and R.F. Daniels. 2004. PTAEDA 3.1: Simulation of individual tree growth, stand development and economic evaluation in loblolly pine plantations. Sch. of For. and Wildl. Res., Va. Polytech Inst. and State Univ. 23 p.

Sharma, M., H.E. Burkhart, and R.L. Amateis. 2002. Modeling the effect of density on the growth of loblolly pine trees. South. J. Appl. For. 26: 124-133.

Table 2.1. Planting density, number of plots across all 4 sites and 12 replications, number of plots per replication, and the spacing for the model fitting dataset.

Planting Density	Number across all 4 sites	Number per replication	Spacing ft.
2722	12	1	4-by-4
1815	24	2	4-by-6 6-by-4
1361	24	2	4-by-8 8-by-4
1210	12	1	6-by-6
907	48	4	4-by-12 6-by-8 8-by-6 12-by-4
680	12	1	8-by-8
605	24	2	6-by-12 12-by-6
453	24	2	8-by-12 12-by-8
302	12	1	12-by-12
	192	16	

Chapter 3

Comparison of methods to estimate Reineke's maximum size-density relationship species boundary line slope

Curtis L. VanderSchaaf and Harold E. Burkhart[1]

[1] Department of Forestry, Virginia Polytechnic Institute and State University

ABSTRACT

Maximum size-density relationships (MSDR) provide natural resource managers useful information about the relationship between tree density and average tree size. Obtaining a valid estimate of how maximum tree density changes with changes in average tree size is necessary to describe these biological relationships accurately. This paper examines three methods to estimate the slope (b) of the MSDR species boundary line across a range of planting densities: ordinary least squares, first-difference model, and the linear mixed-effects model. For this paper, stability refers to the extent to which parameter estimates do not change when the range of planting densities in the fitting dataset changes. When using data from a planting density trial consisting of planting densities ranging from 2722 to 605 seedlings per acre, mixed-effect models produced the most stable estimates of b while OLS resulted in the least stable estimates.

MSDR boundaries have been defined as either a) those that describe the boundaries of individual stands (MSDR dynamic thinning line) or b) those that describe MSDRs common across all sites for a particular species in a certain geographical region (MSDR species boundary line). A further refinement of the MSDR species boundary line is proposed by defining two MSDR species boundary lines, labeled here as **I** and **II**. Although both MSDR species boundary lines are positioned above all observations, one MSDR species boundary line, (**II**), has a slope that can be considered the population average of all MSDR dynamic thinning lines; the other species boundary line (**I**) has a slope that results from positioning the boundary above all observations without accounting for self-thinning patterns of individual stands. A mixed-effects analysis was used to estimate the slope of a MSDR species boundary line **II**.

Keywords: dynamic thinning lines, loblolly pine, Pinus taeda, stand density.

According to the theoretical reasoning behind stand density index (SDI), all stands should eventually approach and track along the same Maximum Size-Density Relationship (MSDR) boundary for a particular species/region combination (Reineke 1933, Drew and Flewelling 1977, Osawa and Sugita 1989, Williams 1996, Harms et al. 2000). The MSDR is commonly expressed in terms of SDI as seen in equation [3.1]:

$$SDI = N(\overline{D}/25.4)^{b} \qquad [3.1]$$

Where:

N – trees per hectare

$\overline{D}$ – quadratic mean diameter (cm)

b = MSDR boundary coefficient

Generally, for the model form used in equation [3.1], *b* is close to 1.6. Usually, *b* is obtained by regressing LnN against $\text{Ln}\,\overline{D}$ which gives a negative *b*, where Ln is the natural logarithm. Williams (1996) shows how equation [3.1] is derived from the LnN-$\text{Ln}\,\overline{D}$ regression and how *b* becomes positive when used in equation [3.1]. Although this study pertains to estimating the *b* of Reineke's MSDR, this analysis also applies to the well-known Self-thinning rule (Westoby 1984, Weller 1987, Zeide 1987) which uses average volume or average biomass rather than average diameter.

Reineke (1933) conceptualized the MSDR boundary as a linear asymptote on the log-log scale that all stands would eventually approach and track along for a particular species/region combination. Since that time ecologists and foresters have proposed modifications to the theory behind the self thinning concept. This sparked debates between several authors including Weller (1987, 1990), and Osawa and Sugita (1989). For the remainder of this paper, the terminology of Weller (1990) will be used:

1. Individual stand MSDR boundaries will be referred to as MSDR dynamic thinning line boundaries.
2. The MSDR species boundary line **I** shall be defined as a static upper limit of maximum tree density – average tree size relationships (or conversely maximum average tree size – tree density relationships) that applies to all stands of a certain species within a particular geographical area.

For the MSDR species boundary line **I**, "static" refers to the fact that mid-rotation and regeneration management techniques, site quality, genetics, etc., have no impact on this boundary line as opposed to MSDR dynamic thinning lines which can be affected by genetic stock and silvicultural treatments (Weller 1990, VanderSchaaf 2004). The MSDR species boundary line **I** is a line of constant slope connecting maximum tree densities across a range of average tree sizes regardless of site quality, planting density, genetics, thinnings, etc. Maximum tree densities across the range of average tree sizes can be a conglomeration from many stands and the maximum tree densities are not necessarily obtained from an individual stand (Figure 3.1). Conversely, the axes can be rotated such that the MSDR species boundary line **I** is a line of constant slope that connects the maximum average tree size for a given tree density regardless of site quality, planting density, genetics, thinnings, etc.

As shown in Figure 3.1, size-density trajectories for stands of high planting densities begin to diverge from their MSDR dynamic thinning line boundaries before other stands have even reached their MSDR dynamic thinning line boundaries. Thus, if one uses the definition of Weller (1990) to define the MSDR species boundary line - [the MSDR species boundary line **I**] **-** the *b* of this line would not on average reflect the self-thinning pattern of an individual stand (Table 3.1). However, the MSDR species boundary line **I** has been interpreted as a description of individual stand development since it is often assumed that all stands have a constant boundary level and *b* for a given species and particular geographic region. Thus, a third type of MSDR boundary line - [MSDR species boundary line **II**] needs to be defined. The difference between the MSDR species boundary line **II** and MSDR dynamic thinning lines is that each dynamic thinning line has its own *b* while the *b* of **II** can be thought of as an estimate of the MSDR dynamic thinning line population average *b*. Additionally, MSDR dynamic thinning lines each have their own boundary level while, similar to the MSDR species boundary line **I**, the MSDR species boundary line **II** has a constant boundary level.

Often, the MSDR species boundary line is used as a limit for stand density in models (Oliver and Powers 1978, Smith and Hann 1984, 1986, Puettmann et al. 1993). Monserud et al. (2005) described the utility of limiting stand density using self-thinning constraints. When using self-thinning constraints, stand development is predicted using equations independent of the self-thinning constraint until the stand reaches the upper boundary. Stand tree density or average tree size is then constrained such that the stand trajectory tracks along this upper boundary either for a limited amount of time before diverging from the boundary or the stand tracks along this upper boundary for the life of the stand. There are several statistical methods to estimate *b* that includes ordinary least squares (OLS), first-difference models, and mixed-models. When growth and yield models are constrained by MSDR species boundary lines using an estimated *b*, an improper estimated value of *b* can produce serious errors in estimation of stand density development since N will be reduced at a rate that is not correct for a particular increase in $\overline{\mathrm{D}}$. These errors will affect estimates of stand yield and ultimately economic decisions.

The objectives of this paper are to: (1) define a third type of MSDR boundary – the MSDR species boundary line **II,** (2) ascertain whether different statistical methods used to estimate the MSDR species boundary line *b* result in varying values, and (3) determine which statistical methods are more appropriate for obtaining estimates of *b* consistent with each of the definitions of the MSDR species boundary lines.

Methods

Data

Tree and stand measurements were obtained from a spacing trial maintained by the Loblolly Pine Growth and Yield Research Cooperative at Virginia Polytechnic Institute and State University (Table 3.1). The spacing trial was established on four sites; two in the Upper Atlantic Coastal Plain and two in the Piedmont. There is one Coastal plain site in both North Carolina and Virginia while both Piedmont sites are in Virginia. Three replicates of a compact factorial block design were established at each location in either 1983 or 1984. Initial planting densities ranged from 747 to 6727 seedlings per hectare. A variety of planting distances between and within rows were used (not all spacings were square). Rather than using a constant plot size, 49 trees were established per plot and thus plot sizes ranged from about 0.007 to 0.07 hectares. See Zhang et al. (1996) for a more comprehensive description of the studies.

Measurements of $\overline{D}$ and N have been conducted annually beginning at age 5 to age 20 on one of the Coastal plain sites and to age 21 on the other site. On the Piedmont sites, measurement ages are to 18 at one location and 21 at the other.

Stages of individual stand development

Within the overall self-thinning stage of stand development, when density-dependent mortality is occurring, there is generally considered to be three stages of stand development:

1. The self-thinning stage of stand development is initially composed of a curved approach to the MSDR dynamic thinning line. During this initial component of self-thinning, mortality is less than the mortality at maximum competition and thus the trajectory has a concave shape (del Rio et al. 2001).

2. With increases in individual tree growth and the death of other trees, eventually the size-density trajectory approximates linear where an increase in $\overline{\mathrm{D}}$ is a function of the maximum value of Reineke's SDI, the change in N, and the MSDR dynamic thinning line *b*. This stage is known as the MSDR dynamic thinning line stage of stand development (Weller 1990), or when a stand is fully-stocked (del Rio et al. 2001) and Reineke's SDI remains relatively constant.
3. Eventually, as trees die, the residual trees cannot maintain full canopy closure and the trajectory diverges from the MSDR dynamic thinning line (Bredenkamp and Burkhart 1990, Zeide 1995, Cao et al. 2000).

Over the entire range of self-thinning the relationship between Ln$\overline{\mathrm{D}}$ and LnN is curvilinear; however, this analysis deals only with the linear stage (or portion) of the trajectory (Cao et al. 2000, del Rio et al. 2001, Yang and Titus 2002, Monserud et al. 2005).

Determining what observations lie along MSDR dynamic thinning line boundaries

Graphs of LnN over Ln$\overline{\mathrm{D}}$ were constructed for each study plot to determine when trajectories had reached a MSDR dynamic thinning line boundary. In order to be consistent with the recommendations of Weller (1987, 1991), a visual inspection of all plots was conducted to ensure only those observations occurring along a MSDR dynamic thinning line boundary were included when estimating the MSDR species boundary line *b* coefficient (Figure 3.2).

Slopes of individual MSDR dynamic thinning line boundaries were greatly affected by observations located within the divergence stage of stand development -- stage 3 of self-thinning. Therefore, these observations were eliminated when determining the MSDR species boundary line *b*. For example, see the last observation of the size-density trajectory shown in Figure 3.2. If a plot had at least two consecutive observations along the MSDR dynamic thinning line – a size-density trajectory moving in a straight line (MSDR dynamic thinning line) to the right – the plot was included in the analysis. Measurement ages occurring along MSDR dynamic thinning line boundaries ranged from 9 to 21 years; greater planting densities generally reached a MSDR dynamic thinning line boundary sooner.

MSDR species boundary line b *estimation methods*

Mean slope calculation method

Rather than using regression analysis techniques, an estimated value of the MSDR species boundary line *b* can be obtained by determining the arithmetic mean of all slopes between two consecutive measurement ages from individual plots at the MSDR stage of stand development, calculated as:

$$b = \frac{\mathrm{Ln}N_{t} - \mathrm{Ln}N_{t-1}}{\mathrm{Ln}\bar{D}_{t} - \mathrm{Ln}\bar{D}_{t-1}} \qquad [3.2]$$

Equation [3.2] quantifies the change in LnN given a change in $\mathrm{Ln}\,\bar{D}$ – the *b* in equation [3.1]. The Mean slope calculation method is used in this paper only as a “reality check” for the estimated *b*’s using the other statistical methods.

Ordinary least squares

Several researchers have used either linear or non-linear regression to estimate the MSDR species boundary line *b* (MacKinney and Chaiken 1935, Oliver and Powers 1978, Smith and Hann 1984, Bredenkamp and Burkhart 1990, Hynynen 1993, Williams 1994, Williams 1996, Wittwer et al. 1998, Cochran and Seidel 1999, Yang and Titus 2002). For this paper, the OLS form will be used:

$$\text{LnN} = b_0 + b_1 \text{Ln}\,\overline{D} + \varepsilon \qquad [3.3]$$

Where:

b_0, b_1 are parameters to be estimated where $b_1 = b$ from equation [3.1].

ε – random error where it is assumed $\varepsilon \sim N(0, \sigma^2 I)$.

When using OLS to estimate the MSDR species boundary line *b,* individual MSDR dynamic thinning line *b*'s are not identified. OLS, and the commonly used form of non-linear regression (e.g. when not directly accounting for autocorrelation among observations) to estimate the MSDR species boundary line *b* do not account for correlations among observations from individual plots. Under autocorrelation, OLS parameter estimates remain unbiased, but the usual OLS estimates of the standard errors of these estimated parameters are biased (Gregoire 1987, Schabenberger and Pierce 2001, pgs. 51-52). For OLS, Proc REG of SAS (SAS 1996) was used to estimate MSDR species boundary line *b*'s.

First-difference model

Wittwer et al. (1998) and Lynch et al. (2004) used a first-difference approach to account for dependencies between observations from the same plot when determining the MSDR species boundary line *b*. A first-difference model is expressed as:

$$\mathrm{Ln}N_2 - \mathrm{Ln}N_1 = b[\mathrm{Ln}\,\overline{D}_2 - \mathrm{Ln}\,\overline{D}_1] + \varepsilon \qquad [3.4]$$

Where:

b is a parameter to be estimated and is equivalent to the *b* from equation [3.1].

ε – random error, where it is assumed ε is normally distributed with a mean of 0.

In this study, the youngest observation occurring along a MSDR dynamic thinning line boundary was not included in the first-difference model analysis since the lag of LnN and lag of Ln $\overline{D}$ did not exist along the MSDR dynamic thinning line boundary (Figure 3.2). Thus, the sample size for this particular method is the same as the Mean slope calculation method and is less than the OLS and linear mixed-effects model analyses. Parameter estimates were obtained using Proc MODEL of SAS (SAS 1988).

Linear mixed-effects model

Although a first-difference model accounts for autocorrelation between successive measurements from the same plot, it fails to account for autocorrelation among many observations from the same plot. Linear mixed-effects analyses can account for correlation among many observations from the same plot (Lappi and Bailey 1988, Schabenberger and Pierce 2001, pg. 408, Eerikäinen 2003). Hynynen (1993) used a mixed-effects analysis to estimate the MSDR species boundary line *b*. The author did not compare this to other ways of estimating the slope, however.

For this analysis, the intercept (b_0) and slope (b_1) terms from equation [3.3] were assumed to be random parameters:

$$\mathrm{LnN} = (b_0 + u_{0i}) + (b_1 + u_{1i})\mathrm{Ln}\,\overline{\mathrm{D}} + \varepsilon \qquad [3.5]$$

Where:

u_{0i}, u_{1i} – are cluster-specific random effects to be predicted and assumed to be $N(0, \sigma_0^2)$ and $N(0, \sigma_1^2)$, respectively. A cluster is an individual plot (indexed by *i*).

ε – random error where it is assumed $\varepsilon \sim N(0, \sigma^2 I)$.

Estimated values were obtained using Proc Mixed of SAS (SAS 1988). For all analyses, an "unstructured" covariance-variance matrix (un) of the random effects (u_{0i}, u_{1i}) was used in Proc Mixed; thus the data were used to estimate the entire covariance-variance structure, e.g. $(\sigma_0^2, \sigma_1^2, \sigma_{01})$. For the random error term, constant variance and independence of observations was assumed because the emphasis is on prediction rather than hypothesis testing (see Schabenberger and Pierce (2001), pgs. 470-471, and pg. 538). All random effects (u_{0i}, u_{1i}) are assumed to be independent of the random error term (ε).

The motivation behind a mixed-effects analysis to estimate the MSDR species boundary line **II** slope is that it accounts for the variability in $\underline{Y}$ due to cluster specific behavior. Although OLS produces unbiased parameter estimates it does not account for cluster specific behavior and is thus not a correct analysis when estimating the slope of the MSDR species boundary line **II**. Due to the random effects, mixed-effects models account for MSDR dynamic thinning line behavior when estimating the MSDR species boundary line **II** slope. The random effects of a particular cluster alter the population average trend which induces correlation between/among observations from that cluster (Schabenberger and Pierce 2001, pgs. 446-448).

Stability of the estimated MSDR species boundary line b *in relation to planting density*

For this paper, stability refers to the extent to which parameter estimates do not change when the range of planting densities in the fitting dataset changes. In order to see how including different planting densities can affect the estimated value of the MSDR species boundary line *b* for a particular statistical method, several analyses were conducted. First, observations from MSDR dynamic thinning lines of all planting densities were included to estimate the MSDR species boundary line *b* using the four statistical methods. Second, to determine if planting density affects the estimated value of the MSDR species boundary line *b*, estimated *b*'s were obtained from datasets containing all planting densities greater than 1976, 2964, 3952, and 4940 seedlings per hectare.

Results

Estimates of the MSDR species boundary line *b* are given in Table 3.2. The OLS parameter estimates were the least stable, varying greatly as the range of planting densities included in the dataset changed. This instability apparently resulted from the lack of independence of observations. Based on the residual and lag residual plots for OLS (Figure 3.3), the data used in this study had a strong presence of positive autocorrelation (Table 3.2). When using the first-difference model the autocorrelation was reduced. However, the parameter estimates using the first-difference model were still relatively unstable as compared to the linear mixed-effects parameter estimates.

The linear mixed-effects analysis produced relatively stable estimates of *b* as planting density changed (*b* ranged only from -1.7265 to -1.6720 when including different planting densities). This statistical method seems to be robust against factors such as planting density that can change the MSDR dynamic thinning line boundary producing unstable MSDR species boundary line *b* estimates when using OLS (e.g. -1.0330 at high planting densities to -2.1240 when including lower planting densities).

The various statistical methods appear to be estimating two different MSDR species boundary line *b*'s. OLS estimates a MSDR species boundary line *b* that allows for a boundary level that bounds all observations and that also lies closer to most observations relative to the other statistical methods (Figure 3.4). Thus, the OLS estimated *b* more closely agrees with the MSDR species boundary line **I** slope. Due to the ability to account for dependency between and among observations, the first-difference and linear mixed-effects models, and the Mean slope calculation method, appear to estimate the *b* for the MSDR species boundary line **II**.

Discussion

Some may argue this paper deals with estimating the *b* of the MSDR species boundary line and thus accounting for MSDR dynamic thinning lines is not necessary. If all we wanted to know was the maximum tree density for a given average tree size across all loblolly pine plantations in the Southeastern US then the OLS estimated *b* would be appropriate. However, beyond determining the maximum tree density for a given average tree size, it is often desired to quantify how, on average, maximum tree density changes for a given change in average tree size for individual plantations – this can also be thought of as the *b* of equation [3.1]. As seen in Table 3.2 and Figure 3.4, the OLS estimated *b* provides a quantification of the upper boundary of the relationship between maximum tree density and average tree size. However, this *b* fails to adequately describe the expected population change (based on the Mean slope calculation method) in maximum tree density given a change in average tree size. Quite often, growth and yield models are constrained using the MSDR species boundary line or the Self-thinning rule. Based on the data used in this analysis, the estimated OLS *b* would, on average, incorrectly predict stand development. Some MSDR dynamic thinning lines may have a *b* close to the estimated OLS *b* though.

Why is the OLS estimated b not sufficient for describing MSDR dynamic thinning lines? When using a *b* near –1.6, stands with low planting densities fall short of the MSDR species boundary line if the boundary level is established using greater planting densities (Figure 3.4). In stands of low planting densities, intraspecific density-dependent mortality occurs at later ages. Trees that die in relation to density-dependent mortality in low planting density stands have greater crown widths associated with the same diameter at breast height (DBH) relative to greater planting densities; thus larger canopy gaps are created when mortality occurs (Bredenkamp and Burkhart 1990, Zeide 1995). This, coupled with the fact that the ability of surviving trees to respond to gaps in the canopy declines with age (Bredenkamp and Burkhart 1990, Zeide 1995), means that MSDR dynamic thinning line boundaries of varying planting densities may not always occur at the MSDR species boundary line when using a *b* near -1.6. To account for differences in MSDR dynamic thinning line boundaries, in addition to adjusting the intercept, OLS adjusts the MSDR species boundary line *b* (Table 3.2).

From a statistical point of view, the OLS estimated MSDR species boundary line *b* fails to adequately describe, on average, the *b* of MSDR dynamic thinning lines because it fails to account for correlation among observations from the same stand (Figure 3.3). By assuming all observations from MSDR dynamic thinning lines are independent, OLS does not estimate the MSDR species boundary line *b* taking into account that MSDR dynamic thinning line boundary levels differ in relation to planting density. For the linear mixed-effects model, the intercept is much less sensitive to the range of planting densities included in the dataset since the intercept is considered random – thus accounting for differences in MSDR dynamic thinning line boundary levels when estimating the MSDR species boundary line *b* (Table 3.2).

When estimating the MSDR species boundary line *b* for western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) stands in the Pacific Northwest, Johnson (2000) found similar results to this study. However, Johnson (2000) failed to explain why the OLS estimated MSDR species boundary line *b* did not adequately describe, on average, MSDR dynamic thinning line boundary *b*'s. When using OLS, Johnson estimated a MSDR species boundary line *b* of -1.902. He then did what can be called the "two-step approach" of accounting for autocorrelation when estimating parameters (Schabenberger and Pierce 2001, pg. 411). Johnson used OLS to estimate the intercept and *b* for each MSDR dynamic thinning line boundary using equation [3.3] – [Step 1]. The average *b* from all MSDR dynamic thinning line boundaries (n = 23) was then considered to be an estimated value of the MSDR species boundary line *b* – [Step 2]. A value of -1.5159 was obtained which is much closer to Reineke's original value of -1.605 -- ultimately Johnson decided to set *b* = -1.605. Schabenberger and Pierce (2001, pg. 411) state the "two-step approach" is inefficient because the method ignores information contributed by other stands when obtaining MSDR dynamic thinning line boundary *b*'s during Step 1.

