

Estimation and Determination of Carrying Capacity in Loblolly Pine

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Abstract

Stand carrying capacity is the maximum size of population for a species under given environmental conditions. Site resources limit the maximum volume or biomass that can be sustained in forest stands. This study was aimed at estimating and determining the carrying capacity in loblolly pine. Maximum stand basal area (BA) that can be sustained over a long period of time can be regarded as a measure of carrying capacity. To quantify and project stand BA carrying capacity, one approach is to use the estimate from a fitted cumulative BA-age equation; another approach is to obtain BA estimates implied by maximum size-density relationships (MSDRs), denoted implied maximum stand BA. The efficacy of three diameter-based MSDR measures: Reineke's self-thinning rule, competition-density rule and Nilson's sparsity index, were evaluated. Estimates from three MSDR measures were compared with estimates from the Chapman-Richards (C-R) equation fitted to the maximum stand BA observed on plots from spacing trials. The spacing trials, established in the two physiographic regions (Piedmont and Coastal Plain), and at two different scales (operational and miniature) were examined and compared, which provides a sound empirical basis for evaluating potential carrying capacity.

Results showed that the stands with high initial planting density approached the stand BA carrying capacity sooner than the stands with lower initial planting density. The maximum stand BA associated with planting density developed similarly at the two scales. The potential carrying capacity in the two physiographic regions was significantly different. The value of implied maximum stand BA converted from three diameter-based MSDR measures was similar to the maximum stand BA curve obtained from the C-R equation. Nilson's sparsity index was the most stable and reliable estimate of stand BA carrying capacity. The flexibility of Nilson's sparsity index can illustrate the effect of physiographic regions on stand BA carrying capacity.

Because some uncontrollable factors on long-term operational experiments can make estimates of stand BA carrying capacity unreliable for loblolly pine, it is suggested that the stand BA carrying capacity could be estimated from high initial planting density stands in a relatively short period of time so that the risk of damages and the costs of experiments could be reduced. For estimating carrying capacity, another attractive option is to choose a miniature scale trial (microcosm) because it shortens the experiment time and reduces costs greatly.

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Chapter 1

Introduction

1.1 Introduction

Site resources limit the maximum volume or biomass that can be sustained in forest stands. Carrying capacity can be regarded as the maximum population size of a species that a certain environment can support given finite resources. Stand basal area (BA) is a commonly-used measure of stand density when predicting tree growth and mortality. Maximum stand basal area that can be sustained over a long period of time can be regarded as a measure of carrying capacity.

To quantify and project stand BA carrying capacity, one approach is to use the estimate from a fitted cumulative BA-age equation; another approach is to obtain BA estimates implied by maximum size-density relationships (MSDRs). The MSDR is a boundary or maximum “trade-off” between the number of trees per unit area and the average tree size that can be sustained in a given stand. The efficacy of three diameter-based MSDR measures: Reineke’s self-thinning rule (STR) (Reineke 1933), Competition-density rule (C-D rule) (Kira, et al. 1953) and Nilson’s sparsity index (Nilson 2006), were evaluated and compared in this study. Indeed, C-D rule and Nilson’s sparsity index haven’t been much cited and examined in the US forestry literature compared to Reineke’s STR but there are still many advantages of both alternate formulations, such as incorporation of dominant tree height implying the quality of sites.

Limiting density is an important concept that can be addressed through spacing trials with a wide range of initial planting densities. The operational spacing trials that were established by the Forest Modeling Research Cooperative with loblolly pine at planting densities of 747 to over

6,727 trees per hectare and measured annually through age 25 provide a sound empirical basis for evaluating potential carrying capacity. The experimental design of this spacing trial is a nonsystematic plaid design developed by Lin and Morse (1975). The effect of physiographic regions on stand dynamics and carrying capacity were assessed and compared using data from operational spacing trials.

In addition, due to the tremendous costs of establishment and maintenance of conventional field experiments, a small scale experiment, so called microcosm or miniature scale trial, has been developed to overcome the shortcomings. This cost-effective experimental tool has potential to reduce the temporal and spatial scale of field experiments to a manageable level. The loblolly pine miniature scale spacing trial established on the Virginia Tech campus is an example. This miniature scale spacing trial employs spacing that is 1/16 of the operational spacing trials which have been described above. The trend of stand competition and dynamics was compared at both miniature and operational scales.

The results of this study should enhance understanding of plant competition, forest stand dynamics, and stand growth and yield. Also, this study provides guidance for managers when making decisions on planting density, thinning schedules and rotation ages.

1.2 Objectives

The main objectives of this study were to estimate and determine the stand BA carrying capacity in loblolly pine. Following is a list of specific objectives:

- (1) Compare the efficacy of three diameter-based maximum size-density relationships measures for estimating stand BA carrying capacity.
- (2) Examine the effect of physiographic regions (Piedmont and Coastal Plain) on stand BA carrying capacity.
- (3) Evaluate the projection of stand competition phenomena from the miniature scale spacing trial (microcosm) to the operational scale spacing trial.

Chapter 2

Literature review

2.1 Stand carrying capacity and maximum stand basal area

Carrying capacity can be regarded as the maximum population size of a species that a certain environment can support given finite resources. Carrying capacity, which originated from livestock science, has been broadly applied and discussed in many fields, such as population ecology, sociology, and anthropology (Wisniewski 1980, Dewar 1984, Price 1999). The concept of carrying capacity contains two meanings: a measure of environmental productivity and a description of equilibrium population density (Dewar 1984). That is, carrying capacity illustrates the environment limits that constrain the size of populations that can safely be attained; populations tend to stabilize at or fluctuate around these limits (Price 1999). In addition to the physical environment limits (i.e.: growing space), carrying capacity is determined by the resource and sink functions of the environment (e.g.: solar radiation, nutrients availability, decomposition rate) (Durham 1991, Harms, et al. 1994) and the composition of the species (e.g.: mixed stands, multiaged stands).

Stockability, or stocking capacity, shares similar concepts with carrying capacity. Hall (1983) and DeBell, et al. (1989) denoted “stockability” to describe the tolerance of a stand to the presence of and/or competition from increasing numbers of trees per unit area. Stand stocking, which is a relative term, refers to the adequacy of a given stand density to meet the desired management objective whereas stand density is a quantitative measurement of the stand, such as number of trees per unit area (Bickford, et al. 1957, Burkhart and Tomé 2012). As a result, a stand might simultaneously be referred to as understocked, fully stocked, or overstocked based

on the management objective. Stands designated as understocked might not have the same stand density. Stand carrying capacity could also be referred to as the maximum possible stocking of trees that a stand can sustain over a long term. In general, stand carrying capacity for a given species is relatively constant. Some silvicultural practices, such as fertilization, and genetic manipulation are helpful to improve the growth rate of reaching carrying capacity so that the years to reach financial returns can be shortened (Fox, et al. 2007).

Stand basal area (BA) is the sum of cross-sectional area of all stems diameters at breast height. BA per unit area is preferred as a measure of stand density and a satisfactory expression of stocking levels (Bickford, et al. 1957) because it integrates the effect of both diameter and number of trees in a stand. Stahelin (1949) computed the percentage of stocking using the actual BA per unit area divided by the desired BA per unit area for prescribing thinning treatment. In addition, due to the allometric relationship, stand BA has been used as a predictor for biomass and aboveground carbon stocks (Burrows, et al. 2000, Balderas Torres and Lovett 2012).

Maximum stand BA that is sustainable over a period of time can be regarded as a measure of stand carrying capacity. It shows the total amount of maximum yield in a stand. Hall (1983) developed a field method, called growth BA, for determining the site potential limitations on stockability. He proposed in essence using BA at which dominant trees grow 25 mm diameter per decade at age 100. DeBell, et al. (1989) used BA and volume production in loblolly pine plantations to compare the stockability between Hawaii and South Carolina. Notably, BA per unit area incorporated with size information (e.g.: size-density relationship) is a useful and improved quantification for input into prescribing silvicultural treatments and for projecting stand growth and yield (Burkhart and Tomé 2012).

2.2 Forest stand dynamics and size-density relationship

2.2.1 Stand dynamics and competition

Forest stand dynamics is the process of stand structural changes through time (Oliver and Larson 1996). Apart from silvicultural intervention or disturbances, forest competition occurs naturally and it is a common phenomenon in forest stand dynamics. Individual trees compete for light, water, and nutrients; when site resources no longer adequately support tree growth, mortality occurs. As trees grow in size, the growing space for each individual shrinks. For even-aged stands, intraspecific competition becomes fierce, initiates self-thinning, and causes the number of trees per unit area to decrease (competition-induced mortality or self-thinning). The canopy gaps created by dead trees will be occupied by the residual neighboring trees. Later, the number of trees per unit area and the average tree size in the stand will reach and then stay on a relatively stable equilibrium for a period of time (VanderSchaaf and Burkhart 2008, Burkhart and Tomé 2012). Then, the ability of residual neighboring trees to fully compensate the canopy gaps decreases gradually (Zeide 1995). Eventually, the number of trees per unit area will be reduced with minor or no increase of average tree size (Cao, et al. 2000). Indeed, most forest stands experience competition but the extent of competition varies, depending on different environmental factors and different species composition and structure.

To describe the extent of competition and stand dynamics, number of trees per unit area, individual trees size, and spatial distribution need to be included (Kikuzawa 1999, Burkhart and Tomé 2012). In practice, number of trees per unit area is the most straightforward and simplest expression of stand competition and crowdedness. However, lack of reference stands or other determined relationships, number of trees per unit area provides limited information of stand

dynamics (Burkhart and Tomé 2012). Therefore, for practical purposes, two quantitative approaches have been developed to explore stand dynamics: size-density relationships and cumulative basal area (BA)-age relationships. Size-density relationships and cumulative BA-age relationships are based on different perspectives. The former focuses on the relationship between the size of the average tree and the number of trees per unit area in a stand; the latter focuses on the total amount of yield over a period of time in a stand. The age of inflection of sigmoidal cumulative BA-age relationship curves is related to crown closure and to the onset of competition (Radtke and Burkhart 1999).

2.2.2 Size-density relationship and its application

In general, there are two stages in the size-density trajectory on a log-log scale shown as Fig. 1: Stage I density-independent mortality stage and Stage II Competition-induced (maximum size-density relationship, or self-thinning) mortality stage (VanderSchaaf and Burkhart 2008). A stand transfers from Stage I to Stage II because of occurrence of competition. The maximum size-density relationship (MSDR) is a boundary or maximum “trade-offs” between the number of trees per unit area and the average tree size that can be sustained in a given stand (Kira, et al. 1953, Lonsdale and Watkinson 1982, Zeide 1995, VanderSchaaf and Burkhart 2008). MSDR can be referred to as an expression of stand carrying capacity (Long and Vacchiano 2014). Further, Weller (1990) separated MSDR into two boundary lines: the species boundary line (static thinning line) and the dynamic boundary line. For a given species, the plant population cannot be denser than a fixed limiting density, whose value depends on time or stage of development (Yoda, et al. 1963). Thus, for a particular species in a certain geographic region, the species boundary line is a static upper limit in any even-aged stands while the dynamic boundary line,

usually below the species boundary line, varies among individual stands. In the further discussion, we will use MSDR as the species boundary line for simplicity.

Due to different physiographic regions, genotypes or phenotypes, or species, size-density trajectories for individual stands vary. There are three common types: (1) For most stands, their size-density trajectories will approach and nearly parallel the MSDR or self-thinning line (i.e.: bounded by dynamic thinning line), shown as Type I in Fig.1. Then, the trajectory will diverge from MSDR as a line or a curve concave down (Zeide 1987, Cao, et al. 2000, VanderSchaaf and Burkhardt 2008); (2) The trend of Type II is similar to Type I while the size-density trajectory of Type II will merge with MSDR (i.e.: species boundary line coincides with dynamic boundary line). Namely, the Type II stands can maintain the maximum population density (i.e.: carrying capacity) for a period of time; (3) For Type III, the size-density trajectory passes across MSDR line temporarily and then diverges farther from MSDR line than Type I and Type II. That is, the overcrowded stands experience serious competition, which then causes the number of trees per unit area to decline rapidly.

Furthermore, MSDRs as a central component in stand dynamics or as a constraint on mortality, have been incorporated into a number of growth and yield models (Burkhardt and Tomé 2012). Tang, et al. (1994) developed a stand growth model by combining a self-thinning model and a basal area increment model to estimate average diameter and stand density at any stand age with any initial stand conditions. Turnblom and Burk (2000) studied self-thinning, growth and mortality in red pine plantations using nonlinear simultaneous differential equations. They indicated that in the Lake States (Minnesota, Michigan and Wisconsin), stands with high initial planting density exhibited lower self-thinning lines than those planted with lower density. High site quality accelerated the progress of stand development. Yang and Titus (2002) used MSDR to

constrain individual tree mortality models in a mixedwood growth model for boreal mixedwood forests. Reyes-Hernandez, et al. (2013) calculated the slope of the dynamic self-thinning line to represent the average stand behavior and to constrain stand density models in boreal mixed and pure aspen and white spruce stands.

For practical uses, one of the most common applications for MSDR and size-density relationships is construction of stand density management diagrams (SDMDs) (e.g.: López-Sánchez and Rodríguez-Soalleiro 2009, VanderSchaaf and Burkhardt 2012, Vacchiano, et al. 2013) for determining management schedules, prescribing silvicultural treatments, evaluating stand conditions and predicting stand development (Jack and Long 1996, Newton 1997). López-Sánchez and Rodríguez-Soalleiro (2009) implemented the isolines of relative spacing index (Hart 1926) in a static SDMD to assess the stability of stands for Douglas-fir in Spain. Vacchiano, et al. (2013) used maximum SDI (Reineke 1933) as a constraint in a SDMD to identify the structure of stands and the resistance to natural disturbances for Norway spruce in temperate Europe. However, VanderSchaaf and Burkhardt (2012) pointed out the inadequacy of traditional SDMD when considering a wide range of initial planting density. Due to the self-thinning beginning at 40-72% of the species maximum SDI for wide-ranged planting densities, they developed a planting density-specific SDMD for loblolly pine in the southern US.