Both MSDR species boundary lines fail to adequately describe self-thinning patterns of most individual stands. The MSDR species boundary line **I** is inadequate to describe self-thinning of individual stands because the relationships between maximum tree density and average tree size are based on a mixture of many sites (Figure 3.1). The

MSDR species boundary line **II** is inadequate to describe self-thinning patterns of individual stands because, when using a *b* near –1.6, all stands do not have MSDR dynamic thinning line boundaries occurring along the MSDR species boundary line (Figure 3.4).

Previous studies that have found a large difference between their estimated MSDR species boundary line *b* and Reineke's original value of -1.605 (or MacKinney and Chaiken's (1935) original value of -1.707) should be reexamined using mixed-models. However, to clarify, the previous statement depends on whether an estimate of the MSDR species boundary line **I** or **II** *b* was desired.

Predicted MSDR dynamic thinning line boundary b's using linear mixed-effects models

Although using equation [3.2] showed there was variability in the MSDR dynamic thinning line *b* (Table 3.1), equation [3.2] will usually fail to quantify the general trend for a particular MSDR dynamic thinning line *b*. Equations [3.2] and [3.4] only calculate the *b* for any two consecutive points along the MSDR dynamic thinning line boundary. For those plots with more than two observations, equations [3.2] and [3.4] do not account for correlation among all observations from an individual plot – e.g. second and third order lags, etc.

Due to the random effects of linear mixed-models, a more complete prediction of the MSDR dynamic thinning line *b* can be obtained because the predicted value will be based on information from all observations for a particular MSDR dynamic thinning line boundary. Using a linear mixed-models approach to estimate cluster specific *b*'s, or MSDR dynamic thinning line *b*'s, the range of MSDR dynamic thinning line *b*'s was -0.9850 to -2.5987 which is a slightly narrower range than equation [3.2] (Table 3.1 and Figure 3.5). Additionally, the MSDR dynamic thinning line *b*'s estimated using the linear mixed-effects models were more centered around the estimated population average (Figure 3.5). Although the Mean slope calculation method was used as the "reality check," in fact, the linear mixed-effects method may be superior to both equations [3.2] and [3.4] when estimating the *b* for the MSDR species boundary line **II**.

However, a word of caution needs to be expressed. Although in linear mixed-effects models having a large number of individual observations is important and each one adds additional information to the analysis, all asymptotic properties of linear mixed-models are based on the number of clusters (e.g., plots). This results from the lack of independence of all observations. Thus, the asymptotic properties in this particular case were dependent on the number of research plots (e.g. MSDR dynamic thinning lines) and not the number of individual observations from MSDR dynamic thinning lines. Additionally, low numbers of clusters may force the modeler to choose random effects covariance-variance structures other than "unstructured [un]" in Proc MIXED (SAS 1988) due to the inability to obtain reliable estimates. The selected structure can impact the estimates of the parameters.

Conclusions

Weller's (1990) definition of the MSDR species boundary line is correct for the MSDR species boundary line **I**, but does not describe the MSDR species boundary line **II**. If one of the two boundary lines is used to constrain or validate growth and yield projections, particular statistical methods should be used to obtain the correct *b* associated with that particular boundary line. For example, results from this study suggest the OLS estimated *b* is more consistent with the definition of the MSDR species boundary line **I** while the first-difference and linear mixed-effects estimated *b*'s are more consistent with the MSDR species boundary line **II**. Based on the data used in this analysis and the linear mixed-effects analysis for the entire dataset (n = 416), foresters some 70 years ago (Reineke 1933 and MacKinney and Chaiken 1935) may well have determined the population average MSDR dynamic thinning line *b* for loblolly pine stands throughout the Southeastern US. However, results from this study suggest that quantifying MSDR dynamic thinning line boundaries and *b*'s will provide a better description of maximum tree density – average tree size relationships for individual plantations.

Literature Cited

Bredenkamp, B.V., and H.E. Burkhart. 1990. An examination of spacing indices for *Eucalyptus grandis*. Can. J. For. Res. 20: 1909-1916.

Cao, Q.V., T.J. Dean, and V.C. Baldwin. 2000. Modeling the size-density relationship in direct-seeded slash pine stands. For. Sci. 46: 317-321.

Cochran, P.H., and K.W. Seidel. 1999. Growth and yield of western larch under controlled levels of stocking in the Blue Mountains of Oregon. USDA For. Serv. Res. Pap. PNW-RP-517. 35 p.

del Rio, M., G. Montero, and F. Bravo. 2001. Analysis of diameter-density relationships and self-thinning in non-thinned even-aged Scots pine stands. For. Ecol. Manage. 142: 79-87.

Drew, T.J., and J.W. Flewelling. 1977. Some recent Japanese theories of yield density relationships and their application to Monterey pine plantations. For. Sci. 23: 517-534.

Eerikäinen, K. 2003. Predicting the height-diameter pattern of planted *Pinus kesiya* stands in Zambia and Zimbabwe. For. Ecol. Manage. 175: 355-366.

Gregoire, T.G. 1987. Generalized error structure for forestry yield models. For. Sci. 33: 423-444.

Harms, W.R., C.D. Whitesell, and D.S. DeBell. 2000. Growth and development of loblolly pine in a spacing trial planted in Hawaii. For. Ecol. Manage. 126: 13-24.

Hynynen, J. 1993. Self-thinning models for even-aged stands of *Pinus sylvestris, Picea abies*, and *Betula penula*. Scand. J. For. Res. 8: 326-336.

Johnson, G. 2000. ORGANON calibration for western hemlock project: Maximum size-density relationships. Willamette Industries, Inc. Internal Research Report. 8 p. Can obtain a pdf file at http://www.cof.orst.edu/cof/fr/research/organon/orgpubdl.htm

Lappi, J., and R.L. Bailey. 1988. A height prediction model with random stand and tree parameters: an alternative to traditional site index methods. For. Sci. 34: 907-927.

Lynch, T.B., R.F. Wittwer, and D.J. Stevenson. 2004. Estimation of Reineke and volume-based maximum size-density lines for shortleaf pine. P. 226 *in* Proc. of the Twelfth biennial southern silvicultural research conference, Connor, K.F., (ed). USDA For. Serv. Gen. Tech. Rep. SRS-GTR-71.

MacKinney, A.L., and L.E. Chaiken. 1935. A method of determining density of loblolly pine stands. USDA For. Serv., Appalachian Forest Experiment Station, Tech. Note 15. 3 p.

Monserud, R.A., T. Ledermann, and H. Sterba. 2005. Are self-thinning constraints needed in a tree-specific mortality model? For. Sci. 50: 848-858.

Oliver, W.W., and R.F. Powers. 1978. Growth models for ponderosa pine: I. Yield of unthinned plantations in northern California. USDA For. Serv. Res. Pap. PSW-RP-133. 21 p.

Osawa, A., and S. Sugita. 1989. The self-thinning rule: another interpretation of Weller's results. Ecology 70: 279-283.

Puettmann, K.J., D.W. Hann, and D.E. Hibbs. 1993. Evaluation of the size-density relationships for pure red alder and Douglas-fir stands. For. Sci. 39: 7-27.

Reineke, L.H. 1933. Perfecting a stand-density index for even-age forests. J. Agri. Res. 46: 627-638.

SAS Institute, Inc. 1988. SAS/ETS user's guide. Version 6. 1st ed. Cary, N.C.: SAS Institute.

SAS Institute, Inc. 1996. SAS/STAT guide for personal computers. Version 6.12. Cary, N.C.: SAS Institute.

Schabenberger, O., and F.J. Pierce. 2001. Contemporary statistical models for the plant and soil sciences. CRC Press, New York, NY. 738 p.

Smith, N.J., and D.W. Hann. 1984. A new analytical model based on the -3/2 power rule of self-thinning. Can. J. For. Res. 14: 605-609.

Smith, N.J., and D.W. Hann. 1986. A growth model based on the self-thinning rule. Can. J. For. Res. 16: 330-334.

VanderSchaaf, C.L. 2004. Can planting density have an effect on the maximum size-density line of loblolly and slash pine? P. 115-126 *in* Proc. of the Northeastern Mensurationist Organization and Southern Mensurationists Joint Conference, Doruska, P.F., and Radtke, P. (comps.). Department of Forestry, Virginia Polytechnic Institute and State University, Blacksburg, VA. Can obtain a pdf file at http://filebox.vt.edu/users/cvanders/

Weller, D.E. 1987. A reevaluation of the -3/2 power rule of plant self-thinning. Ecol. Monogr. 57: 23-43.

Weller, D.E. 1990. Will the real self-thinning rule please stand up? – A reply to Osawa and Sugita. Ecology 71: 1204-1207.

Weller, D.E. 1991. The self-thinning rule: Dead or unsupported? – A reply to Lonsdale. Ecology 72: 747-750.

Westoby, M. 1984. The self-thinning rule. Advances in Ecol. Res. 14: 167- 225.

Williams, R.A. 1994. Stand density management diagram for loblolly pine plantations in north Louisiana. South. J. Appl. For. 18: 40-45.

Williams, R.A. 1996. Stand density index for loblolly pine plantations in north Louisiana. South. J. Appl. For. 20: 110-113.

Wittwer, R.F., T.B. Lynch, and M.M. Huebschmann. 1998. Stand density index for shortleaf pine (*Pinus echinata* Mill.) natural stands. P. 590-596 *in* Proc. of the Ninth biennial southern silvicultural research conference, Waldrop, T.A., (ed). USDA For. Serv. Gen. Tech. Rep. SRS-GTR-20.

Yang, Y. and S.J. Titus. 2002. Maximum-size density relationship for constraining individual tree mortality functions. For. Ecol. Manage. 168; 259-273.

Zeide, B. 1987. Analysis of the 3/2 power law of self-thinning. For. Sci. 33: 517-537.

Zeide, B. 1995. A relationship between size of trees and their number. For. Ecol. Manage. 72: 265-272.

Zhang, S., H.E. Burkhart, and R.L. Amateis. 1996. Modeling individual tree growth for juvenile loblolly pine plantations. For. Ecol. Manage. 89: 157-172.

Table 3.1. Plot-level characteristics for the observations used in this analysis. All observations are located along a MSDR dynamic thinning line boundary. Mean, minimum (Min), and maximum (Max) values for the slope were obtained based on equation [3.2]. SDI was calculated using equation [3.1] with a slope of 1.6. Observations were obtained from 120 plots. Several plots had more than two observations occurring along a MSDR dynamic thinning line and thus the entire dataset is composed of 416 observations. Since the lag of the youngest observation occurring along a MSDR dynamic thinning line did not occur along the MSDR dynamic thinning line, these slopes, as calculated using equation [3.2], were not included when determining the mean slope and thus the sample size equals 248.

Variable	n	Min	Mean	Max
Trees/ha		595	2453	6453
$\overline{D}$ (cm)		7.7	15.4	25.3
SDI	416	525	942	1499
BA (m^2/ha)		26	40	59
SI (m)		15	19	23
Slope	248	-2.6639	-1.6417	-0.9613

Table 3.2. Estimates of the MSDR species boundary line slope (*b*) using several statistical methods for the full dataset and for subsets of the data consisting of varying planting densities.*

Trees/ha	Estimation method	n	np	Intercept	Std. error	*b*	Std. error
>4940	OLS	37	11	9.0617	0.3293	-1.0330	0.2310
	First	23		-	-	-1.8258	0.1148
	Mixed	37		10.0866	0.2201	-1.7265	0.1534
	Mean	23		-	-	-1.8019	0.1086
>3952	OLS	109	32	9.8533	0.1678	-1.6196	0.1084
	First	66		-	-	-1.7721	0.0580
	Mixed	109		9.9621	0.1086	-1.6720	0.0726
	Mean	66		-	-	1.7285	0.0527
>2964	OLS	223	61	10.3378	0.1127	-1.9641	0.0687
	First	138		-	-	-1.7796	0.0385
	Mixed	223		9.9499	0.0880	-1.7032	0.0547
	Mean	138		-	-	-1.7095	0.0363
>1976	OLS	336	92	10.4693	0.0727	-2.0523	0.0421
	First	204		-	-	-1.7361	0.0312
	Mixed	336		9.8746	0.0812	-1.6944	0.0450
	Mean	204		-	-	-1.6747	0.0302
All	OLS	416	120	10.5867	0.0531	-2.1240	0.0295
	First	248		-	-	-1.7085	0.0282
	Mixed	416		9.8066	0.0767	-1.6855	0.0402
	Mean	248		-	-	-1.6417	0.0271

Where: n -- number of observations used in parameter estimation, np -- number of plots that observations were obtained from, Std. error -- standard error of the estimate, OLS -- Ordinary Least Squares method, First -- First-difference model method, Mixed -- Linear mixed-effects model method, Mean -- Mean slope calculation method.

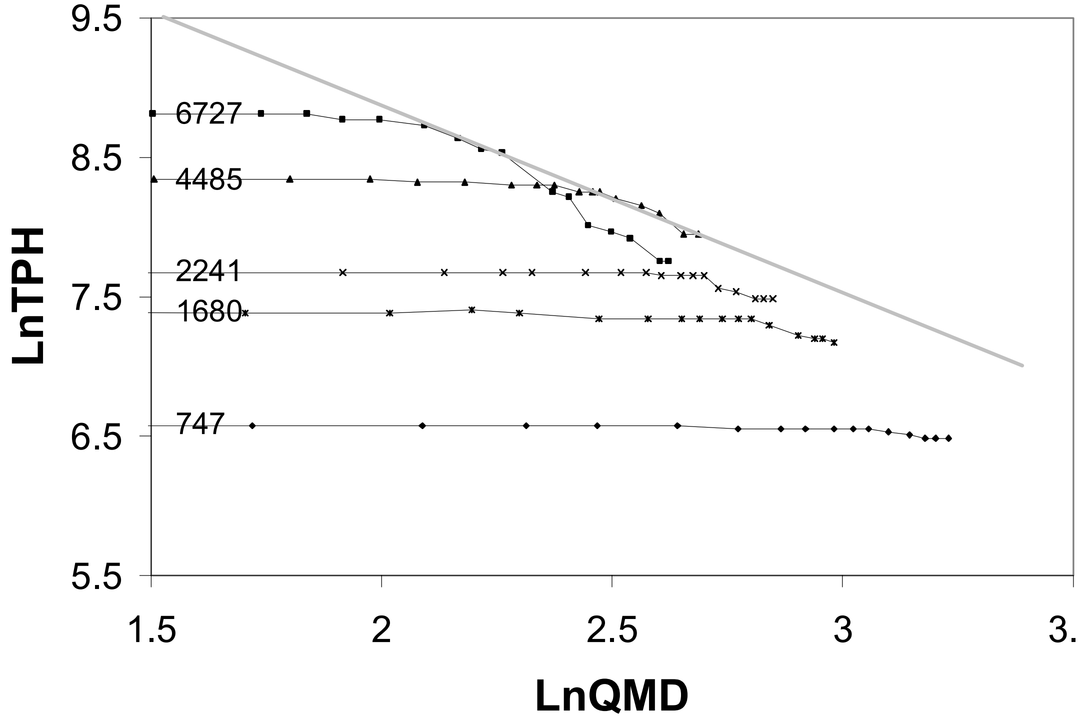


Figure 3.1. Natural logarithmic transformations of trees per hectare (LnN) and quadratic mean diameter ($Ln\,\overline{D}$, cm) for different planting densities (stems/ha) from one replication of a planting density study located near West Point, VA. The gray line is the MSDR dynamic thinning line for the planting density of 6727 seedlings per hectare.

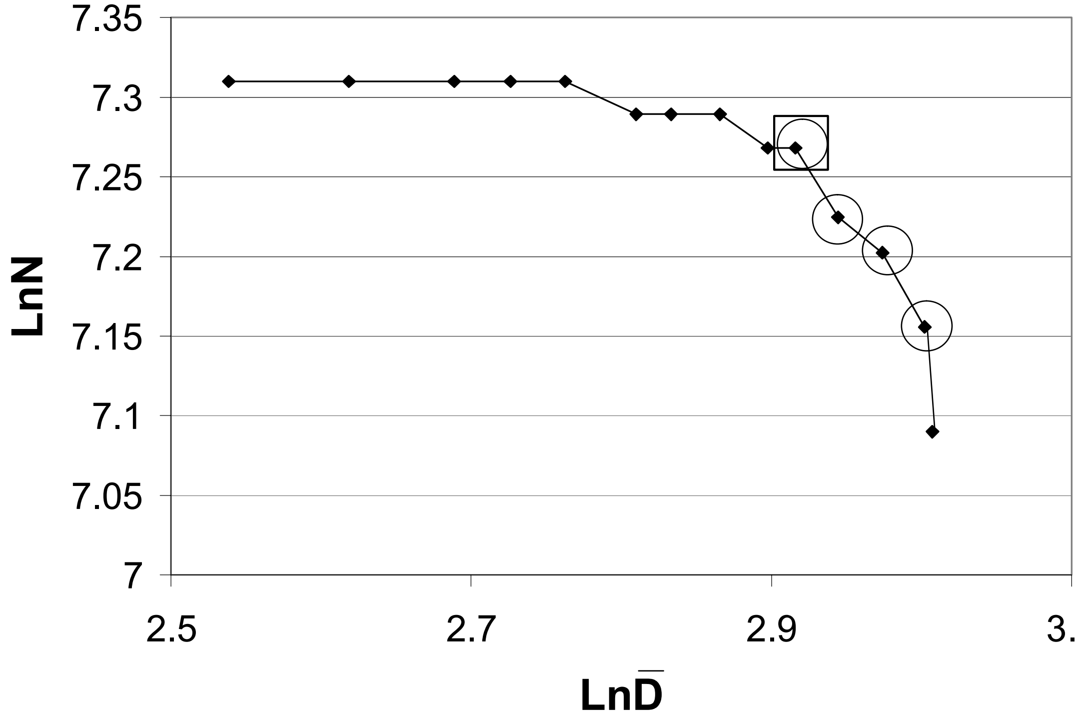


Figure 3.2. Loblolly pine size-density trajectory for a planting density of 1495 seedlings per hectare. Measurement ages with circles around them were used to estimate the *b* for the OLS and mixed-effects analyses while the observation with a square was omitted when determining *b* values between two successive measurement ages for the first-difference model and the Mean slope calculation method.

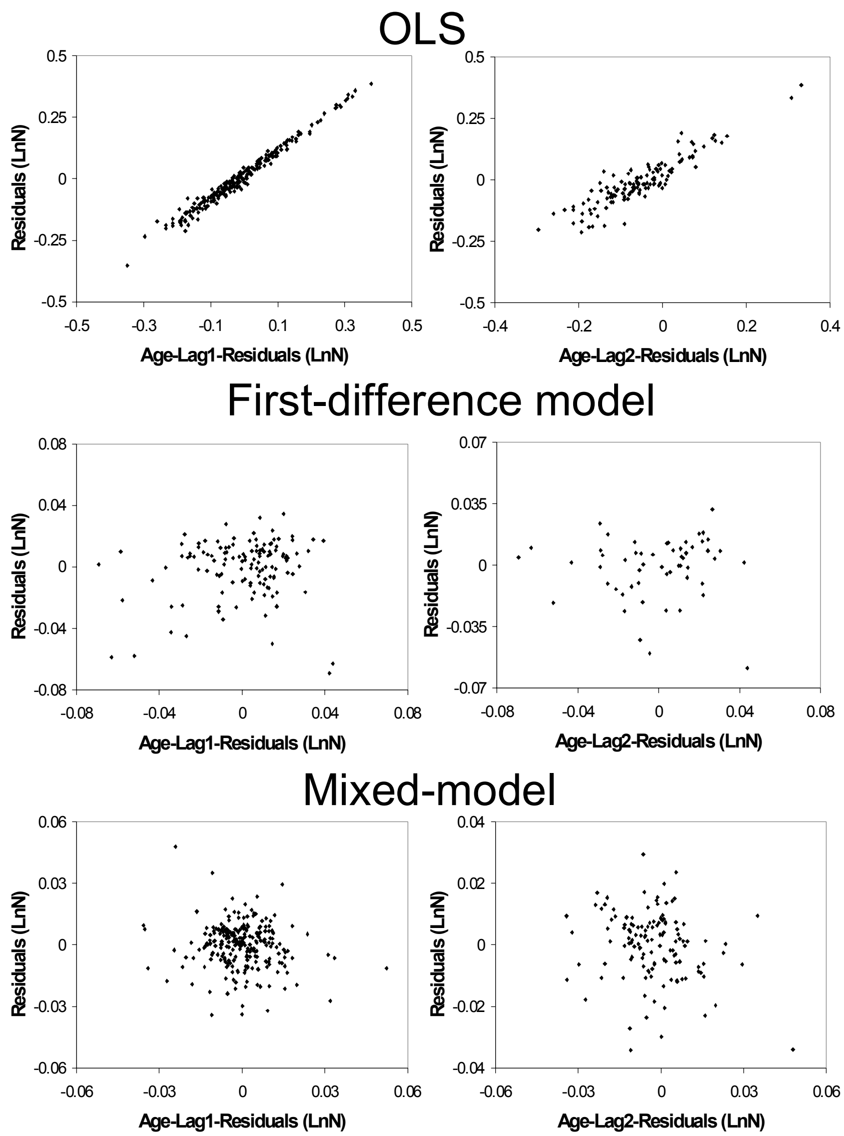


Figure 3.3. Residuals versus Age-Lag1-Residuals and Age-Lag2-Residuals for the OLS, first-difference model, and the mixed-effects model of estimating the MSDR species boundary line *b*. For the OLS and mixed-effects analyses, the Age-Lag1-Residual n = 248 and for Age-Lag2-Residuals n = 128 while for the first-difference model, n = 128 and n = 55 for the Age-Lag1 and Age-Lag2 residuals, respectively.