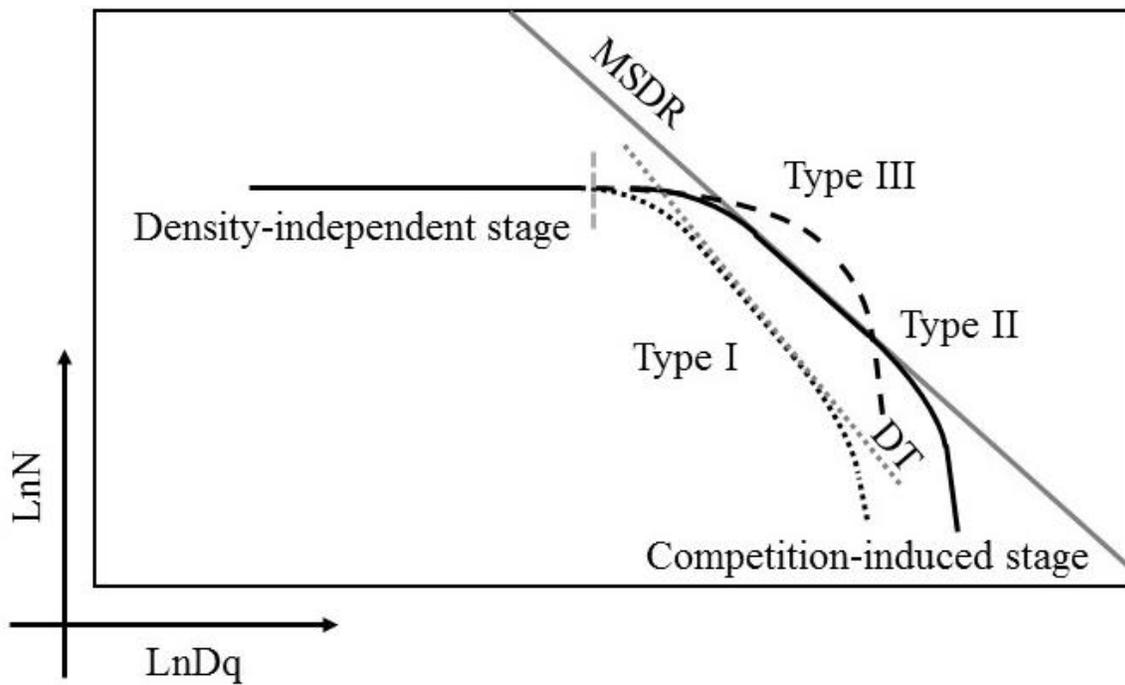


Figure 1 Size-density relationship trajectories on a log-log scale. Grey solid line is maximum size-density relationship (MSDR) line (species boundary line). Grey dotted line is dynamic boundary line (DT) (dynamic thinning line). Grey dashed line is the occurrence of competition-induced mortality. Black dotted, solid, and dashed lines are Type I, Type II, and Type III trajectories.

2.3 Maximum size-density relationship (MSDR) measures

Since maximum size-density relationships (MSDRs) provide essential and useful information for forest managers about stand development and dynamics, many MSDR measures have been developed, such as relative spacing (Hart 1926), $-3/2$ power self-thinning rule (Yoda, et al. 1963), Reineke's self-thinning rule (STR) (Reineke 1933), Competition-density (C-D) rule (Kira, et al. 1953), Nilson's sparsity index (Nilson 2006), crown competition factor (CCF) (Krajicek, et al. 1961), and others. Different MSDR measures are based on different aspects of MSDR and have varying ecological implications. For example, relative spacing focuses on the mean distance between individual trees as a proportion of mean dominant tree height of stands, whereas Yoda's $-3/2$ power self-thinning rule describes the relationship between maximum average plant weight versus number of plants per unit area.

Long and Vacchiano (2014) categorized 10 MSDR measures into three types: at a point of time (e.g: Kira's C-D rule), over time (e.g: Yoda's $-3/2$ power self-thinning rule), and independent of time (e.g: Reineke's STR). Their rationale for classification was in the context of time. However, Curtis (1970) pointed out the similarity of several common MSDR measures, including Reineke's STR, Kira's C-D rule, Krajicek's CCF, and so on. He found that these MSDR measures could be viewed as the expression of available area to individual trees in a stand, relative to that occupied by individual trees growing under a standard density condition and comparable in diameter or other measure of size. In addition, Curtis (1970) emphasized that although the MSDR measures are mainly different in the details of algebraic form and methods of estimation of constants, they are expressed as the same basic relationship. That is, they are practically equivalent.

Another way to categorize MSDR measures is based on the size variables (i.e. the measures of size), such as quadratic mean diameter (e.g: Reineke's STR), average dominant tree height (e.g: relative spacing), or mean tree volume or weight (e.g: Yoda's $-3/2$ power self-thinning rule). An examination of 31 articles from 12 different journals using MSDR measures showed that although 9 different size variables have been used, quadratic mean diameter remains the most common measure of size. Burkhart (2013) compared the efficacy of MSDR measures of three different size variables (quadratic mean diameter, average dominant tree height, and average stem volume) which were derived from a common formulated structure. He indicated while the differences aren't large due to the allometric relationships, quadratic mean diameter still proved most informative and was well ground in theory. Zeide (1991, 1995, 2002, 2010) discussed and analyzed the usefulness of MSDR measures for describing tree crowdedness and stand density. By integrating the knowledge of tree characteristics, stand development and dynamics, he modified and justified the ecological concepts underlying MSDR measures. Zeide (1987, 1995) argued that stem diameter is highly correlated to tree crown size, which is the vital stand variable representing crowding of trees. Furthermore, Zeide (2010) emphasized that average stem diameter as a predictor of number of trees is better than other measures of size, such as height and volume. Therefore, in this study, three well-known and widely employed diameter-based MSDR measures were selected for further analysis: Reineke's STR (Reineke 1933), C-D rule (Kira, et al. 1953), and Nilson's sparsity index (Nilson 2006).

2.3.1 Reineke's self-thinning rule (STR)

Reineke (1933) considered the maximum number of trees for specified average tree sizes in fully stocked even-aged stands. He plotted number of trees and diameter data of various tree species, including red fir, Douglas-fir, white fir, eucalyptus, and loblolly pine, on log-log graph paper. Then, he positioned a upper limiting line with a fixed slope above the clouds of data by hand and concluded that maximum stand density and quadratic mean diameter on a log-log scale followed a linear relationship. That is,

$$\ln N = a + b \cdot \ln \bar{D}_q \quad (1)$$

where

\ln = natural logarithm

N = number of trees per unit area

\bar{D}_q = quadratic mean diameter

a, b = Reineke's coefficients.