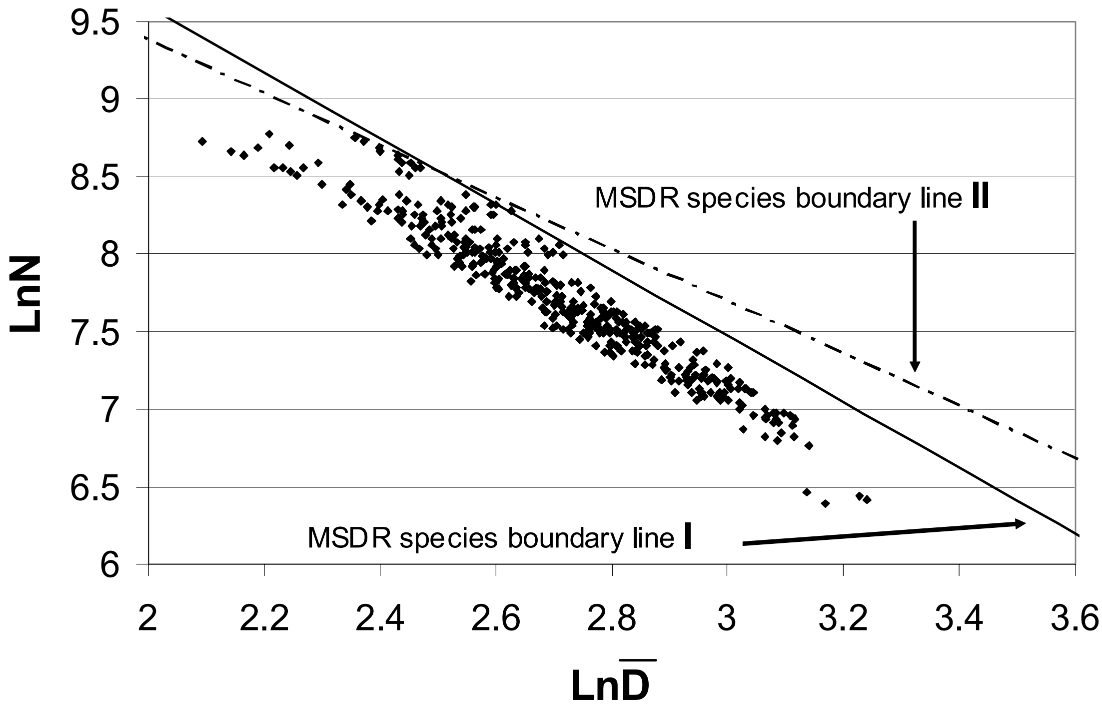
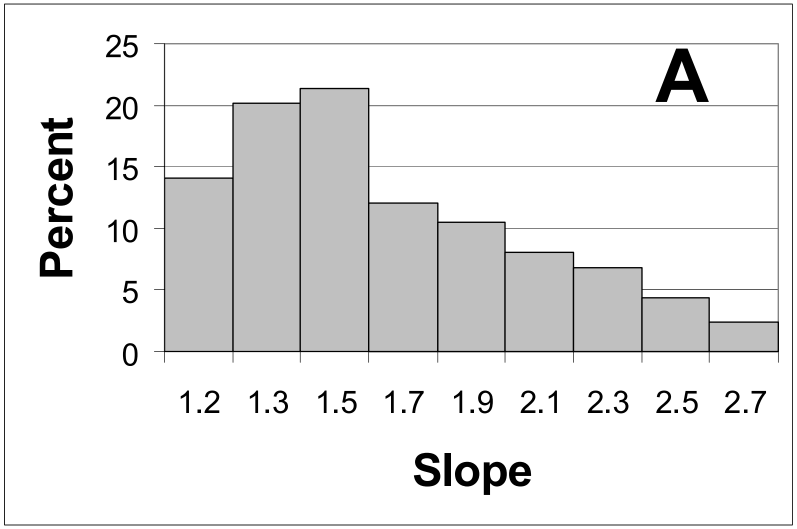


Figure 3.4. Plot of all individual LnN-Ln $\overline{D}$ data points (n = 416) occurring along MSDR dynamic thinning line boundaries. The figure contains a MSDR species boundary line (**I**) that has a *b* of -2.1240 as estimated by OLS. Also on the figure is a MSDR species boundary line (**II**) with a *b* of –1.6855 -- the linear mixed-effects model estimated *b* (dashed line). The boundary lines were visually placed above all points.



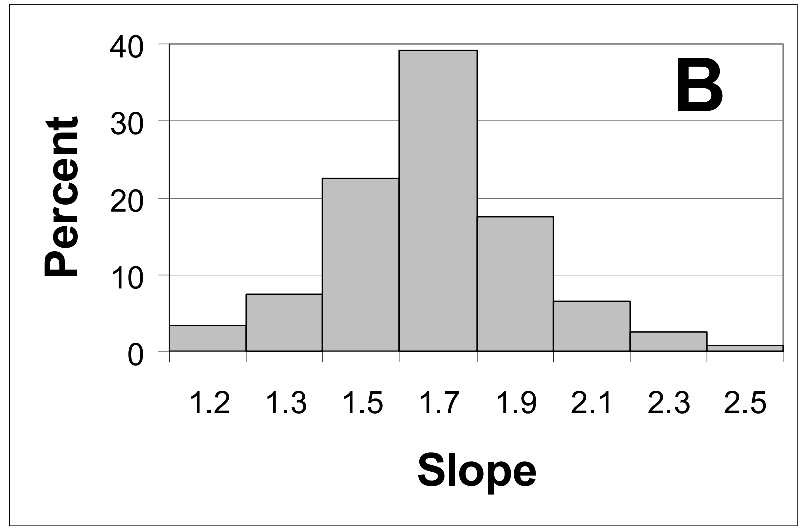


Figure 3.5. Distribution of slopes for the Mean slope calculation method (**A**), equation [3.2], and the predicted MSDR dynamic thinning line boundary *b*'s using a linear mixed-effects model (**B**). Slopes are negative but for clarity have been presented as positive. n = 248 for equation [3.2] and n = 120, the number of clusters, for the mixed-effects distribution.

Chapter 4

Using segmented regression to estimate stages of stand development

Curtis L. VanderSchaaf and Harold E. Burkhart[1]

[1] Department of Forestry, Virginia Polytechnic Institute and State University

ABSTRACT

Size-density trajectories on the natural logarithmic (Ln) scale are generally thought to consist of two major stages. The first major stage is often referred to as the density-independent mortality stage where the probability of mortality is independent of stand density; in the second stage, often referred to as the density-dependent mortality or self-thinning stage, the probability of mortality is related to stand density. Within the self-thinning stage, segments consisting of a non-linear approach to a linear portion, a linear portion, and a divergence from the linear portion are generally assumed. Here, we define the Maximum Size-Density Relationship (MSDR) dynamic thinning line as the linear portion. A loblolly pine (*Pinus taeda* L.) planting density study was used to demonstrate the process of using segmented regression models for estimating stages of stand development. After obtaining results from the segmented regression model analyses, full versus reduced model tests indicated that a portion of self-thinning can be represented as linear. Estimates of the logarithm of quadratic mean diameter ($\text{Ln}\overline{\text{D}}$) and logarithm of trees per unit area (LnN) where the linear component begins and ends were obtained from the segmented regression analyses and used as response variables predicted as a function of planting density. Predicted values of the $\text{Ln}\overline{\text{D}}$s and LnNs allow for the MSDR dynamic thinning line boundary level and slope to be estimated for any planting density.

Estimates showed MSDR dynamic thinning line boundaries did not all attain the same level but varied by planting density.

Keywords: loblolly pine, Pinus taeda, plantations, self-thinning, size-density trajectories.

Self-thinning is a widely studied concept that quantifies the relationship between average tree size and tree density. Understanding self-thinning is important to better grasp intraspecific mortality patterns of a tree species, which can lead to more efficient management of growing stock. For instance, estimating the onset of self-thinning can help resource managers plan thinnings, reduce competition-induced mortality, and allow for limited site resources to be optimally utilized across a rotation. Quantifying Maximum Size-Density Relationships (MSDR), or the maximum obtainable tree density per unit area for a given quadratic mean diameter ($\overline{D}$), should aid resource managers to better understand how different management regimes affect productivity. Additionally, predictions of MSDRs can be used to constrain and verify estimated stand development of process based models and empirical models developed using insufficient data to properly estimate mortality equations. Statistically-based criteria are needed to determine what observations are within various stages of stand development and to estimate the duration of these stages. This paper reports on the application of segmented regression to quantify stages of stand development in loblolly pine (*Pinus taeda* L.) plantations.

Stages of self-thinning

For size-density trajectories on the natural logarithmic (Ln) scale, two major stages of stand development are generally recognized (Drew and Flewelling 1979, McCarter and Long 1986, Williams 1994). An initial stage without significant competition in which mortality is independent of stand density, often referred to as the density-independent mortality stage, and a stage with competition-induced mortality (the self-thinning stage) often referred to as the density-dependent mortality stage. Within the overall self-thinning stage, when density-dependent mortality is occurring, three stages of stand development are generally assumed. The first stage is a non-linear approach to a linear portion, followed by a linear portion, and the third stage is a divergence from the linear portion. A further explanation is given below:

1. The self-thinning stage of stand development is initially composed of a curved approach to the MSDR dynamic thinning line (Figure 4.1 -- Stage **II**). During this initial component of self-thinning, mortality is less than the mortality at maximum competition and thus the trajectory has a concave shape (Harms et al. 2000, del Rio et al. 2001).
2. With increases in tree sizes and the death of other trees, eventually the size-density trajectory is assumed to become linear (Figure 4.1 -- Stage **III**) where an increase in $\overline{D}$ is a function of the stand's maximum value of Reineke's (1933) Stand Density Index (SDI), the change in trees per acre (N, 1 N = 2.471 trees/ha), and the MSDR dynamic thinning line *b*. This stage is known as the MSDR dynamic thinning line stage of stand development (Weller 1990), or when a stand is fully-stocked (del Rio et al. 2001) and Reineke's SDI remains relatively constant.
3. Eventually, as trees die, the residual trees cannot continue to fully occupy canopy gaps and the trajectory diverges (Figure 4.1 -- Stage **IV**) from the MSDR dynamic thinning line (Bredenkamp and Burkhart 1990, Zeide 1995, Cao et al. 2000). Several authors have depicted the divergence from the MSDR dynamic thinning line as linear (Peet and Christensen 1980,

Christensen and Peet 1981, Lonsdale 1990) while others have depicted the divergence as a curve (Zeide 1985, Cao et al. 2000). It should be clarified that the divergence stage of self-thinning does not contain the stand disintegration stage. The stand disintegration stage has mortality that is independent of stand density and thus is not part of the self-thinning stage of stand development. Therefore, whether the divergence can be depicted as linear or a curve is most likely related to the amount of time since the occurrence of the MSDR dynamic thinning line stage (Christensen and Peet 1981, Weller 1991, Cao et al. 2000). For example, the time period immediately after the MSDR dynamic thinning line stage of stand development shows an approximate linear divergence in Figure 4.1. With time, as mortality continues, the divergence becomes curvilinear eventually encompassing the disintegration stage of stand development.

Over the entire range of self-thinning the relationship between LnN and Ln$\overline{D}$ is curvilinear; however, it is commonly assumed there is a linear stage (or portion) during the density-dependent mortality stage of stand development (Zeide 1985, Cao et al. 2000, Johnson 2000, del Rio et al. 2001, Yang and Titus 2002, Monserud et al. 2005).

Many studies have attempted to estimate Reineke's slope using empirical methods (Bredenkamp and Burkhart 1990, Zhang et al. 2005, VanderSchaaf and Burkhart [In review]). A commonly known problem is the determination of what observations are occurring in the self-thinning stage of stand development and, more specifically, what observations occur along the MSDR dynamic thinning line. Several selection methods have been postulated ranging from visually selecting observations (Harms 1981, Zeide 1985, Weller 1987, 1991, Johnson 2000, VanderSchaaf and Burkhart [In review]) to using more statistically based criteria (e.g. Smith and Hann 1984, Bredenkamp and Burkhart 1990, del Rio et al. 2001, Arisman et al. 2004, Zhang et al. 2005). Despite the wide use of MSDRs, there is still not a consensus among foresters and biologists about the selection criteria to use when determining what observations occur along MDSR dynamic thinning lines (Smith and Hann 1984, del Rio et al. 2001, Arisman et al. 2004, Zhang et al. 2005).

Zeide (1987) was one of the first to claim trajectories of self-thinning stands have no linear portion for the LnV-LnN relationship and therefore the slope is never constant, where V is mean tree volume. He mainly based his conclusion on the observation that with increasing age residual trees lose their ability to completely fill canopy gaps following mortality, thus the trajectory is entirely non-linear. In this same paper though, Zeide states LnV-LnN trajectories have a portion that can be roughly approximated by linear regression and the LnN-Ln$\overline{D}$ relationship is less sensitive to canopy gaps. More recently, Zeide (2005) modified Reineke's original equation by including an exponential component to represent residual trees' inability to completely fill canopy gaps following mortality. The exponential modification results in the slope between LnN and Ln$\overline{D}$ never being constant on the Ln-Ln scale.

Maximum size-density relationships are often used as constraints in growth and yield models (Monserud et al. 2005) both for the LnV-LnN relationship (e.g. Smith and Hann 1984, Landsberg and Waring 1997, Turnblom and Burk 2000) and the LnN-$\text{Ln}\,\overline{\text{D}}$ relationship (e.g Hynynen 1993, Johnson 2000). In many model systems, mortality equations are combined with height, diameter, or volume equations to estimate an approach to a linear MSDR constraint. Once the projected stand density is equivalent to the linear constraint, self-thinning occurs such that stand density is maintained equivalent to the linear constraint for some period of time. However, because there is some discrepancy in interpretation of the slope of the entire self-thinning trajectory, there is a need to determine statistically whether the assumption of a linear portion during self-thinning is valid and to estimate the extent of the linear portion if in fact it is exhibited. The first objective of this study was to 1) determine if a portion of self-thinning on the Ln-Ln scale can be represented as linear. The second objective of this study was to 2) use segmented regression to estimate the beginning and duration of the four stages of stand development for size-density trajectories. Finally, the third objective was to 3) determine whether estimates of the $\text{Ln}\,\overline{\text{D}}$ and LnN where MSDR dynamic thinning lines begin and end are related to planting density.

Data

Tree and plot-level measurements were obtained from a spacing trial maintained by the Loblolly Pine Growth and Yield Research Cooperative at Virginia Polytechnic Institute and State University. The spacing trial was established on four cutover sites, two in the Upper Atlantic Coastal Plain and two in the Piedmont. There is one Coastal plain site in

North Carolina and one in Virginia while both Piedmont sites are in Virginia. Three replicates of a compact factorial block design were established at each location in either 1983 or 1984. Sixteen initial planting densities were established ranging from 2722 to 302 trees per acre (6727 to 747 trees/ha). Thus, a total of 192 research plot replicates were established when combining all four sites (4 sites x 3 replications x 16 planting densities). A variety of planting distances between and within rows was used (not all spacings were square). For the planting densities of 2722, 1210, 680, and 302 trees per acre (6727, 2990, 1680, 747 trees/ha) there was one plot established for a particular site and replication combination, for the planting densities of 1815, 1361, 605, and 453 trees per acre (4485, 3363, 1495, 1119 trees/ha) there were two plots established, and for the planting density of 907 trees per acre (2241 trees/ha) there were four plots established (Sharma et al. 2002). Table 4.1 contains summaries of plot-level characteristics for the entire dataset.

Measurements of $\overline{D}$ and N were conducted annually between ages 5 and 21 on one of the Coastal plain sites and to age 22 on the other site. On the Piedmont sites, measurement ages end at 18 at one location and 21 at the other. At the latter Piedmont site, one replication had measurements to 22 years of age. Site quality was quantified using site index defined as the average height of all trees with diameters larger than $\overline{D}$ for the planting densities of 907, 680, and 605 trees per acre (2241, 1680, 1495 trees/ha) by replication (Table 4.1). Plots intermediate in stand density were used when estimating site index for each block in order to avoid any possible effects of high or low number of

N. A site index equation found in Burkhart et al. (2004) was used to project dominant height forward to base age 25.

Using segmented regression to estimate stages of stand development

Based on the four stages of stand development, a segmented regression model was developed to determine what observations of size-density trajectories are within particular stages. The segmented regression model can be written as:

$$\text{LnN} = (b_1)J_1 + (b_1 + b_2[\text{Ln}\overline{\text{D}} - c_1]^2)J_2 + (b_1 + b_2[c_2 - c_1]^2 + b_3[\text{Ln}\overline{\text{D}} - c_2])J_3 + (b_1 + b_2[c_2 - c_1]^2 + b_3[c_3 - c_2] + b_4[\text{Ln}\overline{\text{D}} - c_3])J_4 \quad [4.1]$$

Equation [4.1] can be broken into component parts that represent the various stages of stand development:

$$\begin{aligned}
\text{LnN} = {} & \\
& (b_1)J_1 \\
& + (b_1 + b_2[\text{Ln}\overline{\text{D}} - c_1]^2)J_2 \\
& + (b_1 + b_2[c_2 - c_1]^2 + b_3[\text{Ln}\overline{\text{D}} - c_2])J_3 \\
& + (b_1 + b_2[c_2 - c_1]^2 + b_3[c_3 - c_2] + b_4[\text{Ln}\overline{\text{D}} - c_3])J_4
\end{aligned}$$

Where:

J_1, J_2, J_3, J_4 are indicator variables for the stages of stand development.

$J_1 = 1$ if $\mathrm{Ln}\,\overline{\mathrm{D}}$ is within the density-independent mortality stage of stand development (Stage **I** in Figure 4.1), 0 otherwise,

$J_2 = 1$ if $\mathrm{Ln}\,\overline{\mathrm{D}}$ is within the curved approach to the MSDR dynamic thinning line stage of self-thinning (Stage **II** in Figure 4.1), 0 otherwise,

$J_3 = 1$ if $\mathrm{Ln}\,\overline{\mathrm{D}}$ is within the MSDR dynamic thinning line stage of self-thinning (Stage **III** in Figure 4.1), 0 otherwise, and

$J_4 = 1$ if $\mathrm{Ln}\,\overline{\mathrm{D}}$ is within the divergence stage of self-thinning (Stage **IV** in Figure 4.1), 0 otherwise.

Seven parameters are estimated; one for the initial component (b_1), one for the curved approach to the MSDR dynamic thinning line (b_2), one for the MSDR dynamic thinning line (b_3), one for the divergence from the MSDR dynamic thinning line (b_4), and three for the join points to estimate at what $\mathrm{Ln}\,\overline{\mathrm{D}}$ self-thinning begins (c_1), at what $\mathrm{Ln}\,\overline{\mathrm{D}}$ the MSDR dynamic thinning line stage of stand development begins (c_2), and at what $\mathrm{Ln}\,\overline{\mathrm{D}}$ the divergence from the MSDR dynamic thinning line begins (c_3).

For all subsequent segmented regression model analyses, parameters were estimated using Proc NLMIXED of SAS (SAS 2000) and the Newton-Raphson algorithm (NEWRAP in NLMIXED). Within the SAS program, the code for a particular model is based on methods found in Schabenberger and Pierce (2001, pgs. 256 - 257). Leites and Robinson (2004) used NLMIXED to estimate entirely fixed-effects segmented regression models and Schabenberger and Pierce (2001, pgs. 291, 326, 544) state NLMIXED can be used to estimate entirely fixed-effects nonlinear models. For all subsequent segmented regression model analyses, starting values of the parameters were obtained by examining figures of LnN plotted over Ln$\overline{D}$.

Initially, we tried to fit segmented regression models to each individual research plot but due to variability among size-density trajectories and the lack of sufficient self-thinning for many individual plots, this approach did not currently produce reliable and satisfactory results. Thus, a second approach was used where segmented regression models were fit by planting density for a particular site and replication combination. This allowed us to conduct several analyses to determine if site quality and planting density simultaneously significantly affected the beginning and duration of MSDR dynamic thinning lines. Several studies have concluded MSDR dynamic thinning line boundary levels vary in relation to site quality for many conifer species (Barreto 1989, Hynynen 1993, Pittman and Turnblom 2003) including loblolly pine in South Africa (Strub and Bredenkamp 1985). These studies imply that greater N can occur for a particular $\overline{D}$ on higher quality sites. For these analyses, a portion of self-thinning was assumed linear and thus a MSDR dynamic thinning line was presumed to exist.

All analyses showed that site quality was not statistically significant at the alpha = 0.10 level. Due to a limited range of site qualities (63 to 73 ft, 19.2 to 22.3 m), results of this analysis should not be considered indicative of the impacts of site quality on self-thinning in loblolly pine plantations. To more fully address this question, a broader range of site qualities would need to be included.

For each planting density, since site quality was not shown to impact self-thinning, data were pooled across all planting configurations, replications, and sites and attempts were made to fit equation [4.1]. Initially, two components of equation [4.1] were combined such that a quadratic model was used to depict both Stages **I** and **II** of stand development (Figure 4.1). However, illogical behavior occurred where N was predicted to be greater than the planting densities. Attempts were made to use a quadratic model to depict the divergence from MSDR dynamic thinning lines. Preliminary analyses using a quadratic model consisting of two parameters did not result in both parameters being statistically significant. These results suggest that a linear component, for the current dataset, was sufficient for depicting the divergence stage. Whether the divergence was specified as linear or quadratic had negligible effects on the estimates of the beginning and ending values of MSDR dynamic thinning lines. Finally, attempts were also made to reparameterize equation [4.1]. To clarify, the parameters and join points of equation [4.1] were predicted directly as functions of site quality and/or planting density within the segmented regression model. However, due to the large number of parameters and problems associated with starting values, statistical convergence was not met.

To determine the validity of assuming self-thinning contains a linear portion, full (equation [4.1]) versus reduced (equation [4.2]) model tests were conducted by planting density. The reduced segmented regression model can be written as:

$$\mathrm{LnN} = (b_1)\mathrm{J}_1 + (b_1 + b_2[\mathrm{Ln}\,\overline{\mathrm{D}} - c_1]^2)\mathrm{J}_2 \qquad [4.2]$$

Equation [4.2] can be broken into component parts that represent various stages of stand development:

$$\text{LnN} =$$

$$(b_1)J_1$$

$$+ (b_1 + b_2[\text{Ln}\,\overline{\text{D}} - c_1]^2)J_2$$

Where:

J_1, J_2 are indicator variables for stages of stand development.

$J_1 = 1$ if $\text{Ln}\,\overline{\text{D}}$ is within the density-independent mortality stage of stand development, 0 otherwise, and

$J_2 = 1$ if $\text{Ln}\,\overline{\text{D}}$ is within the self-thinning stage of stand development, 0 otherwise.

For this analysis, since the reduced model (equation [4.2]) is nested within the full model (equation [4.1]), a Likelihood ratio test was used (see Schabenberger and Pierce 2001, pgs. 547, 557). Equation [4.2] consists of the join point determining when self-thinning begins (c_1); the other two parameters are the initial level prior to self-thinning beginning (b_1) and the exponent for the quadratic term describing the self-thinning curve (b_2). Equation [4.2] should be adequate when depicting self-thinning patterns if a linear self-thinning stage is not evident. In all analyses, under the null hypothesis, the test statistic is assumed to follow a χ^2_4 distribution with a critical value of 9.48773 for an alpha level of 0.05. Akaike's Information Criterion (AIC) values were also compared between equations [4.1] and [4.2] by planting density (Akaike 1974). The three join points of equation [4.1] were also examined by planting density to see whether they were statistically significantly different from one another at the alpha = 0.05 level. Finally, the slope of the MSDR dynamic thinning lines and all other parameters were examined for statistical significance. As alternatives to equation [4.2], more complex segmented regression models not consisting of a linear portion during self-thinning were examined; however, all parameters were not significant at the alpha = 0.20 level, and/or the models exhibited illogical behavior during the self-thinning stage, and/or the join point determining where self-thinning is expected to begin was illogical.

Statistical convergence of equation [4.1] was not achieved for planting densities of 453 and 302 trees per acre (1119 and 747 trees/ha) due to a lack of sufficient self-thinning. For all other planting densities statistical convergence was met (Table 4.2 and Figure 4.2). All three join points were significantly different from one another at the alpha = 0.05 level for all planting densities except for 1210 trees per acre (2990 trees/ha) where the join points were significantly different from one another at the 0.10 alpha level. The range of MSDR dynamic thinning line slopes is similar to the range observed in other studies (Zeide 1985, Pretzsch and Biber 2005). Full versus reduced model tests showed equation [4.1] was significantly better for all planting densities (Table 4.3). Additionally, the AIC value for equation [4.1] was always less than that of equation [4.2]. Thus, assuming that each planting density's size-density trajectory contains a linear component during self-thinning is valid.

Based on these results, segmented regression is an effective method to estimate stages of stand development. Segmented regression can be used to more objectively and statistically determine what observations are within the four stages (Figure 4.1).

Predicting MSDR dynamic thinning line beginning and ending points

In order to determine whether the beginning and end of MSDR dynamic thinning lines are related to planting density, a system of linear regression equations was developed and a simultaneous parameter estimation method (Borders 1989) was used. The linear system of equations is:

$$\mathrm{Ln}\,\overline{\mathrm{D}}_{\mathrm{B}} = b_{01} + b_{11}\,\mathrm{Ln}(\mathrm{N}_0) \qquad [4.3]$$

$$\mathrm{Ln}\,\overline{\mathrm{D}}_{\mathrm{E}} = b_{02} + b_{12}\,\mathrm{Ln}\,\overline{\mathrm{D}}_{\mathrm{B}} \qquad [4.4]$$

$$\mathrm{Ln}\,\mathrm{N}_{\mathrm{B}} = b_{03} + b_{13}\,\overline{\mathrm{D}}_{\mathrm{B}} \qquad [4.5]$$

$$\mathrm{Ln}\,\mathrm{N}_{\mathrm{E}} = b_{04} + b_{14}\,\overline{\mathrm{D}}_{\mathrm{E}} \qquad [4.6]$$

Where:

$\mathrm{Ln}\,\overline{\mathrm{D}}_{\mathrm{B}}$ -- $\mathrm{Ln}\,\overline{\mathrm{D}}$ where a particular MSDR dynamic thinning line begins (7 c_2 estimates from Table 4.2).

$\mathrm{Ln}\,\overline{\mathrm{D}}_{\mathrm{E}}$ -- $\mathrm{Ln}\,\overline{\mathrm{D}}$ where a particular MSDR dynamic thinning line ends (7 c_3 estimates from Table 4.2).

$\mathrm{Ln}\,\mathrm{N}_{\mathrm{B}}$ -- LnN where a particular MSDR dynamic thinning line begins.

$\mathrm{Ln}\,\mathrm{N}_{\mathrm{E}}$ -- LnN where a particular MSDR dynamic thinning line ends.

N_0 -- planting density (trees per unit area)

b_{0i}, b_{1i} -- are parameters to be estimated.

Ln N_B and Ln N_E values by planting density (in trees per acre) were derived using the parameter estimates of the segmented regression models shown in Table 4.2. The system of equations will avoid illogical predictions of the response variables, e.g. Ln $\overline{D}_B$ estimated to be greater than Ln $\overline{D}_E$ ($\overline{D}$ in inches in Table 4.4). Using a Ln transformation of planting density to predict Ln $\overline{D}_B$ allows for a non-linear relationship between these variables. Parameter estimates are given in Table 4.4.

Nonlinear trends can be seen for the Ln $\overline{D}$ and LnN values where MSDR dynamic thinning lines begin and end relative to planting density (Figure 4.3). As planting density increases, MSDR dynamic thinning lines begin when trees are younger and smaller due to competition for limited resources occurring at earlier ages.

As opposed to using regression analyses to directly estimate the slope of MSDR dynamic thinning lines, by predicting when MSDR dynamic thinning lines begin and end, an alternative methodology to predict the slope of MSDR dynamic thinning lines can be conducted. Since the Ln $\overline{D}$ s and LnNs where MSDR dynamic thinning lines begin and end are predicted using equations [4.3] through [4.6], an estimate of the MSDR dynamic thinning line slope for any planting density ($\hat{b}$) can be obtained using equation [4.7]:

$$\hat{b} = \frac{\hat{\text{Ln}}N_B - \hat{\text{Ln}}N_E}{\text{Ln}\hat{\bar{D}}_B - \text{Ln}\hat{\bar{D}}_E} \qquad [4.7]$$

Based on this methodology, for the range of planting densities used in fitting equations [4.3] through [4.6], the MSDR dynamic thinning line slope is to some degree related to planting density (Figure 4.4, ranging from -1.3933 to -1.7072). To check whether these predicted slopes are reasonable, the 7 MSDR dynamic thinning line slopes (b_3) from Table 4.2 were plotted along with the expected slopes predicted using equation [4.7]. Based on comparison with the MSDR dynamic thinning line slope estimates of the segmented regression analyses, the simultaneously estimated system of equations, [4.3] through [4.6], and equation [4.7], produce predictions of MSDR dynamic thinning line slopes that are representative of the data used in this study.

Additionally, equation [4.7] can be used along with equation [4.8] to obtain an estimate of the maximum SDI for any planting density:

$$\hat{SDI} = \hat{N}\left[\frac{\hat{\bar{D}}}{c}\right]^{\hat{b}} \qquad [4.8]$$

Where:

$\hat{b}$ -- predicted exponent using equation [4.7].

c -- 10 when using English units and 25.4 when using metric units

$\hat{N}$, $\hat{\overline{D}}$ -- estimated using either the combination of the untransformed predicted values of $\text{Ln}\,N_B$ and $\text{Ln}\,\overline{D}_B$, or $\text{Ln}\,N_E$ and $\text{Ln}\,\overline{D}_E$.

Conclusions

Segmented regression has been shown to provide a reliable statistical estimate of stages of stand development and more specifically when MSDR dynamic thinning lines begin and end. Results from this study show that assuming self-thinning contains a linear component is valid for loblolly pine plantations. There are relatively strong relationships between planting density and MSDR dynamic thinning line boundaries for data used in this study. When using the presented simultaneously estimated system of equations, MSDR dynamic thinning line boundary levels and slopes can be predicted for any planting density. The estimated boundary levels and slopes can be used to constrain stand development of process based models and for more empirical models that lack sufficient data to properly estimate mortality equations (Monserud et al. 2005) and for verifying mortality equations and predicted stand development in general.

The main purpose of this paper was to demonstrate the process of using segmented regression to statistically determine what observations are within the generally accepted stages of stand development. In addition to estimating the beginning, duration, and boundary level of MSDR dynamic thinning lines, results of the segmented regression analyses have many other potential uses. For example, by using estimates of all b_i and c_i from equation [4.1] as response variables predicted as a function of planting density, entire size-density trajectories can be developed. Additionally, an equation to predict when self-thinning is expected to begin can be combined with the equations to estimate MSDR dynamic thinning line boundary levels to produce planting density specific density management diagrams.

Literature Cited

Akaike, H. 1974. A new look at the statistical model identification. IEEE Transaction on Automatic Control, AC-19: 716-723.

Arisman, H., S. Kurinobu, and E. Hardiyanto. 2004. Minimum distance boundary method: maximum size-density lines for unthinned *Acacia mangium* plantations in South Sumatra, Indonesia. J. For. Res. 9: 233-237.

Barreto, L.S. 1989. The '3/2 power law': A comment on the specific constancy of K. Ecol. Model. 45: 237-242.

Borders, B.E. 1989. Systems of equations in forest stand modeling. For. Sci. 35: 548-556.

Bredenkamp, B.V., and H.E. Burkhart. 1990. An examination of spacing indices for *Eucalyptus grandis*. Can. J. For. Res. 20: 1909-1916.

Burkhart, H.E., R.L. Amateis, J.A. Westfall, and R.F. Daniels. 2004. PTAEDA 3.1: Simulation of individual tree growth, stand development and economic evaluation in loblolly pine plantations. Sch. of For. and Wildl. Res., Va. Polytech Inst. and State Univ. 23 p.

Cao, Q.V., T.J. Dean, and V.C. Baldwin. 2000. Modeling the size-density relationship in direct-seeded slash pine stands. For. Sci. 46: 317-321.

Christensen, N.L., and R.K. Peet. 1981. Secondary forest succession on the North Carolina Piedmont. P. 230-245 *in* Forest Succession: concepts and application, West, D.C., H.H. Shugart, and D.B. Botkin (eds). Springer-Verlag, New York.

del Rio, M., G. Montero, and F. Bravo. 2001. Analysis of diameter-density relationships and self-thinning in non-thinned even-aged Scots pine stands. For. Ecol. Manage. 142: 79-87.

Drew, T.J., and J.W. Flewelling. 1979. Stand density management: an alternative approach and its application to Douglas-fir plantations. For. Sci. 25: 518-532.

Harms, W.R. 1981. A competition function for tree and stand growth models. P. 179-183 *in* Proc. of the First biennial southern silvicultural research conference, Barnett, J.P., (ed). USDA For. Serv. Gen. Tech. Rep. SO-GTR-34.

Harms, W.R., C.D. Whitesell, and D.S. DeBell. 2000. Growth and development of loblolly pine in a spacing trial planted in Hawaii. For. Ecol. Manage. 126: 13-24.

Hynynen, J. 1993. Self-thinning models for even-aged stands of *Pinus sylvestris, Picea abies*, and *Betula penula*. Scand. J. For. Res. 8: 326-336.

Johnson, G. 2000. ORGANON calibration for western hemlock project: Maximum size-density relationships. Willamette Industries, Inc. Internal Research Report. 8 p. Can obtain a pdf file at http://www.cof.orst.edu/cof/fr/research/organon/orgpubdl.htm

Landsberg, J.J., and R.H. Waring. 1997. A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. For. Ecol. Manage. 95: 209-228.

Leites, L.P., and A.P. Robinson. 2004. Improving taper equations of loblolly pine with crown dimensions in a mixed-effects modeling framework. For. Sci. 50: 204-212.

Lonsdale, W.M. 1990. The self-thinning rule: dead or alive? Ecology 71: 1373-1388.

McCarter, J.B., and J.N. Long. 1986. A lodgepole pine density management diagram. West. J. Appl. For. 1: 6-11.

MacKinney, A.L., and L.E. Chaiken. 1935. A method of determining density of loblolly pine stands. USDA For. Serv., Appalachian Forest Experiment Station, Tech. Note 15. 3 p.

Monserud, R.A., T. Ledermann, and H. Sterba. 2005. Are self-thinning constraints needed in a tree-specific mortality model? For. Sci. 50: 848-858.

Peet, R.K., and N.L. Christensen. 1980. Succession: a population process. Vegetatio 43: 131-140.

Pittman, S.D., and E.C. Turnblom. 2003. A study of self-thinning using coupled allometric equations: implications for coastal Douglas-fir stand dynamics. Can. J. For. Res. 33: 1661-1669.

Pretzsch, H., and P. Biber. 2005. A re-evaluation of Reineke's rule and stand density index. For. Sci. 51: 304-320.

Reineke, L.H. 1933. Perfecting a stand-density index for even-age forests. J. Agri. Res. 46: 627-638.

SAS Institute Inc. 2000. SAS OnlineDoc (RTM), Version 8.

Schabenberger, O., and F.J. Pierce. 2001. Contemporary statistical models for the plant and soil sciences. CRC Press, Boca Raton, FL. 738 p.

Sharma, M., H.E. Burkhart, and R.L. Amateis. 2002. Modeling the effect of density on the growth of loblolly pine trees. South. J. Appl. For. 26: 124-133.

Smith, N.J., and D.W. Hann. 1984. A new analytical model based on the -3/2 power rule of self-thinning. Can. J. For. Res. 14: 605-609.

Strub, M.R., and B.V. Bredenkamp. 1985. Carrying capacity and thinning response of *Pinus taeda* in the CCT experiments. South African For. J. 2: 6-11.

Turnblom, E.C., and T.E. Burk. 2000. Modeling self-thinning of unthinned Lake States red pine stands using nonlinear simultaneous differential equations. Can. J. For. Res. 30: 1410-1418.

VanderSchaaf, C.L., and H.E. Burkhart. In review. Comparison of methods to estimate Reineke's maximum size-density relationship species boundary line slope. Submitted to For. Sci.

Weller, D.E. 1987. A reevaluation of the -3/2 power rule of plant self-thinning. Ecol. Monogr. 57: 23-43.

Weller, D.E. 1990. Will the real self-thinning rule please stand up? – A reply to Osawa and Sugita. Ecology 71: 1204-1207.

Weller, D.E. 1991. The self-thinning rule: Dead or unsupported? – A reply to Lonsdale. Ecology 72: 747-750.

Williams, R.A. 1994. Stand density management diagram for loblolly pine plantations in north Louisiana. South. J. Appl. For. 18: 40-45.

Yang, Y. and S.J. Titus. 2002. Maximum size-density relationship for constraining individual tree mortality functions. For. Ecol. Manage. 168; 259-273.

Zeide, B. 1985. Tolerance and self-tolerance of trees. For. Ecol. Manage. 13: 149-166.

Zeide, B. 1987. Analysis of the 3/2 power law of self-thinning. For. Sci. 33: 517-537.

Zeide, B. 1995. A relationship between size of trees and their number. For. Ecol. Manage. 72: 265-272.

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

Zhang, L., Bi, H., Gove, J.H., Heath, L.S. 2005. A comparison of alternative methods for estimating the self-thinning boundary line. Can. J. For. Res. 35: 1-8.

Table 4.1. Plot-level characteristics for the entire dataset (n = 2977).

Variable	Minimum	Mean	Maximum
Trees (acre^{-1}, ha^{-1})	228, 563	917, 2266	2722, 6727
QMD (in., cm)	1.1, 2.8	5.4, 13.7	10.8, 27.4
BA (ft^2/acre, m^2/ha)	0.1, 0.02	122, 28	258, 59
SI (ft, m)	63, 19.2	68, 20.7	73, 22.3

Table 4.2. Parameter estimates for the Full (Equation [4.1]) segmented regression model by planting density in trees/ac and quadratic mean diameter in inches. To convert trees/ac to trees/ha multiply by 2.47; in. to cm multiply by 2.54. Where: -LL -- negative log-likelihood, * specifies that the two join points (c_2, c_3) were significantly different from one another at the alpha = 0.10 level.

Equation [4.1] -- 2722, n = 198

	Estimate	Approx. Std. Error	Sign.
b_1	7.8833	0.01544	<.0001
b_2	-1.8300	0.3762	<.0001
b_3	-1.8852	0.4722	<.0001
b_4	-3.7231	0.1450	<.0001
c_1	1.1103	0.03097	<.0001
c_2	1.3737	0.005598	<.0001
c_3	1.4855	0.02797	<.0001

-LL -123.7

Equation [4.1] -- 1815, n = 376

	Estimate	Approx. Std. Error	Sign.
b_1	7.4773	0.009708	<.0001
b_2	-1.3237	0.5149	0.0105
b_3	-1.6777	0.2177	<.0001
b_4	-3.4829	0.1715	<.0001
c_1	1.2228	0.06501	<.0001
c_2	1.5691	0.000276	<.0001
c_3	1.6649	0.000169	<.0001

-LL -377.452

Equation [4.1] -- 1361, n = 382

	Estimate	Approx. Std. Error	Sign.
b_1	7.1886	0.009028	<.0001
b_2	-1.3897	0.7198	0.0543
b_3	-1.1109	0.4344	0.0109
b_4	-2.7154	0.1518	<.0001
c_1	1.3536	0.07241	<.0001
c_2	1.6535	0.000645	<.0001
c_3	1.7335	0.01904	<.0001

-LL -374.162

Table 4.2. (cont.)

Equation [4.1] -- 1210, n = 179

	Estimate	Approx. Std. Error	Sign.
b_1	7.0648	0.01165	<.0001
b_2	-1.1343	0.7823	0.1488
b_3	-1.4331	0.488	0.0038
b_4	-4.394	0.5164	<.0001
c_1	1.3868	0.09966	<.0001
c_2	1.7104*	0.05148	<.0001
c_3	1.8228*	0.01609	<.0001

-LL -193.008

Equation [4.1] -- 907, n = 690

	Estimate	Approx. Std. Error	Sign.
b_1	6.7691	0.005000	<.0001
b_2	-1.0541	0.5443	0.0532
b_3	-1.7074	0.3616	<.0001
b_4	-1.9898	0.1094	<.0001
c_1	1.5551	0.06402	<.0001
c_2	1.8382	0.01689	<.0001
c_3	1.8940	0.000407	<.0001

-LL -819.912

Equation [4.1] -- 680, n = 198

	Estimate	Approx. Std. Error	Sign.
b_1	6.5001	0.007022	<.0001
b_2	-0.5454	0.3036	0.074
b_3	-1.4385	0.1986	<.0001
b_4	-13.7855	6.0312	0.0233
c_1	1.5554	0.1041	<.0001
c_2	1.9674	0.0181	<.0001
c_3	2.0994	0.000076	<.0001

-LL -312.668

Table 4.2. (cont.)

Equation [4.1] -- 605, n = 378			
	Estimate	Approx. Std. Error	Sign.
b_1	6.3635	0.005550	<.0001
b_2	-0.5607	0.2860	0.0507
b_3	-1.6226	0.4917	0.0011
b_4	-2.2319	0.5229	<.0001
c_1	1.6532	0.08610	<.0001
c_2	2.0320	0.01783	<.0001
c_3	2.0908	0.000320	<.0001

-LL -520.739

Table 4.3. Results of Full (Equation [4.1]) versus Reduced (Equation [4.2]) segmented regression model tests by planting density. Where: Full and Reduced are the negative log-likelihood values for each segmented regression model, Test Statistic -- is the negative of twice the Diff and is compared to a critical value of 9.48773 -- $\chi^2_{0.05,4}$, AIC -- Akaike's information criterion (smaller is better).

Planting density							AIC	
trees/ac	trees/ha	Full	Reduced	Diff	Test Statistic	p-value	Full	Reduced
2722	6727	-125.824	-112.875	-10.8251	21.65016	0.00024	-231.4	-217.7
1815	4485	-377.452	-367.187	-10.265	20.53004	0.00039	-738.9	-726.4
1361	3363	-374.162	-365.789	-8.37335	16.7467	0.00216	-732.3	-723.6
1210	2990	-193.008	-185.704	-7.30464	14.60928	0.00558	-370	-363.4
907	2241	-819.912	-812.182	-7.72963	15.45926	0.00384	-1624	-1616
680	1680	-312.668	-305.4	-7.26733	14.53466	0.00577	-609.3	-602.8
605	1495	-520.739	-514.209	-6.52945	13.0589	0.01099	-1025	-1020

Table 4.4. Simultaneous parameter estimates for a system of equations predicting when MSDR dynamic thinning lines begin and end. Where: N_0 -- planting density per acre, Std. error -- standard error of the estimate, Sign. -- significance level, RMSE -- root mean square error, Adj. R^2 -- adjusted R^2 value. n = 7 for all equations.