He indicated that the slope (b), close to -1.605, is generally consistent among species and locations but the value of the intercept (a) varies. Further, he proposed an index, called stand density index (SDI), for estimating and comparing the degree of stocking in even-aged stands. SDI is defined as the number of trees when quadratic mean diameter is equal to 10 inches (25.4 cm) (Eq.2). Reineke's SDI is expressed in the form

$$SDI = N \left(\frac{25.4}{\bar{D}_q} \right)^b \quad (2)$$

where all the symbols have been defined in Eq. 1.

In addition, Yoda, et al. (1963) indicated that if we assume the average plant weight is proportional to the 2.5th power of DBH, the Reineke's equation could be algebraically transformed to -3/2 power self-thinning rule. Yoda's assumption of an allometric relationship between plant weight and DBH is a reasonable approximation for many species (reviewed in White 1981). Zeide and Semevski (2007) found that the overall bias of Reineke's equation is less than Yoda's -3/2 power self-thinning rule by applying two-stage least regressions while Bégin, et al. (2001) showed Yoda's rule is useful to describe the size-density relationship of Balsam fir stands among different ecological regions.

However, subsequent studies revealed the inconsistency between self-thinning theory and empirical results, and questioned the assumption of constant slope (Zeide 1985, Weller 1987, 1987, Lonsdale 1990). Some argued that the slope should be regarded as a useful variable instead of a constant to describe the ecological differences among stands or species (Zeide 1985, Weller 1987). A number of studies have shown that the slope (b) varies among site qualities (Binkley 1984, Weiskittel, et al. 2009, Zhang, et al. 2013), tree species (e.g.: Douglas-fir, Norway spruce, Southern pine) (Hynynen 1993, Puettmann, et al. 1993, Xue, et al. 1999, Weiskittel, et al. 2009, Comeau, et al. 2010), forest types (pure or mixed) (Reyes-Hernandez, et al. 2013), and silvicultural treatments (VanderSchaaf and Burkhart 2007, 2012). As a result, Reineke's SDI might be questioned for comparing across species and locations if the constant slope, -1.605, is assumed.

Notably, the various statistical procedures of data screening and estimating Reineke's coefficients will affect the values obtained. Their statistical validity has been debated considerably over a period of time. Bi and Turvey (1997) indicated that there is no agreed upon method for selecting appropriate plots. They divided the data points into a specific number of

intervals and selected the point having maximum biomass from each interval for fitting the line. The estimates of the line were obtained by repeating the process several times. Burkhart (2013) selected plots for fitting by computing the relative spacing and Reineke's STR from normal yield tables of fully stocked natural stands and using plot data that were equal to or exceeded stand density as indicated in normal yield tables.

A number of statistical techniques for estimating Reineke's coefficients have been discussed and proposed in several studies (Zhang, et al. 2005, VanderSchaaf and Burkhart 2007). Burkhart (2013) used ordinary least-squares regression (OLS) for estimation of coefficients of MSDR measures. Leduc (1987) indicated that least-squares regression is generally acknowledged the best method to estimate the conditional mean of one variable given a fixed value for another while reduced major axis (RMA) regression is more applicable to interpret the functional relationship between parameters in bivariate data. RMA has been used to establish MSDR lines for three mixed softwood forest types (hemlock-red spruce, spruce-fir, and cedar-black spruce) in the northeastern US (Solomon and Zhang 2002). Bi, et al. (2000) and Bi (2004) adopted stochastic frontier functions (SFF), which originated in economics, to estimate MSDR for even-aged radiata pine stands in Australia. Further, Zhang, et al. (2005) compared six methods, including OLS, RMA, SFF, quantile regression (QR), deterministic frontier function (DFF), and corrected OLS (COLS), for eastern white pine stands. They noted that OLS, RMA, and COLS are sensitive to the screening data while SFF, QR and DFF have the potential to produce the MSDR without predefined criteria of data selection. They recommended SFF as an ideal method because SFF easily produced the statistics for inference on the model coefficients, given that there are no significant departures from underlying distributional assumptions. Another comparison of statistical methods is that of VanderSchaaf and Burkhart (2007). They

used data from a spacing trial to examine the stability of Reineke's coefficients estimates. Among three methods (OLS, first-difference model and the linear mixed-effects model), OLS resulted in the least stable estimates while the mixed model approach produced the most stable estimates.

2.3.2 Competition-density (C-D) rule

C-D rule is another MSDR measure based on diameter, which shares the same concept with Reineke's STR. Kira, et al. (1953) installed a spacing field experiment with cultivated soybeans in five grades of initial planting spacing without applying irrigation and fertilization. They observed a linear relationship between the mean plant dry weight and the number of plants per unit area on a log-log scale and called it "Competition-density (C-D) rule." At each point along growing stages, the product of the mean plant dry weight and the number of plants to a specific power (p) is equal to a constant (K). That is,

$$WN^p = K \quad (3)$$

where

W = mean plant dry weight

N = number of trees per unit area

p = C-D coefficient

K = constant.

The C-D coefficient (p) can be regarded as an expression of intensity of competition. With the intensity of competition among individuals increasing, the value of the C-D coefficient

(p) increases from zero and approaches one. Namely, the C-D coefficient (p) will increase with plant population development (i.e. the C-D coefficient is a function of time). When the value of the C-D coefficient is equal to one, the mean plant dry weight is inversely proportional to number of plants per unit area. Furthermore, if mean plant dry weight is replaced by total plant yield per unit area, the C-D coefficient (p) can be used to determine the optimal planting density for commercial practice (Kira, et al. 1953).

Because the growth of a plant follows a logistic curve, Shinozaki and Kira (1956) modified the Eq. 3 and proposed a logistic form of the C-D rule. Later, the C-D rule was introduced for describing of trees competition and thinning behavior (Tadaki 1963). Mean plant dry weight and C-D coefficient were replaced by quadratic mean diameter and average dominant tree height (Ando 1968, Ando, et al. 1968, Goulding 1972) because dominant tree height can be regarded as a measure of age (reviewed in Sterba 1987, Hasenauer, et al. 1994, Vospernik and Sterba 2014). The expression has been modified as a four-parameter equation:

$$\bar{D}_q = \frac{1}{\alpha_0 \cdot \bar{H}_d^{\alpha_1} \cdot N + \beta_0 \cdot \bar{H}_d^{\beta_1}} \quad (4)$$

where

N = number of trees per unit area

\bar{D}_q = quadratic mean diameter

\bar{H}_d = mean dominant tree height

$\alpha_0, \alpha_1, \beta_0, \beta_1$ = C-D coefficients.

Theoretically, the coefficients of the C-D rule and Reineke's STR are algebraically interchangeable. That is,

$$b = \frac{\alpha_1}{\beta_1} - 1 \quad (5)$$

$$a = \text{Ln}\left(\frac{\beta_0}{\alpha_0} (2\beta_0)^b\right) \quad (6)$$

where all symbols have been defined above and a, b are Reineke's coefficients. This implies that the coefficients of Reineke's STR can be estimated from the four parameter C-D equation.