Equation	Estimate	Std. error	Sign.	Estimate	Std. error	Sign.	RMSE	Adj. R^2
		b_{01}			b_{11}			
$\ln \bar{D}_B = b_{01} + b_{11} \ln(N_0)$	4.766335	0.0799	<.0001	-0.42899	0.0113	<.0001	0.0149	0.9958
		b_{02}			b_{12}			
$\ln \bar{D}_E = b_{02} + b_{12} \ln \bar{D}_B$	0.151668	0.0885	0.1472	0.965822	0.0506	<.0001	0.0302	0.9818
		b_{03}			b_{13}			
$\ln N_B = b_{03} + b_{13} \ln \bar{D}_B$	11.01013	0.1470	<.0001	-2.34843	0.0840	<.0001	0.0504	0.9913
		b_{04}			b_{14}			
$\ln N_E = b_{04} + b_{14} \ln \bar{D}_E$	11.04924	0.1332	<.0001	-2.32946	0.0723	<.0001	0.0446	0.9926

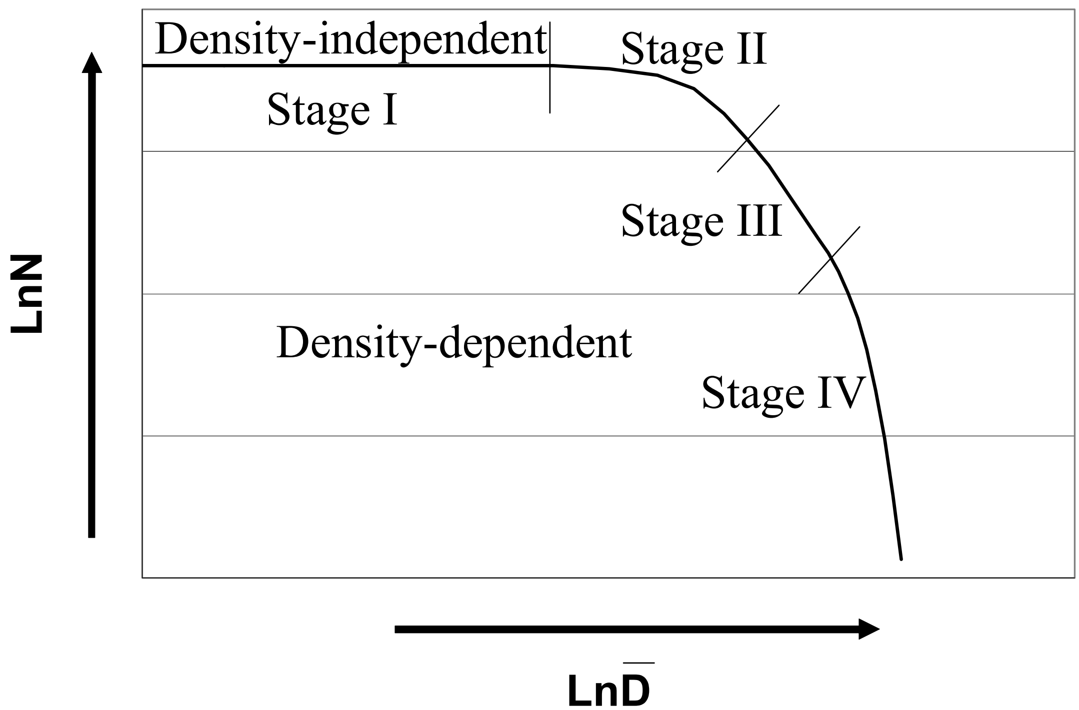


Figure 4.1. Depiction of a size-density trajectory for an individual stand. Two major stages of stand development are shown -- Density-independent mortality and Density-dependent mortality. Within the density-dependent mortality stage three stages of stand development are shown.

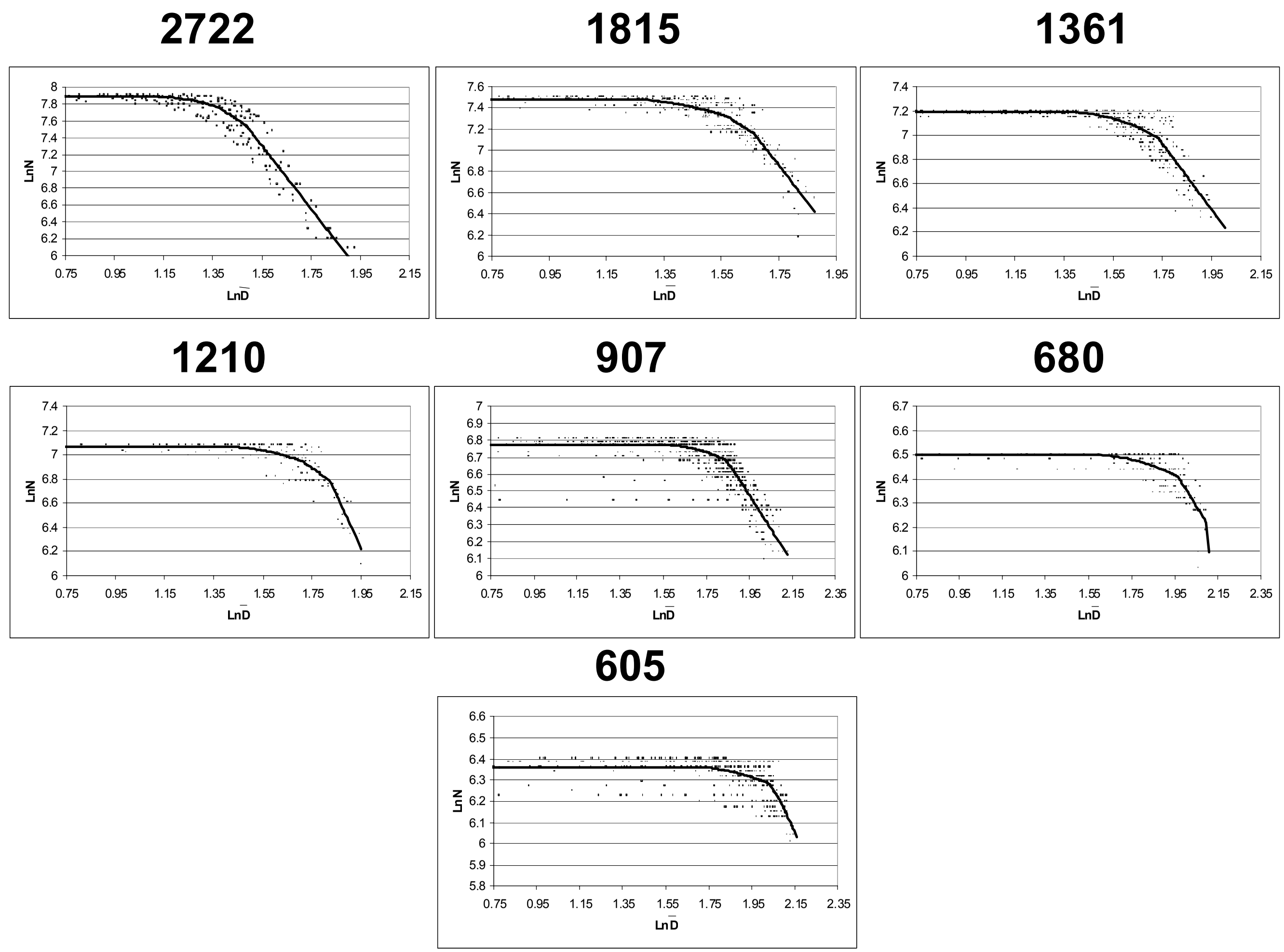


Figure 4.2. Predicted size-density trajectories of seven planting densities, where N is trees per acre and $\overline{D}$ is quadratic mean diameter in inches. All trajectories consist of a linear component representing stand growth prior to the beginning of self-thinning, a non-linear approach to a linear portion, a linear portion which is the MSDR dynamic thinning line, and a divergence from the MSDR dynamic thinning line. To convert trees/ac to trees/ha, multiply by 2.47; $\overline{D}$ in inches can be converted to $\overline{D}$ in cm by multiplying by 2.54. The number of observations differs by planting density.

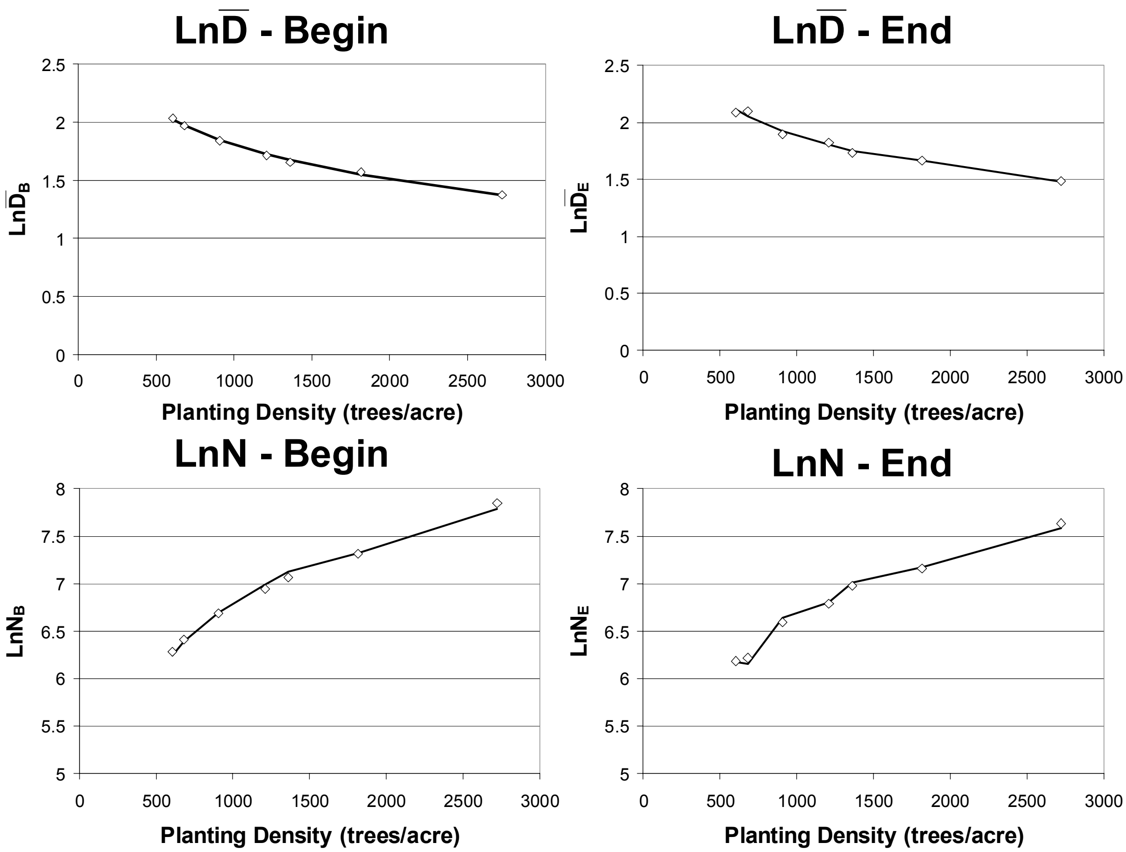


Figure 4.3. MSDR dynamic thinning line attributes over planting density per acre. Ln $\overline{D}$ - Begin -- Ln $\overline{D}$ where MSDR dynamic thinning lines begin, Ln $\overline{D}$ - End -- Ln $\overline{D}$ where MSDR dynamic thinning lines end, LnN - Begin -- LnN where MSDR dynamic thinning lines begin, LnN - End -- LnN where MSDR dynamic thinning lines end, n = 7 (to convert trees/ac to trees/ha, multiply by 2.47; $\overline{D}$ in inches can be converted to $\overline{D}$ in cm by multiplying by 2.54).

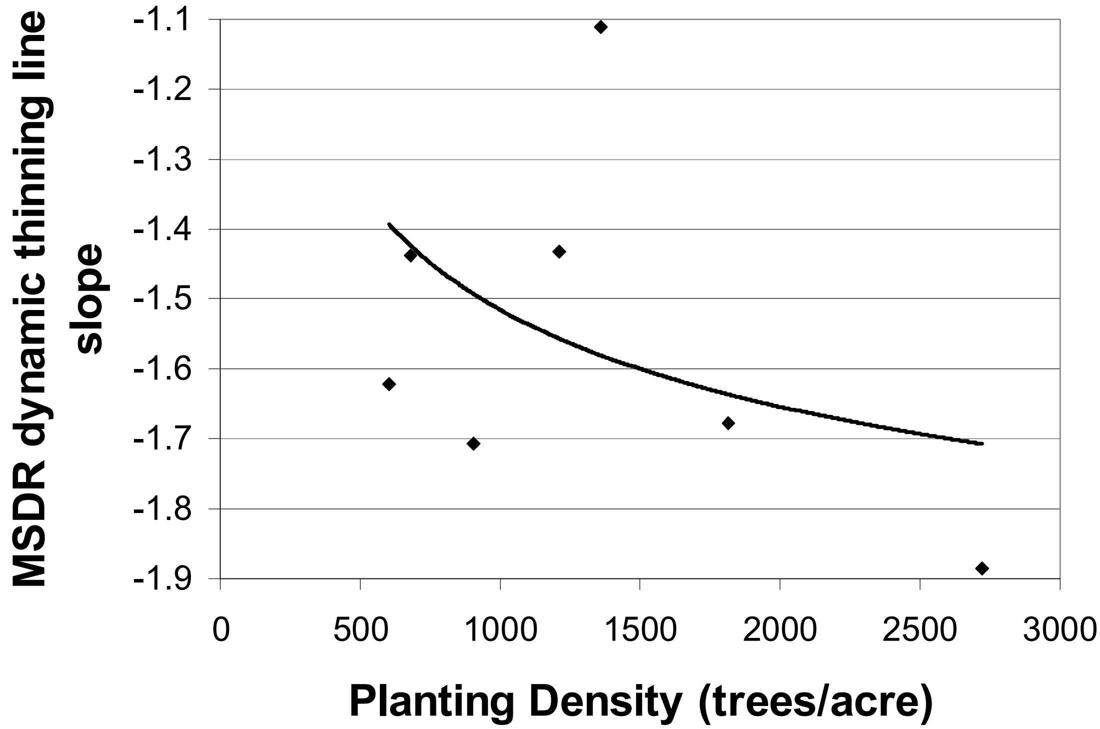


Figure 4.4. Predicted MSDR dynamic thinning line slopes across planting density. The black curve is slopes predicted using equation [4.7] while the black diamonds are the slopes as estimated by the segmented regression analyses (to convert trees/ac to trees/ha, multiply by 2.47; $\overline{D}$ in inches can be converted to $\overline{D}$ in cm by multiplying by 2.54).

Chapter 5

Impact of alternative methods to estimate maximum size-density relationships on density management diagrams for loblolly pine plantations

Curtis L. VanderSchaaf and Harold E. Burkhart[1]

[1] Department of Forestry, Virginia Polytechnic Institute and State University

ABSTRACT

Maximum size-density relationships (MSDRs) quantify the maximum tree density for a given average tree size. In this paper, we review and compare two previously presented alternative methods to estimate loblolly pine (*Pinus taeda* L.) plantation individual stand MSDR boundaries and slopes, termed MSDR dynamic thinning line boundary levels and slopes, respectively. One method estimates expected slopes for individual planting densities, while the second method uses an estimate of the population average slope of all MSDR dynamic thinning lines across a range of planting densities. Data used in model fitting were obtained from a loblolly pine planting density trial located in the Piedmont and Atlantic Coastal Plain physiographic regions and consisting of planting densities ranging from 2722 to 302 seedlings per acre. Validation analyses were conducted using data from a mid-rotation thinning study located throughout the southeastern US. The validation results showed that predicted maximum values of Reineke's Stand Density Index (SDI) had less error when using a constant slope across all MSDR dynamic thinning lines. The analyses also showed, on average, maximum SDI was overpredicted for stands of relatively low site quality, that were mid-rotation thinned, and located in the Western Gulf.

By relating planting density specific Zone of Imminent Competition Mortality boundaries to a MSDR species boundary line, self-thinning was found to begin at differing levels of relative SDI. Density Management Diagrams (DMD) that accounted for initial planting density showed that self-thinning began at 40 to 72% of maximum SDI for planting densities of 605 and 2722 seedlings per acre, respectively.

Keywords: density management diagrams, mixed models, Pinus taeda, stand density index, Zone of Imminent Competition Mortality.

Loblolly pine (*Pinus taeda* L.) is one of the most commercially valuable and widely planted tree species in the Southeastern US. Understanding self-thinning patterns of this species is important to making prudent management decisions such as determining optimum planting density and mid-rotation thinning regimes. Maximum size-density relationships (MSDRs) quantify the maximum tree density for a given average tree size. Weller (1990) defined two types of MSDRs (*i*) individual stand MSDR boundaries referred to as MSDR dynamic thinning line boundaries and (*ii*) the MSDR species boundary line defined as a static upper limit of maximum tree density – average tree size relationships that applies to all stands of a certain species within a particular geographical area.

VanderSchaaf and Burkhart (In review) further clarified Weller's definition of the species boundary line by defining what they called the MSDR species boundary line **II** while Weller's original species boundary line definition was referred to as the MSDR species boundary line **I**. Similar to the MSDR species boundary line **I**, **II** has a constant boundary level but has a slope that can be considered the population average of MSDR dynamic thinning line slopes for a particular species and geographic area. In part, this paper addresses the relative merits of using MSDRs as constraints (Monserud et al. 2005) for predicted stand density development when using MSDR dynamic thinning lines and two slope estimation alternatives, slopes that vary in relation to planting density and a population average MSDR dynamic thinning line slope.

Estimation of MSDR dynamic thinning line slopes

VanderSchaaf and Burkhart (In preparation) used segmented regression to estimate stages of stand development on the natural logarithmic (Ln) scale for planting densities ranging from 2722 to 605 seedlings per acre. The segmented regression models statistically determine where MSDR dynamic thinning lines begin and end allowing for these values to be predicted as a function of regressors, in this particular case planting density. Thus, they presented a system of simultaneously estimated linear regression equations to predict the beginning and ending values of MSDR dynamic thinning lines:

$$\text{Ln}\,\overline{D}_B = 4.766335 - 0.42899\ \text{Ln}(N_0) \quad [5.1]$$

$$\text{Ln}\,\overline{D}_E = 0.151668 + 0.965822\ \text{Ln}\,\overline{D}_B \quad [5.2]$$

$$\text{Ln}\,N_B = 11.01013 - 2.34843\ \text{Ln}\,\overline{D}_B \quad [5.3]$$

$$\text{Ln}\,N_E = 11.04924 - 2.32946\ \text{Ln}\,\overline{D}_E \quad [5.4]$$

Where:

$\text{Ln}\,\overline{D}_B$ -- logarithm of quadratic mean diameter (in) where a particular MSDR dynamic thinning line begins.

$\text{Ln}\,\overline{D}_E$ -- logarithm of quadratic mean diameter where a particular MSDR dynamic thinning line ends.

$\text{Ln}\,N_B$ -- logarithm of trees per acre where a particular MSDR dynamic thinning line begins.

$Ln\,N_E$ -- logarithm of trees per acre where a particular MSDR dynamic thinning line ends.

N_0 -- planting density per acre

Equations [5.1] through [5.4] can be used to predict the expected MSDR dynamic thinning line slope for any planting density by using equation [5.5]:

$$b = \frac{LnN_B - LnN_E}{Ln\overline{D}_B - Ln\overline{D}_E} \qquad [5.5]$$

When using the estimated slope as an exponent in Reineke's (1933) Stand Density Index (SDI) equation:

$$SDI = N\left[\frac{\overline{D}}{10}\right]^b \qquad [5.6]$$

Where:

b -- predicted exponent using equation [5.5].

an estimate of the expected maximum SDI can be obtained for any planting density by using $Ln\,\overline{D}_B$ and $Ln\,N_B$ (or alternatively $Ln\,\overline{D}_E$ and $Ln\,N_E$) untransformed in place of N and $\overline{D}$ in equation [5.6]. The exponent obtained from equation [5.5] is used to standardize to a $\overline{D}$ of 10 inches. A maximum SDI is analogous to quantifying MSDR dynamic thinning line boundary levels on the Ln-Ln scale.

Estimation of a population average MSDR dynamic thinning line slope

VanderSchaaf and Burkhart (In review) used linear mixed-models to estimate the MSDR species boundary line **II** slope. Since individual stand trajectory boundary levels vary relative to site quality (Weller 1990) and planting density (VanderSchaaf and Burkhart [In review]), when using Ordinary Least Squares which assumes independence of all observations, the estimated MSDR species boundary line **I** slope can be sensitive to the range of site qualities and planting densities used in model fitting. In mixed-models, since the boundary level can be considered random accounting for differences in MSDR dynamic thinning line boundary levels, the estimated MSDR species boundary line **II** slope is less sensitive to the range of site qualities and planting densities in the model fitting dataset. When using the mixed-models approach, an estimate of -1.6855 was obtained for the MSDR species boundary line **II** slope, which can be considered an estimate of the population average MSDR dynamic thinning line slope.

Data used in model fitting of slope estimation alternatives

For the two alternative MSDR slope estimation methods, the same overall dataset was used when estimating parameters. Tree and stand measurements were obtained from a spacing trial maintained by the Loblolly Pine Growth and Yield Research Cooperative at Virginia Polytechnic Institute and State University. The spacing trial was established on four cutover sites, two in the Upper Atlantic Coastal Plain and two in the Piedmont.

There is one Coastal plain site in both North Carolina and Virginia while both Piedmont sites are in Virginia. Three replicates of a compact factorial block design were established at each location in either 1983 or 1984. Sixteen initial planting densities were established ranging from 2722 to 302 seedlings per acre. Thus, a total of 192 research plot replicates were established when combining all four sites (4 sites x 3 replications x 16 planting densities). A variety of planting distances between and within rows were used (not all spacings were square). For the planting densities of 2722, 1210, 680, and 302 there was one plot established for a particular site and replication combination, for the planting densities of 1815, 1361, 605, and 453 there were two plots established, and for the planting density of 907 there were four plots established (Sharma et al. (2002) provide a more comprehensive description of this study). Site quality was quantified using site index defined as the average height of all trees with diameters larger than the $\overline{D}$ for the planting densities of 907, 680, and 605 by replication (Table 5.1). A site index equation found in Burkhart et al. (2004) was used to project dominant height forward to base age 25. Plots intermediate in stand density were used when estimating site index in order to avoid any possible effects of high or low number of N. Table 5.1 contains summaries of plot-level characteristics for the entire dataset.

Measurements of $\overline{D}$ and N have been conducted annually beginning at age 5 to age 21 on one of the Coastal plain sites and to age 22 on the other site. On the Piedmont sites, measurement ages end at 18 at one location and 21 at the other. At the latter Piedmont site, one replication had measurements to 22 years of age.

Since segmented regression models may contain many parameters, and observations may not exist in all stages of stand development for a particular experimental unit, statistical convergence can be a problem. For example, convergence was not met for the planting densities of 453 and 302, and therefore observations from those planting densities were not included when estimating parameters of equations [5.1] through [5.4] (VanderSchaaf and Burkhart [In preparation]). VanderSchaaf and Burkhart (In review) visually determined what observations occurred along MSDR dynamic thinning lines based on recommendations found in Weller (1987, 1991). Thus, observations occurring along a MSDR dynamic thinning line were obtained from a total of 8 and 2 plots for the planting densities of 453 and 302, respectively.

The objectives of this paper are to 1) review and compare previously presented alternative methods to estimate the slope of MSDRs, 2) present validation analysis results when using equations [5.1] through [5.6] to estimate the maximum SDI for populations of loblolly pine plantations different than those used in model fitting and compare results to using a constant slope for all planting densities, and 3) discuss implications of using non-constant MSDR boundary levels and alternatively estimated slopes when developing Density Management Diagrams (DMDs).

VALIDATION ANALYSES

Estimates of the maximum SDI using either slope estimation alternative can be used to constrain stand development of process based models and for more empirical models that lack sufficient data to properly estimate mortality equations (Monserud et al. 2005) and for verifying mortality equations and predicted stand development in general. Thus, we wanted to see whether our model system produces reasonable estimates of the maximum SDI for a variety of site conditions across the Southeastern US. In addition, validation analyses were conducted to determine the advantages of using planting density specific MSDR dynamic thinning line slopes as opposed to using a population average MSDR dynamic thinning line slope.

Data used in model validation were obtained from a long-term loblolly pine plantation thinning study established on cutover sites throughout the Southeastern United States (Burkhart et al. 1985). Study plots were established in 1980-1982 at 186 locations. At each study location, three plots were established; one was left unthinned and the two other plots were thinned; a lightly thinned plot and a heavily thinned plot. Thinnings were generally from below and the light thinning removed approximately one-third of the plot basal area while the heavy thinning removed approximately one-half of the plot basal area. The three experimental plots were located so as to minimize variation among the plots due to microsite differences. For sites where planting density is known, planting density ranged from 1223 to 570 seedlings per acre and measurement ages ranged from 8 to 43 years old. Inventories were conducted every three years. Dominant height was determined for plots by calculating the average height of all trees with DBHs greater than $\overline{D}$ for the age closest to the base age of 25; an equation was then used to obtain site index (Burkhart et al. 2004).

The validation process followed the methodology proposed by Arabatzis and Burkhart (1992) where the difference between the observed and predicted maximum SDI ($\text{Bias}_k = \text{SDI}_k - \hat{\text{SDI}}_k$) for each individual research plot (*k*) was calculated. The mean residual ($\overline{\text{Bias}}$) and the sample variance (s^2) of residuals were then computed which were considered to be estimates of bias and precision, respectively. An estimate of mean square error (MSE) was obtained by combining the bias and precision measures using the following formula:

$$\text{MSE} = \overline{\text{Bias}}^2 + s^2 \qquad [5.7]$$

In order to validate equations [5.1] through [5.6], only those plots where planting density is known can be used. Additionally, plots were examined to ensure those with excessive mortality due to ice storms, bug kills, etc., were removed – our purpose was to validate intraspecific self-thinning patterns and to avoid catastrophic mortality. To make sure that a maximum SDI had been reached for a particular trajectory, plots of LnN over Ln$\overline{\text{D}}$ were examined in a similar fashion as explained by VanderSchaaf and Burkhart (In review) using recommendations found in Weller (1987, 1991). These examinations were based on the concept that for observations occurring along a MSDR dynamic thinning line on the Ln-Ln scale, when plotting SDI over age for those observations and if the true exponent was known, SDI would be constant. LnN-Ln$\overline{\text{D}}$ trajectories were only checked to ensure that a maximum SDI should have been reached when using either slope estimation alternative (exponents that vary relative to planting density or a constant exponent, 1.6855), not to estimate the slope of the trajectory during the MSDR dynamic thinning line stage of stand development. The maximum observed SDI for a plot was the greatest value of SDI for a particular slope estimation alternative for those observations visually determined to occur along MSDR dynamic thinning lines. Based on the above criteria, a total of 65 plots were selected for validation analyses whose planting densities ranged from 1223 to 570 per acre. Site indexes, using the definition previously given, ranged from 43 to 78 feet.

Errors in predicting maximum SDIs for any size-density trajectory can result from two factors. The first factor is an incorrect prediction of the MSDR dynamic thinning line boundary slope, which is equivalent to the SDI exponent (see Williams 1994). An incorrect exponent can result in prediction errors of the maximum SDI since we standardize to a $\overline{D}$ of 10 inches. Assuming the SDI exponent is correctly predicted, the second factor is properly predicting the MSDR dynamic thinning line boundary level, which is equivalent to the maximum SDI. Since the true MSDR dynamic thinning line slope is not known, the two error factors cannot be separated. If an approximately correct SDI exponent is used, SDI will be constant, or nearly constant, when plotted over age for some period of time since the LnN-Ln $\overline{D}$ relationship will be linear for a period of time. SDI trajectories over age were examined using both slope estimation alternatives and in some cases a relatively constant maximum SDI was not reached, for variable slopes this occurred for 23 plots and when using a population average slope this occurred for 27 plots. Thus, assuming observations truly occurred along a MSDR dynamic thinning line boundary on the Ln-Ln scale, both slope estimation alternatives did not always correctly predict the slopes of trajectories.

Validation of maximum SDI prediction using exponents which vary by planting density

For unthinned plantations with site indexes greater than 63 feet (base age 25) located in either the Piedmont or Atlantic Coastal Plain physiographic regions (East in Table 5.2), our model reasonably predicts maximum SDI (Table 5.2 and Figure 5.1). To determine if equations [5.1] through [5.6] provide an unbiased estimate of maximum SDI, one sample t-tests were conducted where the null hypothesis is that $\overline{\text{Bias}}$ is not significantly different from 0. For all analyses, based on t-test results, our model system produced biased estimates of maximum SDI except for unthinned plantations with site indexes greater than 63 feet and thinned plantations with site indexes less than 63 feet located in the East. The t-test result for the thinned plantations with site indexes less than 63 feet is somewhat misleading though. Although the t-test result shows no significant difference from 0, the bias is -53.4 where three observations were overpredicted, -24.9, -71.6, and -119.6, while a fourth was slightly underpredicted, 2.4. It is reasonable to assume that our model system, on average, will overpredict the maximum SDI for such stands which is explained below. Therefore, the power of the test was calculated for a detectable difference of 20 and 40 N for a two-tailed test and an alpha level equal to 0.05 using methods found in Kirk (1995, pg. 60). The dependent variable is N since Reineke's SDI equates the current stand density (and based on the form of equation [5.6]) to the trees per acre (N) for a stand of equivalent density with a $\overline{\text{D}}$ of 10 inches (see Zeide 2005). In both cases, the power of the test was very low due to extreme variability in SDI prediction error.

It has been found that, on average, stands located in the Western Gulf tend to have lower maximum SDIs (Hasenauer et al. 1994, Amateis et al. 2006). There are several possible reasons for this ranging from genetic stock, higher probabilities of droughts later in the growing season, etc., (see VanderSchaaf and Prisley (In press) for a review of the literature). Our validation analyses provide further evidence that, on average, MSDRs are lower for Western Gulf plantations. All data used in model fitting are from sites located in the Piedmont or Atlantic Coastal Plain regions which may cause our model system, on average, to overpredict maximum SDIs for plantations located in the Western Gulf.

These validation analyses also seem to suggest the maximum SDI is dependent on site quality (Strub and Bredenkamp 1985). Our model system was developed using data from plantations with site indexes ranging from 63 to 73 feet and thus may generally overpredict maximum SDIs for stands with site indexes less than 63 feet. Finally, our model system tends to overpredict maximum SDIs of stands that have been mid-rotation thinned. To the best of our knowledge, no one has previously reported that mid-rotation thinning affects the MSDR dynamic thinning line boundary level. Similar to the reasoning given by VanderSchaaf and Burkhart (In review) as to why lower planting densities don't reach the same boundary level as greater planting densities, mid-rotation thinning, in a sense, produces mortality later in a rotation and residual trees do not have the capacity to fully occupy the canopy (Bredenkamp and Burkhart 1990, Zeide 1995). The impact of mid-rotation thinning probably depends on the severity of the thinning and the age at which the treatment is conducted.

Overprediction may also have occurred since some of the validation plots were established using minimal regeneration scenarios and were established only in stands planted with genetically unimproved seedling stock, unlike the study sites used in model fitting where weed control and genetic stock were relatively superior for the time period when the stands were established. Users should also be aware of the non-planted loblolly pine composition in their stands when using our model system since plantations used in model fitting were basically pure planted loblolly pine. Even non-planted loblolly pine can produce prediction errors since the estimated maximum SDI depends upon planting density.

Comparing results of using slopes that vary relative to planting density versus using a constant MSDR dynamic thinning line slope

Rather than using MSDR dynamic thinning line slopes that vary by planting density, or using variable exponents in equation [5.6], a constant slope can be used. For our example, -1.6855 was used as an estimate of the MSDR dynamic thinning line population average slope (VanderSchaaf and Burkhart [In review]). The MSDR species boundary line **II** slope is defined as the population average of all MSDR dynamic thinning line slopes and thus this species boundary line slope, on average, should be reflective of self-thinning patterns of loblolly pine plantations. Since the available data used in fitting equations [5.1] through [5.4] were the same as the data used to obtain the slope estimate of -1.6855, comparing results of the two MSDR slope estimate alternatives is valid. Other slopes could also have been used such as Reineke's (-1.605) or MacKinney and Chaiken's (1935) of -1.7070. To obtain an estimate of the maximum SDI for any planting density, $\text{Ln}\,\overline{D}_B$ and $\text{Ln}\,N_B$ (or alternatively $\text{Ln}\,\overline{D}_E$ and $\text{Ln}\,N_E$ could have been used) were untransformed and used to estimate the boundary level while 1.6855 was used to standardize to a $\overline{D}$ of 10 inches.

Validation analysis results when using a constant slope across all planting densities are shown in Table 5.3 and Figure 5.2. When comparing model predictions of maximum SDI to observed maximum SDI for plots most similar to those used in model fitting, site indexes greater than 63 feet in the Piedmont or Atlantic Coastal Plain physiographic regions, a constant slope across all planting densities was superior in all prediction criteria. For both slope estimation alternatives, and based on t-tests, SDI estimates are unbiased. The power of both t-tests is reasonable, but a larger sample size is certainly desirable. Although statisticians generally recommend a minimum power of 0.8 (Kirk 1995, pg. 59), foresters have suggested a power near 0.5 is more practical (Zedaker et al. 1993, South and VanderSchaaf 2006). Using a constant slope tended to underpredict maximum SDI while using variable slopes tended to overpredict maximum SDI.

Across all categories and prediction criteria, neither MSDR dynamic thinning line slope estimation alternative was superior but using a constant exponent of 1.6855 generally produced better results. It appears our planting density specific slope estimates are not representative, on average, of self-thinning patterns for the validation dataset. This is particularly true for stands located in the Western Gulf. Due to differences in growing conditions and genetic stock among the model fitting and model validation datasets, future research needs to concentrate on including factors such as site quality into equations [5.1] through [5.4] and fitting those equations using data from stands located in the Western Gulf region.

IMPLICATIONS TO DENSITY MANAGEMENT DIAGRAMS

DMDs provide a relatively easy to use tool when managing stands to achieve a particular management objective. Several DMDs have been created for a variety of conifer species using the LnV-LnN (Drew and Flewelling 1979) and the Ln$\overline{D}$-LnN relationships (Long 1985, Saunders and Puettmann 2000, Long and Shaw 2005, Mack and Burk 2005), where V is mean tree volume. DMDs have also been created for loblolly pine plantations located in the Western Gulf of the Southeastern US (Dean and Baldwin 1993, Williams 1994) using the Ln$\overline{D}$-LnN relationship. Most DMDs consist of a MSDR species boundary line and three management boundaries positioned based on relative stand densities to the MSDR species boundary line (Drew and Flewelling 1979, Saunders and Puettmann 2000, Long and Shaw 2005). The first boundary is the Onset of Competition, the second boundary is Full Site Occupancy, and the final boundary is the Zone of Imminent Competition Mortality sometimes referred to as the Lower Limit of Self-thinning. The Zone of Imminent Competition Mortality is synonymous with the occurrence of self-thinning, when density-dependent mortality is expected to occur (Drew and Flewelling 1979, Hibbs 1987, Long and Shaw 2005). Since capturing density-dependent mortality is an objective of most foresters, in part, DMDs are useful because they provide a means to lessen the loss in recovered stand yield across a rotation due to self-thinning.

In general, the relative stand density boundaries are thought to parallel the slope of the MSDR species boundary line on the Ln-Ln scale. However, Saunders and Puettmann (2000) presented a DMD where the Onset of Competition was curvilinear but the two other boundaries were parallel to the MSDR species boundary line. Based on the segmented regression model analysis results presented in VanderSchaaf and Burkhart (In preparation), we can estimate when self-thinning is expected to occur relative to planting density and when using equations [5.1] through [5.6] we can estimate a maximum SDI for any planting density. Therefore, we can determine whether planting density specific Zone of Imminent Competition Mortality boundaries parallel a MSDR species boundary line. Additionally, unlike current DMDs, we can develop separate DMDs for individual planting densities. Due to the limitations of the segmented regression analyses, we can not determine whether the Onset of Competition and Full Site Occupancy boundaries parallel the MSDR.

In order to predict the SDI at which the Zone of Imminent Competition Mortality begins for a particular planting density, equation [5.8] was fitted using the estimates of $\mathrm{Ln}\,\overline{\mathrm{D}}$ when self-thinning first occurs based on segmented regression analyses (VanderSchaaf and Burkhart [In preparation]):

$$\mathrm{Ln}\,\overline{\mathrm{D}}_{\mathrm{S}} = 3.949656 - 0.36006\mathrm{LnN}_0 \qquad [5.8]$$

Where:

$\mathrm{Ln}\,\overline{\mathrm{D}}_{\mathrm{S}}$ -- logarithm of quadratic mean diameter where self-thinning begins.

Adjusted R^2 is equal to 0.9673, n = 7.

Equation [5.8] is simple and provides a nonlinear relationship between Ln $\overline{D}_S$ and planting density (Figure 5.3). Both parameters were significant at the < 0.0001 alpha level. Using equations [5.5], [5.6], and [5.8], an estimate of the SDI where self-thinning is expected to begin for a particular planting density can be calculated. For Reineke's SDI equation, since density-dependent mortality is not expected to occur until Ln $\overline{D}_S$ is reached, we make the simplifying assumption that N equals planting density (McCarter and Long 1986) while $\overline{D}$ equals Ln $\overline{D}_S$ untransformed. To determine the relative relationship between planting density specific Zone of Imminent Competition Mortality boundaries and MSDR dynamic thinning lines on the Ln-Ln scale, we can calculate the relative density between the expected SDI when self-thinning begins and the expected maximum SDI for any planting density on the untransformed scale (Figure 5.4). Rather than using planting density specific exponents, alternatively we can also calculate relative SDIs when using a constant exponent of 1.6855 (Figure 5.5).

Verifying predicted maximum SDIs and Zone of Imminent Competition Mortality SDIs

In order for any recommendations or conclusions about DMDs found during this study to be relevant, we first need to verify that the estimates of the maximum SDI and the Zone of Imminent Competition Mortality SDI are representative of the data for the range of planting densities used in model fitting. Figures 5.4 and 5.5 both include the observed average SDI for those observations estimated to occur along the MSDR dynamic thinning line boundary for a particular planting density based on the segmented regression analyses (VanderSchaaf and Burkhart [In preparation]). Additionally, both figures include the minimum SDI for those observations estimated to be within the self-thinning stage of stand development, or the Zone of Imminent Competition Mortality, based on the segmented regression analyses. For Figure 5.4, the exponent used in calculating both values of SDI is the same but varies by planting density while for Figure 5.5 the SDI values are calculated using an exponent of 1.6855. Figure 5.6 contains estimated size-density trajectories based on the segmented regression analysis results found in VanderSchaaf and Burkhart (In preparation) for the planting densities used in fitting equations [5.1] through [5.4]. The MSDR species boundary line was positioned at a SDI of 502 using a slope of -1.6855 while the Zone of Imminent Competition Mortality boundary was located using the values of $\text{Ln}\,\overline{D}$ where self-thinning is expected to begin, $\text{Ln}\,\overline{D}_S$.

When using equations [5.1] through [5.6], reasonable maximum SDI estimates occurred (Figure 5.4) while reasonable predictions were also obtained when using $\text{Ln}\,\overline{D}_B$ and $\text{Ln}\,N_B$ to determine the MSDR dynamic thinning line boundary level and then using an exponent of 1.6855 in Reineke's equation (Figure 5.5). When using varying slopes, the average error was 9.7 N while for a constant slope the average error was 9.8 N (based on the definition of SDI, N is the dependent variable). For both slope estimation alternatives, the predicted SDI where the Zone of Imminent Competition Mortality begins exceeded the observed minimum SDI for those observations estimated to be within the self-thinning stage of stand development using segmented regression analyses. However, the overpredictions are not severe, average of 25.9 N for varying slopes and an average of 22.1 N for a constant slope, and most likely result from the fact that we assumed no mortality occurs until after a stand's trajectory has exceeded the $\text{Ln}\,\overline{D}_S$. For several individual research plots, mortality occurred prior to trajectories reaching the predicted $\text{Ln}\,\overline{D}_S$ for a particular planting density. Regardless, conclusions and recommendations provided in this paper about DMDs can be considered representative of plantations growing in the Piedmont and Atlantic Coastal Plain regions since our models predict stand development adequately for the observations used in model fitting. For either slope estimation alternative, based on model validation analyses, our model system reasonably predicts the maximum SDI for plantations located in the Piedmont and Atlantic Coastal Plain regions. Thus, providing further evidence that conclusions and recommendations provided in this paper about DMDs should be applicable to most plantations in the Piedmont and Atlantic Coastal Plain regions.

Planting density specific DMDs

When using varying slopes, the relative SDI of the expected individual stand maximum SDI and expected individual stand SDI where self-thinning begins is essentially constant across the range of planting densities used in fitting equations [5.1] through [5.4] and [5.8], ranging from 68% to 71%. Fairly similar results are seen in Figure 5.5 when using a constant exponent, relative SDIs range from 61% to 72%. These relative SDIs generally exceed those published by others (e.g. Drew and Flewelling 1979, Dean and Baldwin 1993, Williams 1994, Mack and Burk 2005) but our relative SDIs may be greater since we made the assumption that no mortality occurs until a trajectory enters the

Zone of Imminent Competition Mortality. When using a constant exponent of 1.6855, relative SDIs for lower planting densities in our study are close to that proposed for a variety of western US conifer species, 60% (Long 1985, McCarter and Long 1986, and Long and Shaw 2005). Williams (1994) recommended a relative SDI of 55% for loblolly pine plantations in the Western Gulf. Based on our results where the MSDR boundary level varies relative to planting density, the Zone of Imminent Competition Mortality boundary level is generally positioned too low. Relative Zone of Imminent Competition Mortality boundary levels being positioned at 40 to 60% of the MSDR dynamic thinning line boundary level will result in losses of total volume yield when trying to reduce the likelihood of self-thinning because thinnings will either be too frequent or too severe. However, when comparing our results to other studies, variability in growing patterns among conifer species, growing conditions, and genetic stock may cause self-thinning patterns in our data to be different. More importantly, most other DMDs relate the Zone of Imminent Competition Mortality to a MSDR species boundary line.

Either slope estimation alternative produces a nearly constant relative relationship between MSDR dynamic thinning lines and Zone of Imminent Competition Mortality boundaries but when varying the slope relative to planting density, the relative relationship is more constant, about 70%. Thus, which slope estimation alternative to use is somewhat ambiguous. If it is merely desired to obtain an estimate of a maximum SDI, based on the model validation analyses, a constant exponent of 1.6855 should be used. However, if planting density specific DMDs are desired, it may be best to use exponents that vary relative to planting density. For both applications, the use of either slope estimation alternative will generally produce reasonable results.