Vospernik and Sterba (2014) indicated that the four-parameter C-D equation could be reduced to a three-parameter equation (Eq.7) by substituting one parameter β_1 with the slope (b), -1.605 in Reineke's STR. The three-parameter equation is more robust (Vospernik and Sterba 2014).

$$\bar{D}_q = \frac{1}{\alpha_0 \cdot \bar{H}_d^{\alpha_1} \cdot N + \beta_0 \cdot \bar{H}_d^{-\frac{\alpha_1}{0.605}}} \quad (7)$$

Vospernik and Sterba (2014) showed that for Norway spruce, the slope obtained from the four-parameter C-D equation is similar to that of Reineke's STR, -1.605. Due to the inclusion of three stand variables (quadratic mean diameter, stand density and dominant tree height), the C-D rule is more applicable than Reineke's STR (Vospernik and Sterba 2014).

2.3.3 Nilson's sparsity index

Nilson's sparsity index (Nilson 2006) focuses on the average distance between trees. In the case of regular square spacing, the stand sparsity is the square root of number of meter square in a hectare divided by number of trees per hectare; this equation is similar to the relative spacing index. Nilson (2006) assumed a linear relationship between stand sparsity (L) and quadratic mean diameter, that is,

$$L = \sqrt{\frac{10000}{N}} \quad (8)$$

$$L = c_0 + c_1 \cdot \bar{D}_q \quad (9)$$

where

L = stand sparsity

N = number of trees per unit area

\bar{D}_q = quadratic mean diameter

c_0, c_1 = Nilson's coefficients.

For a given a species, each stand will approach the MSDR line on the L-D plane. By combining Eqs. 8 and 9, Zeide (2010) showed that Nilson's equation could be represented in logarithmic form, which is similar to Reineke's equation:

$$\ln N = -2 \ln \left(\bar{D}_q + \frac{c_0}{c_1} \right) + \ln \left(\frac{100}{c_1} \right)^2 \quad (10)$$

Thus, the derivative of Reineke's equation will be

$$\frac{d(\text{Ln}N)}{d(\text{Ln}\bar{D}_q)} = b \quad (11)$$

and the derivative of Nilson's equation is

$$\frac{d(\text{Ln}N)}{d\left(\text{Ln}\left(\bar{D}_q + \frac{c_0}{c_1}\right)\right)} = -2 \quad (12)$$

For comparison, Zeide (2010) multiplied both sides by $d(\text{Ln}\left(\bar{D}_q + \frac{c_0}{c_1}\right))/d(\text{Ln}\bar{D}_q)$ in Eq. 12:

$$\frac{d(\text{Ln}N)}{d(\text{Ln}\bar{D}_q)} = -2 \frac{d\left(\text{Ln}\left(\bar{D}_q + \frac{c_0}{c_1}\right)\right)}{d(\text{Ln}\bar{D}_q)} = -\frac{2\bar{D}_q}{\bar{D}_q + \frac{c_0}{c_1}} \quad (13)$$

Zeide (2010) indicated that unlike the constant slope (b) in Reineke's equation, the slope computed from Nilson's equation ranges from 0 to -2, which is more flexible. Another strength of Nilson's sparsity index is that the dependent variable changes in the same direction with the independent variable of length dimension (Nilson 2006).

However, despite the advantages, Zeide (2010) pointed out the deficiency of Nilson's sparsity index. When the number of trees continuously declines, the influence of quadratic mean diameter on the number of trees vanishes. That is, when stand sparsity becomes larger, quadratic mean diameter remains nearly constant, which means c_0 tends to infinity. Gadow, et al. (2014) found Nilson's assumption of a linear relationship for a *Pinus patula* Correlated curve trend (CCT) experiment wasn't valid when mortality increased but not from intraspecific competition.

2.4 Spacing experiments and miniature scale trials

2.4.1 Initial planting density and the common experimental designs

Initial planting density has a decisive impact on tree growth, stand development and yields. Tree spacing is one of the most important decisions that have to be made at the time of plantation establishment. Initial planting density affects the schedule of intermediate silvicultural treatments and the quality and quantity of anticipated wood production (Zhang, et al. 2002, Amateis and Burkhart 2012). Accordingly, to achieve the management objective, an appropriate initial planting density is essential and indispensable.

The effects of initial planting density on stand attributes have been considerably discussed and examined for various species, locations and experimental designs. Generally, in the absence of thinning treatment, average stem diameter, height and stem volume increase with decreasing initial planting density whereas the total basal area, volume and biomass increase with increasing initial planting density until the stands reach its carrying capacity (Kerr 2003, Amateis and Burkhart 2012, Antón-Fernández, et al. 2012). DeBell, et al. (1989) showed that despite the difference in stockability between Hawaii and South Carolina, the pattern of diameter or height growth among different initial planting density are similar. VanderSchaaf and Burkhart (2012) indicated that the quadratic mean diameter at the onset of self-thinning increases with a reduction of initial planting density for loblolly pine observations in a spacing trial. MacFarlane, et al. (2000) and Antón-Fernández, et al. (2011) found that height growth of dominant trees is dependent on initial planting density for loblolly pine, and they suggested site index is confounded with stand density. Schönau and Coetzee (1989) reviewed several studies for eucalyptus plantations and concluded that for initial planting density between 1000 and 2000

trees per hectare, the mean tree height increases with decreasing planting density but the top height doesn't. However, Scott, et al. (1998) examined coastal Douglas-fir spacing experiments in western Washington and Oregon and indicated that early tree growth at closer spacings is faster than at wider spacings (i.e.: larger average height and diameter in close spacings). They didn't have a firm explanation for this result, however. Burkhart and Tomé (2012) indicated that it is difficult to assess the impact of stand density on height growth without designed experiments that are measured over a long time periods because stand density is confounded with site factors.

Over the years, several different kinds of spacing experiments have been established. There are five common experimental designs: randomized block design, Latin square design, correlated curve trend (CCT) design, Nelder systematic design, and plaid design.

The use of randomized block design is found in many spacing experiments (e.g.: Bernardo, et al. 1998, Scott, et al. 1998, Pretzsch and Biber 2005, Cardoso, et al. 2013). One of the advantages of this design is that if the block-treatment additivity assumption holds, it provides unbiased estimates of mean and of the variance of treatment effects. Another advantage is that if the random errors are assumed independent and normally distributed, several statistical methods, such as ANOVA, hypothesis testing, and regression, can be used for analysis. There are two possible ways to implement this design: one is various plot sizes with the constant number of trees; conversely, the other one is fixed plot size with various numbers of trees (Amateis, et al. 1988). One possible type of fixed plot size design was shown in Fig. 2(a). By using various plot sizes, number of trees can be controlled but the different unequal-sized plots are hard to fit into a compact block; by using various number of trees, a fixed plot size may have an unnecessarily large number of trees at close spacing. For the randomized block design, the

disadvantage is that large block sizes are difficult to install and replicate on relatively uniform sites.

Latin square design is another widely-used experimental design (e.g.: Whitesell 1970, Okojie, et al. 1988, Moore, et al. 2009). The assumption of normally distributed random errors and of block-treatment additivity in Latin square design are the same as for randomized block designs. In the randomized block design, there is one block factor, while in the Latin square design, there are two block factors and the factors are crossed. The block factors are usually environmental gradients, such as the soil type, soil fertility, or slope. Latin square designs are interlocked block-wise randomization. As shown in Fig. 2(b), the number of treatments should be the same as the number of row blocks and the number of column blocks. Compared to randomized block designs, the advantages of Latin square design are that more variation can be controlled and all blocks fit together into a compact square. The disadvantage of this design lies in the number of treatments. If the number of treatments is less than five, the random error's degrees of freedom will be too small. Although the random error's degrees of freedom can be increased by repeating squares, in practice, it will be difficult to control for uniform sites among squares.

The correlated curved trend (CCT) design was conceived by O'Connor (1935). CCT has been well-known for spacing studies, especially those in South Africa (e.g.: van Laar 1982, Strub and Bredenkamp 1985, Bredenkamp 1987). O'Connor (1935) aimed to design a spacing experiment with a limited number of plots that can yield comprehensive information for the effect of growing space and thinning treatment on trees. A CCT experiment can be divided into two sections: unthinned plots and thinned plots, as shown in Fig 2(c). The unthinned plots are referred to as the basic series, which provide information about the growth of thinned plots.

Planting density among the unthinned plots is initially equal and much denser than the desired stand density. Based on the different desired stand density, each unthinned plot will be “thinned” progressively before the onset of intraspecific competition. For the thinned plots, the various thinning treatments are applied, with timing and intensity depending on the interests of the studies. In practice, it may take more than six years to install the whole CCT design, and the investment on manpower is tremendous. For the CCT design, one of the shortcomings is to determine the onset of competition. Some criteria have been suggested, such as comparing rates of diameter growth (van Laar 1978) or comparing DBH between plots (Omule 1984), but there is no standard criterion. Another shortcoming is the selection of trees to be removed. Bredenkamp (1988) indicated that a random selection might result in an undesired spatial arrangement. In addition, Schönau and Coetzee (1989) pointed out the controversy of the CCT design because the results and analyses of growth performance can draw two completely opposite conclusions from the same data.

To overcome some disadvantages of randomized block designs, Nelder (1962) developed a systematic experimental design and Bleasdale (1967) provided all steps of calculation for such installations. Type I(a) of Nelder’s design is broadly used in spacing studies (e.g.: Hummel 2000, Kerr 2003, Kuehne, et al. 2013, Vanclay, et al. 2013). In this type of design, each tree (or a grid) is planted at the intersection of concentric circles (or arcs) and spokes. The spokes radiate out from the center of the circles, as shown in Fig. 2(d). On a top view, the arrangement of trees is like the spoked wheels. The constant number of trees are equally-spaced at each circle (i.e.: the same distance between neighboring trees at each circle). At each spoke, the distance between neighboring trees systematically increases at a fixed rate ρ from the center outward, namely:

$$r_n = r_1 \rho^n \quad (14)$$

where

r_n = the radius of n^{th} circle (arc)

r_1 = the radius of the innermost circle (arc)

ρ = radius increasing rate

n = the circle's number.

Accordingly, the initial planting density increases with the increase of radius of the circle. Based on different locations and research budgets, the design could be fit into a circular, semicircular or rectangular block. However, the key problem of this design is to decide the value of ρ . Nelder (1962) suggested the value should be less than 1.1. Otherwise, the results might be biased due to a shelter effect or exploitation of additional growing space by trees in the higher density (reviewed by Schönau and Coetzee 1989). Furthermore, one of the disadvantages is that the real growing space or the optimum spacing is hard to estimate or determine. Due to the invalid assumption of normally distributed random errors, hypothesis testing or ANOVA can't be used appropriately. However, as Amateis, et al. (1988) indicated, Nelder's design is often efficient for acquiring data for performing regression analyses.

The plaid design developed by Lin and Morse (1975) offers an agreeable compromise between the statistical advantages of certain experimental designs, such as Nelder's design, and the practical advantages of others (Burkhart 2002). The plaid design is well-known for the loblolly pine spacing trials in the Southeastern US (e.g.: Amateis, et al. 2009, Amateis and Burkhart 2012). This design is nonsystematic, allowing the spacing to be varied in two dimensions on a factorial basis with a fixed number of trees in each plot. Details of this design will be discussed in Chapter 3. In this plaid design, the unequal-sized plots are fit in a compact

block. Although the unequal-sized plots will create difficulties with the error variance structure, this design, in practice, makes efficient use of land area and plant material. Amateis, et al. (1988) indicated this consideration is important for long-term forestry spacing studies due to the tremendous maintenance and remeasurement costs. Furthermore, the nonsystematic arrangement provides unbiased estimates of the means and permits to use conventional analysis of variance techniques. Indeed, the plaid design has many of the advantages associated with randomized block designs and it doesn't have the shortcomings of statistical analyses of Nelder's systematic design.