Traditional DMDs

The DMDs presented in Figures 5.4 and 5.5 relate the Zone of Imminent Competition Mortality across a range of planting densities to MSDR dynamic thinning line boundary levels. However, when relating planting density specific Zone of Imminent Competition Mortality boundaries to a MSDR species boundary line, the relative SDIs have a much greater range (Figures 5.6 and 5.7), relative SDIs range from 40% to 72%. This is the traditional approach of developing DMDs, calculating the maximum SDI for a given dataset based on a selected exponent, in our case 1.6855, and establishing management zone boundaries relative to the maximum SDI. The greater range in relative SDIs occurs because planting density specific values of the Zone of Imminent Competition Mortality do not parallel a constant maximum SDI.

SUMMARY AND RECOMMENDATIONS

Previously presented alternative methods of estimating MSDR dynamic thinning line slopes were examined for their ability to predict maximum SDIs for a range of site conditions of loblolly pine plantations across the Southeastern US. The use of a constant slope across planting densities produced better results for independent validation data most similar to that used in model fitting, site indexes greater than 63 feet in either the Piedmont or Atlantic Coastal Plain physiographic regions. Thus, when a prediction of the maximum SDI is desired for plantations located in the Piedmont or Atlantic Coastal Plain regions, a constant exponent of 1.6855 should be used.

Our model fitting and validation analyses clearly show that MSDR dynamic thinning line boundary levels of loblolly pine plantations on cutover sites vary relative to planting density, site quality, and mid-rotation thinning treatments. In some cases our model system will produce reasonable estimates of the maximum SDI for unthinned Western Gulf plantations with site indexes greater than 63 feet. However, on average, our model system will overpredict SDI for these stands, regardless of slope estimation alternative. Additionally, neither slope estimation alternative should be used to predict maximum SDIs for plantations with site indexes less than 63 feet nor which have been mid-rotation thinned.

Recommendations for DMDs

Based on our results, the positioning of the boundary level for the Zone of Imminent Competition Mortality is more complicated than previously depicted. For instance, when using a constant relative SDI of 50 or 60% of the species maximum SDI to establish the Zone of Imminent Competition Mortality, since maximum SDIs are less for lower planting densities, self-thinning would be expected to occur for lower planting densities. The Zone of Imminent Competition Mortality could be positioned at a relative SDI of 40% to avoid self-thinning across the range of planting densities from 2722 to 605 per acre. However, the relative SDI would result in less than optimum density management regimes for higher planting densities since thinnings would be conducted more frequently or would be more severe than needed to avoid self-thinning, assuming maximizing total volume yield is the management objective. Thus, we recommend future DMDs be developed around the concept of establishing maximum SDIs, or MSDR dynamic thinning lines, and Zone of Imminent Competition Mortality boundaries, relative to factors such as planting density and site quality and to avoid the use of MSDR species boundary lines. If possible, it would also be best to estimate exponents of Reineke's SDI relative to planting density and site quality since this slope estimation alternative seems to provide the most stable relationships between the maximum SDI and the Zone of Imminent Competition Mortality SDI boundary. The planting density specific DMDs for loblolly pine plantations presented here can be applied in either the Piedmont or Atlantic Coastal Plain physiographic regions.

LITERATURE CITED

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. South. J. Appl. For. 30: 147-153.

Arabatzis, A.A., and H.E. Burkhart. 1992. An evaluation of sampling methods and model forms for estimating height-diameter relationships in loblolly pine plantations. For. Sci. 38: 192-198.

Bredenkamp, B.V., and H.E. Burkhart. 1990. An examination of spacing indices for *Eucalyptus grandis*. Can. J. For. Res. 20: 1909-1916.

Burkhart, H.E., D.C. Cloeren, and R.L. Amateis. 1985. Yield relationships in unthinned loblolly pine plantations on cutover, site-prepared lands. South. J. Appl. For. 9: 84-91.

Burkhart, H.E., R.L. Amateis, J.A. Westfall, and R.F. Daniels. 2004. PTAEDA 3.1: Simulation of individual tree growth, stand development and economic evaluation in loblolly pine plantations. Sch. of For. and Wildl. Res., Va. Polytech Inst. and State Univ. 23 p.

Dean, T.J., and V.C. Baldwin. 1993. Using a stand density-management diagram to develop thinning schedules for loblolly pine plantations. USDA For. Serv. Res. Pap. SO-275. 7 p.

Drew, T.J., and J.W. Flewelling. 1979. Stand density management: an alternative approach and its application to Douglas-fir plantations. For. Sci. 25: 518-532.

Hasenauer, H., H.E. Burkhart, and H. Sterba. 1994. Variation in potential volume yield of loblolly pine plantations. For. Sci. 40: 162-176.

Hibbs, D.E. 1987. The self-thinning rule and red alder management. For. Ecol. Manage. 18: 273-281.

Kirk, R.E. 1995. Experimental design: procedures for the behavioral sciences. 3rd ed., Brooks/Cole Publishing Company, Pacific Grove, Ca. 921 p.

Long, J.N. 1985. A practical approach to density management. For. Chron. 61: 23-27.

Long, J.N., and J.D. Shaw. 2005. A density management diagram for even-aged ponderosa pine stands. West. J. Appl. For. 20: 205-215.

MacKinney, A.L., and L.E. Chaiken. 1935. A method of determining density of loblolly pine stands. USDA For. Serv., Appalachian Forest Experiment Station, Tech. Note 15. 3 p.

McCarter, J.B., and J.N. Long. 1986. A lodgepole pine density management diagram. West. J. Appl. For. 1: 6-11.

Mack, T.J., and T.E. Burk. 2005. A model-based approach to developing density management diagrams illustrated with Lake States red pine. North. J. Appl. For. 22: 117-123.

Monserud, R.A., T. Ledermann, and H. Sterba. 2005. Are self-thinning constraints needed in a tree-specific mortality model? For. Sci. 50: 848-858.

Reineke, L.H. 1933. Perfecting a stand-density index for even-age forests. J. Agri. Res. 46: 627-638.

Saunders, M.R., and K.J. Puettmann. 2000. A preliminary white spruce density management diagram for the Lake States. Univ. of Minnesota Staff Paper Series No. 145, St. Paul, MN. 14 p.

Sharma, M., H.E. Burkhart, and R.L. Amateis. 2002. Modeling the effect of density on the growth of loblolly pine trees. South. J. Appl. For. 26: 124-133.

South, D.B., and C.L. VanderSchaaf. 2006. The statistical reason why some researchers say some silvicultural treatments "wash-out" over time. P. 333-337 *in* Proc. of the Thirteenth biennial southern silvicultural research conference, Connor, K.F., (ed). USDA For. Serv. Gen. Tech. Rep. SRS-GTR-92.

Strub, M.R., and B.V. Bredenkamp. 1985. Carrying capacity and thinning response of *Pinus taeda* in the CCT experiments. South African For. J. 2: 6-11.

VanderSchaaf, C.L., and H.E. Burkhart. In review. Comparison of methods to estimate Reineke's maximum size-density relationship species boundary line slope. Submitted to For. Sci.

VanderSchaaf, C.L., and H.E. Burkhart. In preparation. Using segmented regression to estimate stages of stand development. To be submitted to For. Sci.

VanderSchaaf, C.L., and S.P. Prisley. In press. Factors affecting site productivity of loblolly pine plantations across the Southeastern United States. To be published in the Proceedings of the Southern Forestry and Natural Resource Management GIS Conference. Virginia Polytechnic Institute and State University.

Weller, D.E. 1987. A reevaluation of the -3/2 power rule of plant self-thinning. Ecol. Monogr. 57: 23-43.

Weller, D.E. 1990. Will the real self-thinning rule please stand up? – A reply to Osawa and Sugita. Ecology 71: 1204-1207.

Weller, D.E. 1991. The self-thinning rule: Dead or unsupported? – A reply to Lonsdale. Ecology 72: 747-750.

Williams, R.A. 1994. Stand density management diagram for loblolly pine plantations in north Louisiana. South. J. Appl. For. 18: 40-45.

Zedaker, S.M., T.G. Gregoire, and J.H. Miller. 1993. Sample-size needs for forestry herbicide trials. Can. J. For. Res. 23: 2153-2158.

Zeide, B. 1995. A relationship between size of trees and their number. For. Ecol. Manage. 72: 265-272.

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

Table 5.1. Plot-level characteristics for the entire dataset (n = 2977).

Variable	Minimum	Mean	Maximum
Trees/ac	228	917	2722
$\overline{D}$ (in)	1.1	5.4	10.8
BA (ft^2/ac)	0.1	122	258
SI (ft)	63	68	73

Table 5.2. Model validation analysis results when comparing observed maximum values of Reineke's SDI, using variable exponents, obtained from a Thinning study established throughout the Southeastern US versus predicted maximum values. Where: $\overline{\text{Bias}}$ -- observed maximum SDI minus predicted SDI, s^2 -- variance, MSE -- mean square error, 63 refers to a site index of 63 feet at base age 25, East -- a plantation was located in either the Piedmont or Atlantic Coastal Plain physiographic regions, West -- a plantation was located in the Western Gulf physiographic region, Sign. -- p-value corresponding to the t-test examining whether $\overline{\text{Bias}}$ is significantly different from 0, Power -- is the ability of the t-tests to detect a difference at the 0.05 alpha level if one actually existed.

			Error		t-test	Power	
Group	n	$\overline{\text{Bias}}$	s^2	MSE	Sign.	20 N	40 N
Unthinned, > 63	18	-28.9	3017	3852	0.0394	-	-
East	9	-14.7	2852	3069	0.4317	0.1657	0.5071
West	9	-43.1	3109	4963	0.0492	-	-
Unthinned, < 63	26	-51.2	3323	5948	0.0001	-	-
East	13	-45.0	2502	4524	0.0071	-	-
West	13	-57.5	4335	7643	0.0084	-	-
Thinned, > 63	9	-74.8	1818	7420	0.0008	-	-
East	4	-76.5	2337	8192	0.0506	-	-
West	5	-73.5	1879	7283	0.0192	-	-
Thinned, < 63	12	-84.0	2292	9342	<0.0001	-	-
East	4	-53.4	2883	5738	0.1406	0.0788	0.1930
West	8	-99.2	1568	11413	0.0002	-	-
All	65	-54.4	3130	6086	<0.0001	-	-
East	30	-41.2	2778	4479	0.0002	-	-
West	35	-65.6	3240	7546	<0.0001	-	-

Table 5.3. Model validation analysis results when comparing observed maximum values of Reineke's SDI, using a constant exponent of 1.6855, obtained from a Thinning study established throughout the Southeastern US versus predicted maximum values. Where: $\overline{\text{Bias}}$ -- observed maximum SDI minus predicted SDI, s^2 -- variance, MSE -- mean square error, 63 refers to a site index of 63 feet at base age 25, East -- a plantation was located in either the Piedmont or Atlantic Coastal Plain physiographic regions, West -- a plantation was located in the Western Gulf physiographic region, Sign. -- p-value corresponding to the t-test examining whether $\overline{\text{Bias}}$ is significantly different from 0, Power -- is the ability of the t-tests to detect a difference at the 0.05 alpha level if one actually existed.

			Error		t-test	Power	
Group	n	$\overline{\text{Bias}}$	s^2	MSE	Sign.	20 N	40 N
Unthinned, > 63	18	-11.2	3278	3404	0.4175	0.2853	0.7955
East	9	1.5	2710	2712	0.9336	0.1721	0.5275
West	9	-23.9	3892	4465	0.2833	0.1327	0.3948
Unthinned, < 63	26	-38.9	3633	5144	0.0030	-	-
East	13	-33.3	2788	3894	0.0424	-	-
West	13	-44.5	4713	6691	0.0377	-	-
Thinned, > 63	9	-61.6	1854	5651	0.0026	-	-
East	4	-69.4	1688	6509	0.0431	-	-
West	5	-55.4	2332	5399	0.0624	0.1090	0.3071
Thinned, < 63	12	-75.5	1700	7406	<.0001	-	-
East	4	-57.3	1560	4842	0.0625	0.1118	0.3178
West	8	-84.7	1716	8886	0.0007	-	-
All	65	-41.1	3349	5040	<.0001	-	-
East	30	-30.9	2866	3819	0.0037	-	-
West	35	-49.9	3686	6179	<.0001	-	-

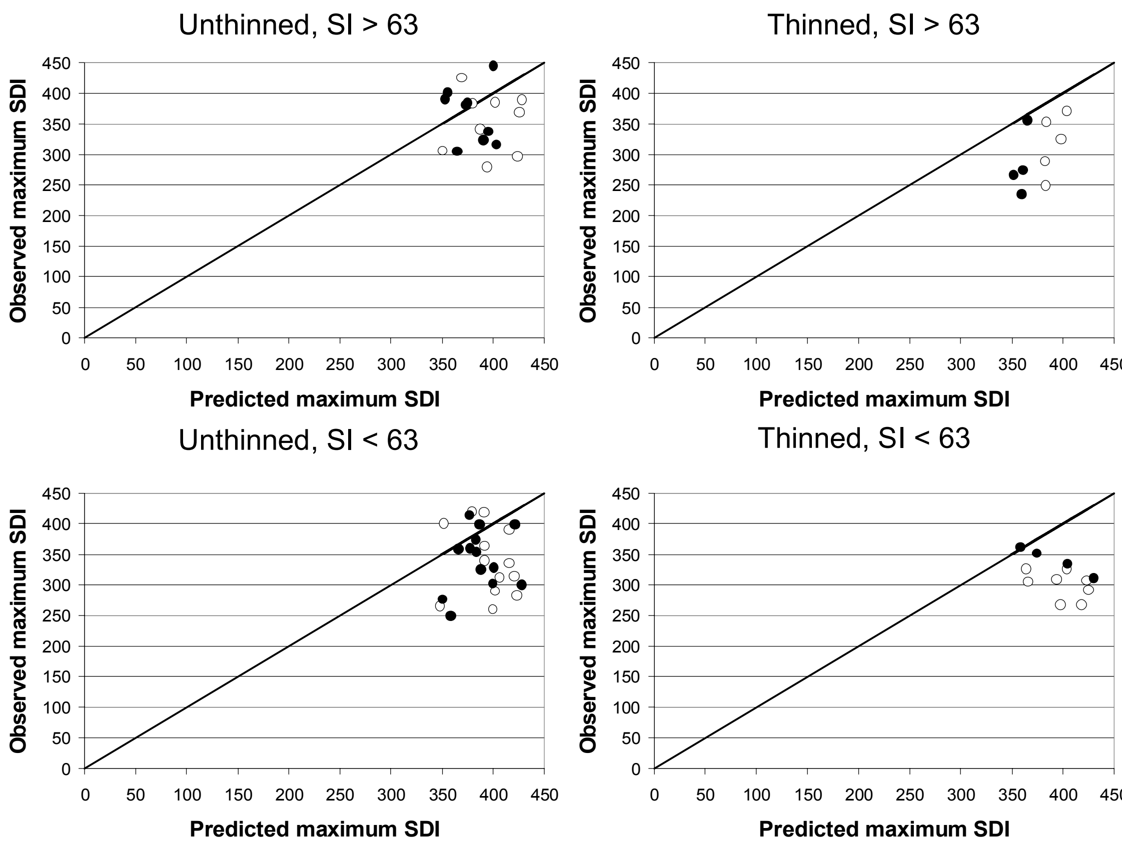


Figure 5.1. Observed maximum Reineke SDI of individual research plots plotted over predicted maximum SDI using exponents that vary relative to planting density as predicted using equation [5.5]. The line is a one-to-one relationship for the predicted maximum SDI values. Where: black filled circles -- observations from the Piedmont or Atlantic Coastal Plain physiographic regions (East in Table 5.2), unfilled circles -- observations from the Western Gulf Coastal Plain region (West in Table 5,2), SI -- site index in feet.

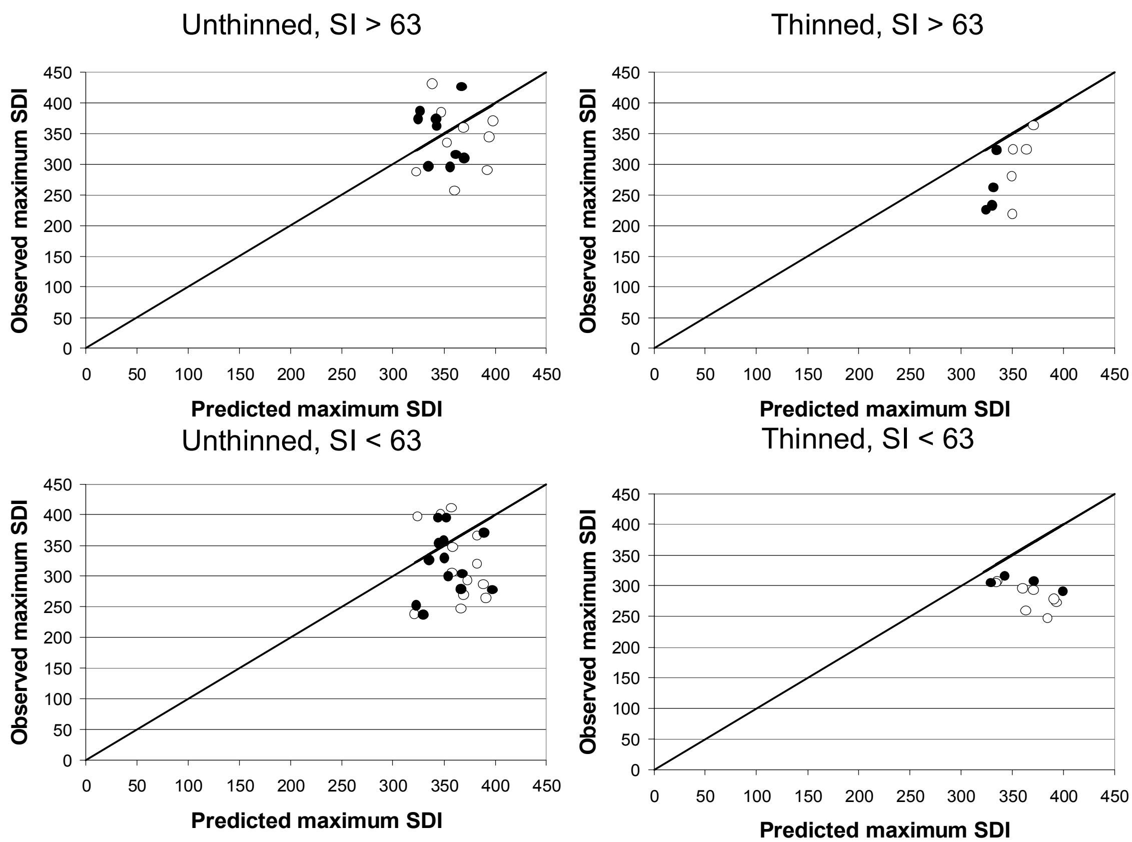


Figure 5.2. Observed maximum Reineke SDI of individual research plots plotted over predicted maximum SDI using a constant exponent of 1.6855. The line is a one-to-one relationship for the predicted maximum SDI values. Where: black filled circles -- observations from the Piedmont or Atlantic Coastal Plain physiographic regions (East in Table 5.3), unfilled circles -- observations from the Western Gulf Coastal Plain region (West in Table 5.3), SI -- site index in feet.

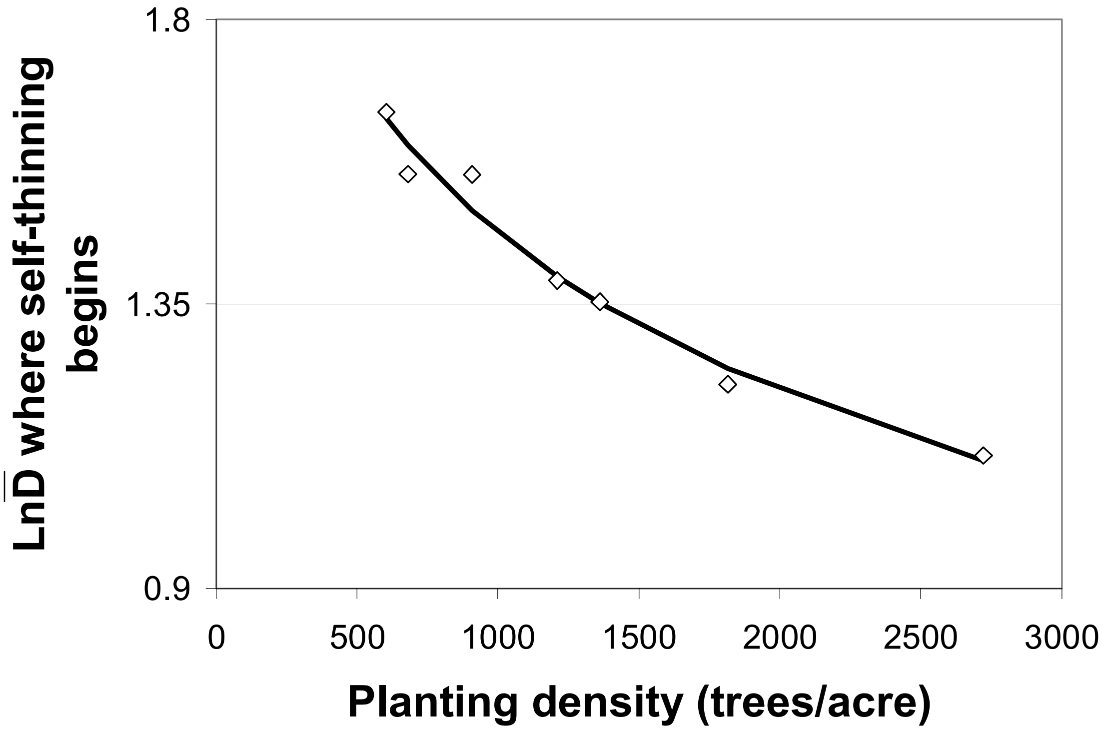


Figure 5.3. Plot of the Ln $\overline{D}$ where self-thinning begins over planting density. n = 7.