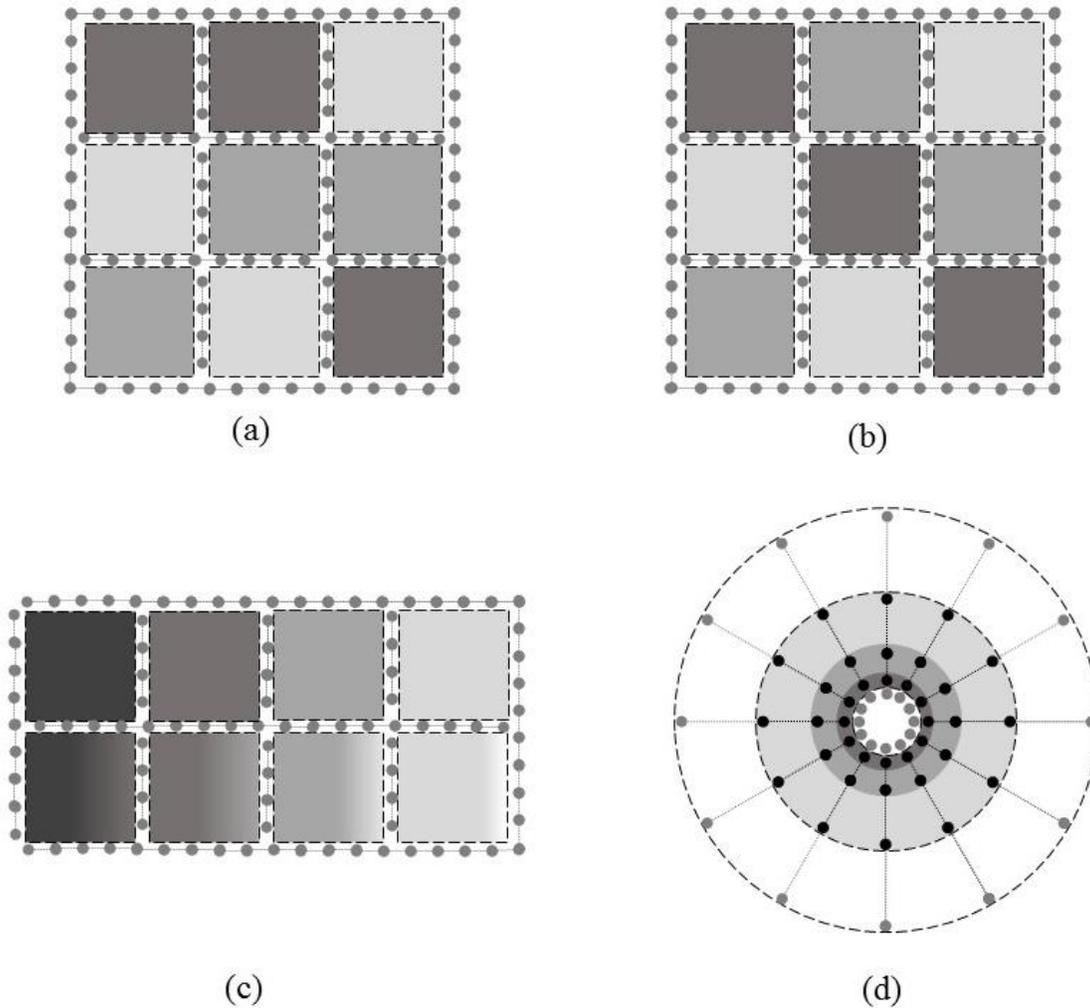


Figure 2 Examples of four types experimental designs. Black dots (●) are measurement trees. Grey dots (●) are guard trees. The fill color represents the stand density of each treatment (plot). The denser the darker, the sparser the lighter. (a) is a randomized block design with 3 columned blocks (1 block factor), and 3 treatments in each block. (b) is a 3×3 Latin square design, with 2 block factors (row and column) and 3 treatments in each block. (c) is a correlated curve trend (CCT) design, with unthinned plots (first row) and thinned plots (second row). The color gradient of the plot at second row represents thinning applied. (d) is a Nelder's type 1a design, with 3 concentric circles (arcs) and 12 spokes.

2.4.2 Microcosms and miniature scale trials

Establishment and maintenance of conventional field experiments are costly investments over an extended period of time. It may take forest researchers several decades on data collection, analyses and reporting, which makes it difficult to provide timely information for forest management. Uncontrollable and unpredictable disturbances can compromise results, increase experimental errors and even collapse trial installations. For some regions, in addition, it is hard to control homogeneity of sites when installing replications of experiments. As a result, small scale experiments, so called microcosms or miniature scale trials, have been implemented to overcome the shortcomings of conventional field experiments. This cost-effective experimental tool has potential to reduce the temporal and spatial scale of field experiments to a manageable level.

Microcosms can be referred to as simplified and isolated ecosystems under controlled conditions. A microcosm can be a closed or open, terrestrial or aquatic system. This experimental tool speeds up the research and its high replicability and controllability is beneficial to researchers (Carpenter 1996). Microcosms have been widely implemented and discussed in many disciplines over a long period of time (Daehler and Strong 1996), including community and ecosystem ecology, evolutionary ecology, ecotoxicology, molecular biology, and physiology (e.g.: Robinson and Dickerson 1987, Naeem, et al. 1994, Wui, et al. 2002, Yoshida, et al. 2003, Jiang and Patel 2008, He, et al. 2015). Amateis, et al. (2003b) indicated that microcosm experiments saved travel time to plot sites and security costs. Notably, despite several advantages of microcosms, the rapid results from microcosms need to be cautiously interpreted and extrapolated when predicting for the full scale ecosystems (Carpenter 1999). Microcosms aren't used to mimic the full complexity of nature (Kareiva 1994). Integrating results from

multiple-scale experiments might, however, provide a broader picture of an ecosystem process or dynamics (Carpenter 1996, Drenner and Mazumder 1999).

Some microcosms have been used for forest soil nutrients and tree physiology studies (Groninger, et al. 1996, Watt, et al. 2005, Davis, et al. 2007, Fernández-Delgado Juárez, et al. 2015) while other microcosms have been designed for forest growth research (e.g.: Smith and Hann 1984, Avila 1993). An example is the loblolly pine miniature scale spacing trial installed on the Virginia Tech campus. This miniature scale spacing trial, 1/16 to operational spacing trials previously established, has been proven a useful experimental tool to simulate stand development. Detailed information of these spacing trials' design will be provided in Chapter 3. Sharma, et al. (2003) applied similarity theory to examine stand development at both full and miniature scales and found that the scaling function is useful in the forest system studied. Amateis, et al. (2003a, 2003b) indicated that important stand characteristics, height and diameter, associated with forest productivity developed similarly at both miniature and operational scale spacing trials. Further, stand development processes for loblolly pine over 16 years at an operational spacing trial corresponded roughly to the same development over 4 years at a miniature scale spacing trial (Amateis, et al. 2003a, 2003b). Sharma, et al. (2007) compared the predictive accuracy of two taper equations by using stem analysis data from close- and conventionally-spaced trials. They reported that the segmented polynomial taper equation (Max and Burkhart 1976) was better than the dimensionally compatible taper equation (Sharma and Oderwald 2001) in scaling the taper relationship. Russell, et al. (2009) observed that the trends of biomass partitioning at both spacing trial types were similar and pointed out the effect of spacing on the allometry of loblolly pine.

Notably, the above studies of miniature scale spacing trials are mainly based on the principles of similarity theory. By reviewing several applications of similarity theory for vegetation community study, Feoli and Orloci (2011) concluded that similarity theory can be a general theory of plant community development. Similarity theory is referred to as a linkage between the physical-chemical environment and plant communities at different scales of generalization (Feoli and Orloci 2011). The phenomenon or behavior of the desired system can be measured and estimated by the corresponding characters or variables from another similar system. Thus, it could be useful to compare and project stand behavior or dynamic occurring at two different scales of stands.