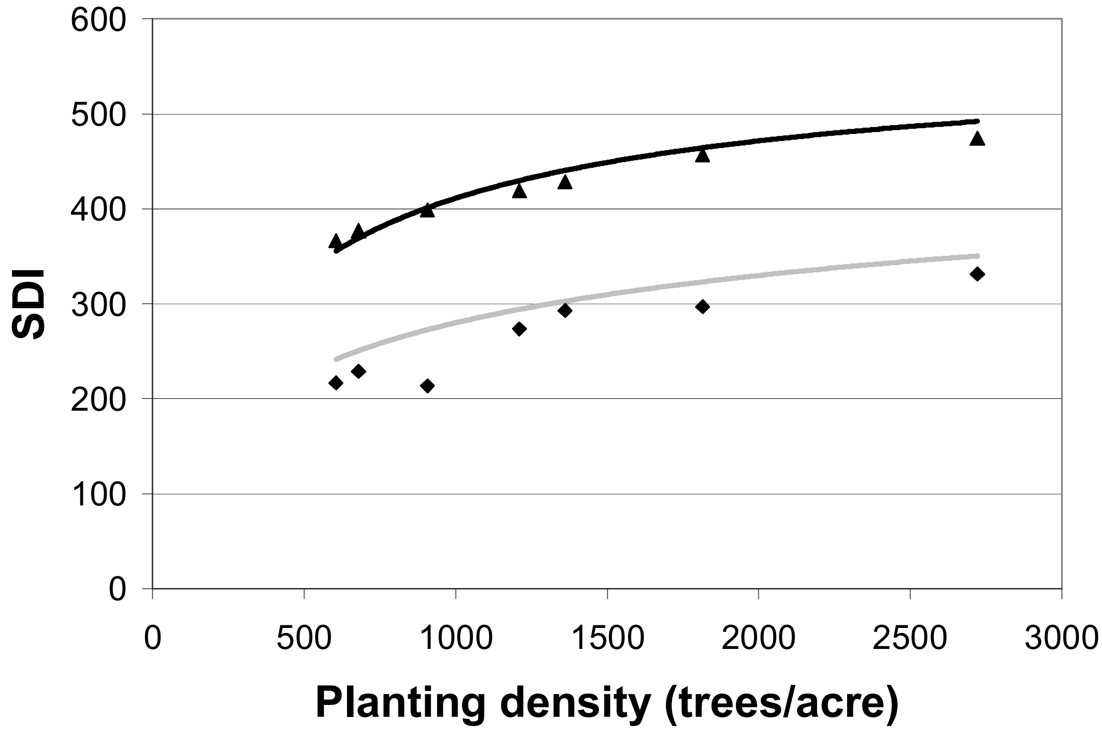


Figure 5.4. Predicted maximum SDI (black curve) and the SDI where the Zone of Imminent Competition Mortality begins (gray curve) across the range of planting densities (2722 to 605 seedlings per acre) used in fitting equations [5.1] through [5.4] and [5.8]. Exponents used in calculating SDI vary across planting density as predicted using equation [5.5]. Black triangles are the average SDI of all observations estimated to be within the MSDR dynamic thinning line stage of stand development for a particular planting density while black diamonds are the minimum SDI values of all observations estimated to be within the self-thinning stage of stand development for a particular planting density using segmented regression analyses.

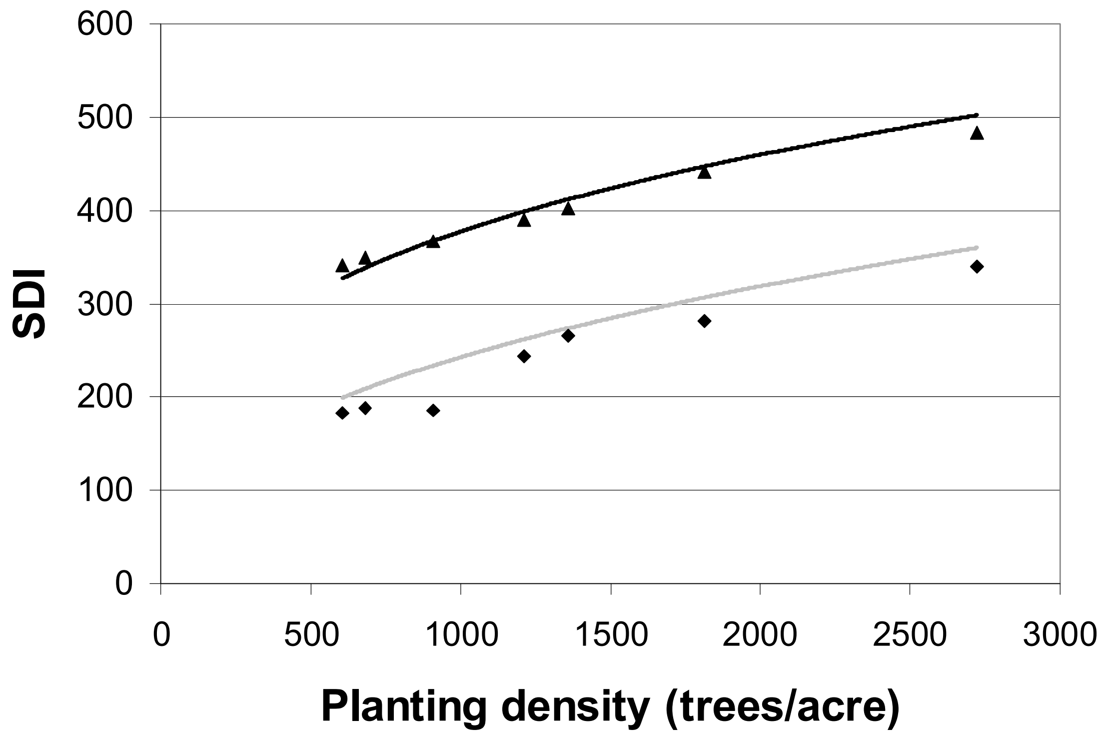


Figure 5.5. Predicted maximum SDI (black curve) and the SDI where the Zone of Imminent Competition Mortality begins (gray curve) across the range of planting densities (2722 to 605 seedlings per acre) used in fitting equations [5.1] through [5.4] and [5.8]. An exponent of 1.6855 was used for all planting densities. Black triangles are the average SDI of all observations estimated to be within the MSDR dynamic thinning line stage of stand development for a particular planting density while black diamonds are the minimum SDI values of all observations estimated to be within the self-thinning stage of stand development for a particular planting density using segmented regression analyses.

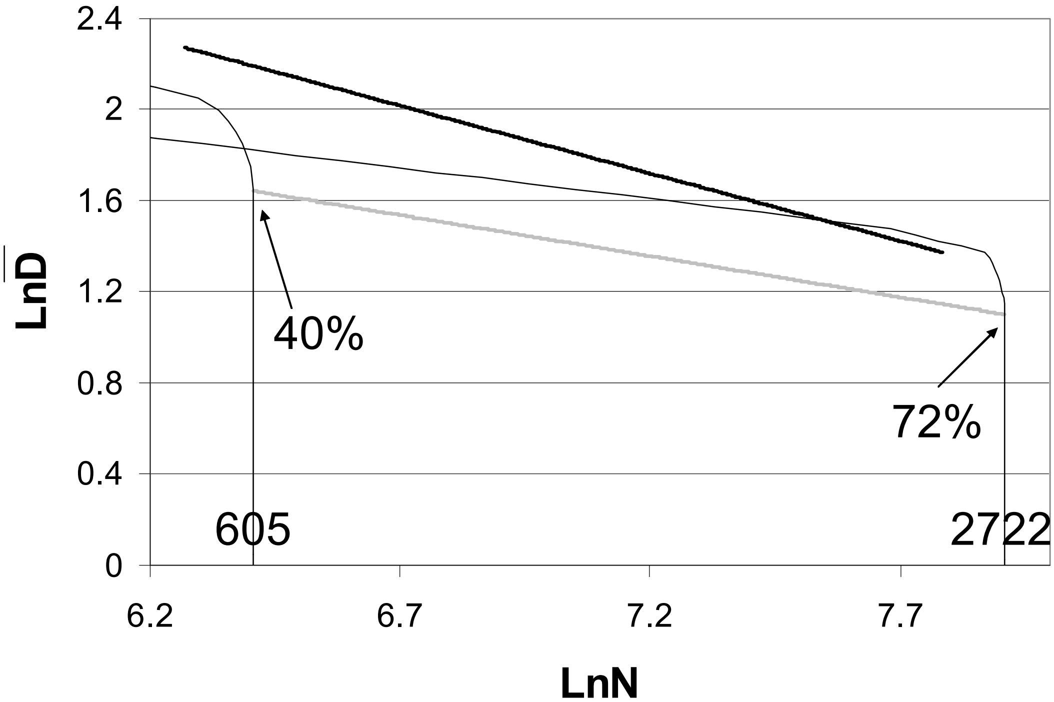


Figure 5.6. Predicted size-density trajectories based on segmented regression analyses of two planting densities, 2722 and 605 seedlings per acre. A constant MSDR species boundary line with a SDI of 502 using a slope of -1.6855 is plotted along with a Zone of Imminent Competition Mortality boundary developed based on predictions of when self-thinning is expected to occur using equation [5.8]. Forty percent and 72% are the relative values of the Zone of Imminent Competition Mortality to the MSDR species boundary line for the planting densities of 605 and 2722 seedlings per acre, respectively.

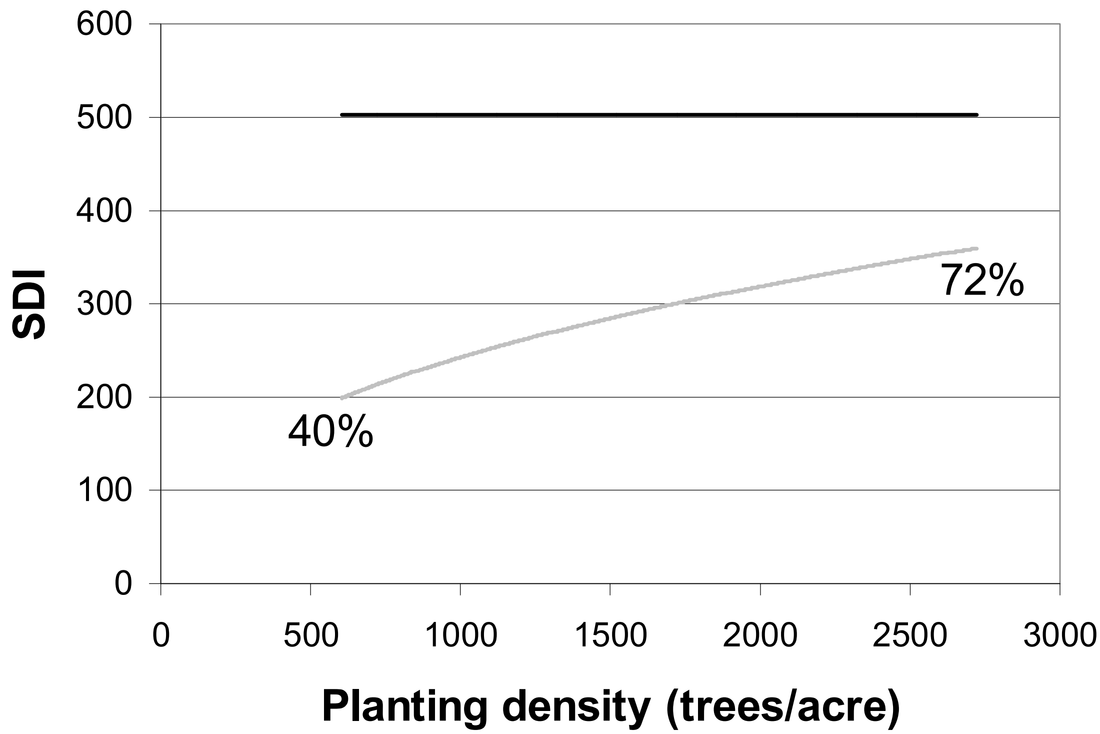


Figure 5.7. Predicted maximum SDI equal to 502 (black line), and the SDI where the Zone of Imminent Competition Mortality begins (gray curve), across the range of planting densities used in fitting equations [5.1] through [5.4] and [5.8], 2722 to 605 seedlings per acre. An exponent of 1.6855 was used for all planting densities. Forty percent and 72% are the relative values of the Zone of Imminent Competition Mortality to the MSDR species boundary line for the planting densities of 605 and 2722 seedlings per acre, respectively.

Chapter 6

Summary and Recommendations

Summary

Expanding upon Weller, a second MSDR species boundary line was defined, the MSDR species boundary line **II**. By using mixed models, an estimate of the population average MSDR dynamic thinning line slope can be obtained that will provide a more meaningful quantification of how stands, on the average, self-thin. Thus, the MSDR species boundary line **II** slope, unlike the MSDR species boundary line **I** slope, can be used to quantify MSDR dynamic thinning line slopes.

Segmented regression was applied as a means to more objectively and statistically determine stand development stages of size-density trajectories, and, more specifically, what observations occur along MSDR dynamic thinning lines. The segmented regression analyses allow for MSDR dynamic thinning line boundary levels to be estimated as a function of planting density. Based on these analyses, an alternative methodology was presented to estimate MSDR dynamic thinning line slopes. Finally, the segmented regression model analyses provided a means to develop a model to estimate at what $\text{Ln}\,\overline{\text{D}}$ self-thinning is expected to begin relative to planting density.

The two alternative methods to depict MSDR dynamic thinning line slopes were compared, using planting density specific slopes or an estimate of the MSDR dynamic thinning line population average slope, and their implications to Density Management Diagrams (DMDs) were examined. Model validation analyses of an independent dataset showed for plantations most similar to those used in model fitting, unthinned plantations of relatively high site quality located in the Piedmont or Atlantic Coastal Plain physiographic regions, that a constant slope across all planting densities produced the most accurate predictions of MSDR dynamic thinning line boundary levels. Neither MSDR dynamic thinning line slope estimation alternative, on the average, produced satisfactory predictions of MSDR dynamic thinning line boundary levels for plantations that were mid-rotation thinned, had a low site quality, or were located in the Western Gulf physiographic region. When estimating MSDR dynamic thinning line boundary levels and slopes and the expected beginning of self-thinning as a function of planting density, a relatively constant relationship was shown to occur between the boundary level and the Zone of Imminent Competition Mortality, approximately 70%. However, when relating planting density specific Zones of Imminent Competition Mortality to a single MSDR species boundary line, but assuming a constant relative relationship of 50% or greater between all planting density specific Zones of Imminent Competition Mortality and the species boundary line, it was shown that self-thinning will likely occur for lower planting densities.

When examining model validation results and the development of planting density specific DMDs, neither slope estimation alternative is consistently superior for unthinned stands of relatively high site quality located in the Piedmont or Atlantic Coastal Plain physiographic regions. If it is merely desired to obtain a prediction of the maximum SDI, on average, an exponent of 1.6855 will produce the best results. When developing planting density specific DMDs, on average, slopes that vary relative to planting density will attain the most constant relative relationship between MSDR dynamic thinning lines and their corresponding planting density specific Zone of Imminent Competition Mortality boundaries. However, for both applications, a constant exponent (or slope) across all planting densities or exponents (or slope) that vary relative to planting density will produce reasonable results.

Recommendations

As often occurs during research, results open many avenues for future investigation. Segmented regression was shown to provide a more objective and statistical method to determine what observations occur within a particular stage of stand development. As self-thinning continues within the plots used to fit models presented in this dissertation, segmented regression models can be fit for the planting densities of 453 and 302 seedlings per acre and for each individual plot of all planting densities. Therefore, models estimating at what $\mathrm{Ln}\,\overline{\mathrm{D}}$ self-thinning is expected to begin and the two values of $\mathrm{Ln}\,\overline{\mathrm{D}}$ when MSDR dynamic thinning lines are expected to begin and end can be fitted using a broader range of planting densities. When fitting by individual plot, site quality and physiographic region can be included when modeling MSDR dynamic thinning line slopes and boundary levels. Data used in fitting models presented in this dissertation could be combined with data from a broader range of site qualities, genetic stock, site preparation treatments, mid-rotation treatments, etc. and from plantations located in the Western Gulf to develop more widely applicable self-thinning and MSDR models. These models would produce more detailed and realistic MSDR constraints. Based on the segmented regression analyses, models describing stand development during the divergence stage can also be developed.

Linear mixed-effects models were shown to account for differences in MSDR dynamic thinning line boundary levels and slopes when estimating MSDR species boundary line slopes. If MSDR species boundary lines are to be estimated, linear mixed models can be used to obtain an estimate of the population average MSDR dynamic thinning line slope and how plantations, on the average, self-thin during the linear stage of self-thinning. Other studies that have found a substantial difference between their estimated MSDR species boundary line slope and those slopes of Reineke (1933) or MacKinney and Chaiken (1935) should be reanalyzed; perhaps the impacts of MSDR dynamic thinning line slopes and boundary levels on the estimated species boundary line slope were not accounted for.

Models presented in this dissertation have provided a foundation for developing more meaningful and complete DMDs. Future work should concentrate on developing more site-specific DMDs; e.g., DMDs more representative of specific combinations of site quality and planting density. Even factors such as genetic or clonal stock, and site preparation, fertilization, and herbicide treatments could be included when developing DMDs. Additionally, future work will need to quantify the Onset of Competition and Full Site Occupancy management boundaries relative to planting density and site quality.

Appendix. Statistical Analysis Software (SAS) code for linear mixed-models and fixed-effect segmented regression models.

SAS code for a simple linear mixed-effects model with varying number of random effects. Clusters would need to be identified (observ in this case) within the dataset (termed j1 for this example). Proc MIXED assumes the data are normally distributed.

No random effect

```
proc mixed data = j1  ;
class observ ;
model lntpa = lnqmd /solution outpred = p ;
run ;
```

Intercept random

```
proc mixed data = j1  ;
class observ ;
model lntpa = lnqmd /solution outpred = p ;
random intercept /subject = observ solution ;
ods output solutionr = solr ;
ods output solutionf = solf ;
run ;
```

Intercept and slope random

By specifying `type = un` for the random effects variance-covariance matrix, a covariance is assumed between the intercept and random effects.

```
proc mixed data = j1  ;
class observ ;
model lntpa = lnqmd /solution outpred = p ;
random intercept lnqmd /subject = observ type = un solution ;
ods output solutionr = solr ;
ods output solutionf = solf ;
run ;
```

SAS code for the full and reduced segmented regression models as explained in Chapter 4 of this dissertation. The `lntpa ~ normal` code stipulates the data are assumed to be normally distributed. Other distributions can be assumed such as the binomial or Poisson. By specifying `tech = newrap`, the Newton-Raphson method is used to obtain parameter estimates by maximizing an approximation to the likelihood. Resvar refers to the residual variance which is estimated within the likelihood approximation and thus a starting value must be specified.

```
proc nlmixed data = j1 tech = newrap ;
parameters b0 = 7.8784 b2 = -3.5949 a1 = 1.1533 resvar = 0.01872 ;
firstterm = b0 ;
secondterm = b0+b2*(lnqmd-a1)**2 ;
model lntpa ~ normal(firstterm*(lnqmd <=a1) + secondterm*(lnqmd >a1),
resvar) ;
run ;

proc nlmixed data = j1 tech = newrap ;
parameters b0 = 7.8821 b2 = -0.57 b3 = -1.9 b4 = -3.5 a1 = 1 a2 = 1.3
a3 = 1.5 resvar = 0.019 ;
firstterm = b0 ;
secondterm = b0+b2*(lnqmd-a1)**2 ;
thirdterm = b0+b2*(a2-a1)**2+b3*(lnqmd-a2) ;
fourthterm = b0+b2*(a2-a1)**2+b3*(a3-a2)+b4*(lnqmd-a3) ;
model lntpa ~ normal(firstterm*(lnqmd <=a1) + secondterm*((lnqmd >a1)
and(lnqmd<=a2))+thirdterm*((lnqmd>a2)and(lnqmd<=a3))+fourthterm*(lnqmd>
a3), resvar) ;
run ;
```

Vita

Curtis L. VanderSchaaf was born on February 11, 1973 in Omaha, Nebraska. He was raised in several locations across the United States including Carol Stream, Rockford, S. Beloit, IL, New Orleans, LA, Jackson, MI, North Platte and Omaha, NE, Reno and Las Vegas, NV, and he graduated from Las Cruces High School in Las Cruces, NM in May 1991. After graduating from high school, he attended Southwestern College in Winfield, KS and Abilene Christian University in Abilene, TX before obtaining his bachelors degree in Forest Management from Stephen F. Austin State University in Nacogdoches, TX in May 1996. Curtis obtained his masters degree in Silviculture from the University of Idaho in Moscow, ID in May 1999. He then worked at the University of Arkansas-Monticello in Monticello, AR and Auburn University in Auburn, AL as a research assistant and research associate, respectively. Curtis obtained his Ph.D. in Forest Biometrics from Virginia Polytechnic Institute and State University in December 2006. During his studies at Virginia Tech University he worked as both a Graduate Teaching Assistant and Graduate Research Assistant. He accepted a faculty position as a Forest Biometrician at the University of Arkansas-Monticello.