Chapter 3

Materials and Methods

3.1 Spacing trials

3.1.1 Operational trials

Measurements were obtained from a loblolly pine spacing trial that employed the plaid nonsystematic design from Lin and Morse (1975). The spacing trial was established in 1983 and maintained by Forest Modeling Research Cooperative at Virginia Polytechnic Institute and State University. There were four cutover sites, two in the upper Coastal Plain and two in the Piedmont. One in the Coastal Plain was in North Carolina, whereas other sites were in Virginia. Each site received an operational chop and burn site preparation treatment before planting. Three nearly contiguous and compact factorial blocks were established at each site. In each block, a spacing factor(F) of 1.2 m (4 ft) was applied. Four levels of the factor were chosen (1F, 1.5F, 2F, and 3F) and randomly assigned to row and column positions. Therefore, there are sixteen initial planting configurations in each block: four square plots (1.2×1.2 , 1.8×1.8 , 2.4×2.4 , 3.6×3.6 m), and 12 rectangular plots (1.2×1.8 , 1.2×2.4 , 1.2×3.6 , 1.8×1.2 , 1.8×2.4 , 1.8×3.6 , 2.4×1.2 , 2.4×1.8 , 2.4×3.6 , 3.6×1.2 , 3.6×1.8 , 3.6×2.4 m). There were 49 trees planted in each plot, but the size of each plot varied by planting density with the 16 plots fitting together in a compact block. Each block occupied approximately 1 hectare. An example of plot arrangement and planting density in each block has been shown in Fig. 3.

In each plot, an equal number of seedlings (49 seedlings) were planted in seven rows and seven columns and measured annually. To reduce the effect from adjacent plots, each plot was separated by two rows of guard trees, three rows and columns guard trees surrounded each block.

Initial planting density varied from 747 (trees/hectare) to 6,727 (trees/hectare). In total, there were 192 plots (4 sites \times 3 blocks \times 16 plots).

The loblolly pine seedlings were 1-0 genetically improved stock from the same nursery. During the first year, the dead seedlings were replaced by seedlings planted on the site. Except for chemical herbicides controlling both competing woody and herbaceous vegetation in the first three years, no management treatments were applied. Groundline diameter (GLD) was measured at age 1-5 and diameter at breast height (DBH) was annually recorded for ages five through age 25. Total height was measured annually for ages 1-10 and biennially for ages 12-25. Through age 10, height to live crown, crown width between rows, crown width within rows, and the maximum crown width were recorded annually. After age 10, crown height was measured biennially. In addition, the health condition (e.g.: disease, insect, other damage) of each tree was examined and assigned a code. Due to the damage of plots by ice storms or other serious disturbances after age 18, only the measurements from age 5-18 were selected for analysis. Quadratic mean diameter, average dominant tree height, numbers of trees per unit area and BA per unit area were computed.

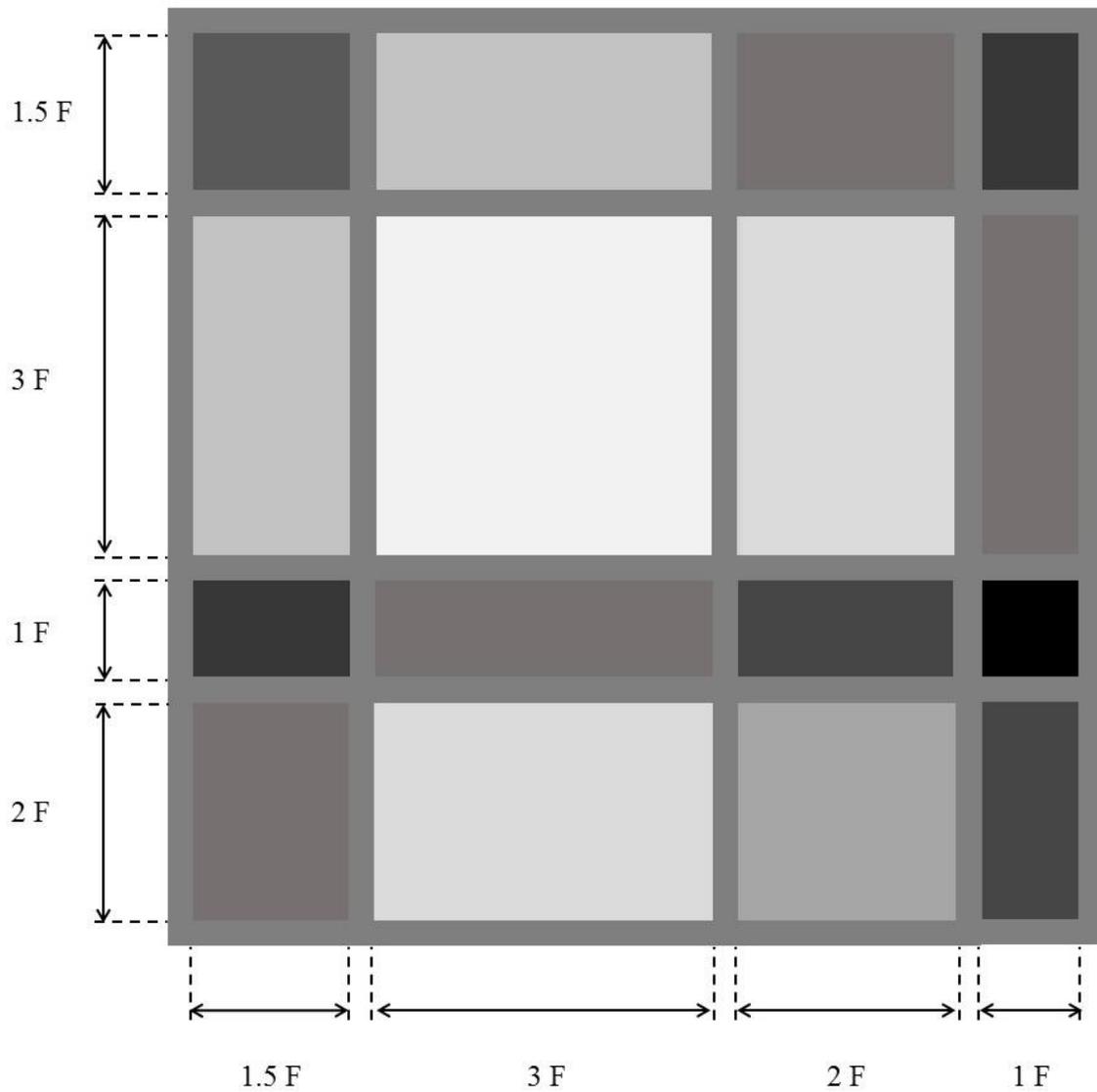


Figure 3 An example of a compact block with sixteen plots. Four levels of the spacing factor were chosen (1F, 1.5F, 2F, and 3F) and randomly assigned to row and column positions. The fill color represents the initial planting density of each plot. The denser the darker, the sparser the lighter. Grey stripes between plots represent the guard trees.

3.1.2 Miniature scale trials

The miniature scale trials, or microcosms, were established on Virginia Polytechnic Institute and State University campus in the spring of 1989 and 1998. The experimental design was the same as the operational trials while the spacing factor(F) was 7.6 cm (3 inch), that is, 1/16 of the operational trials. The four levels of the factor were 7.6 cm, 11.4 cm, 15.2 cm, and 22.8 cm. In each block (installation), 49 seedlings were planted in each plot with two rows of guard trees separating the neighboring plots. The seeds were germinated in a greenhouse and then planted as germinals in May, 1989, of the first replicate and May, 1998, for the second. Measurements, including groundline diameters (GLD), height to live crown, total height and tree condition (alive or dead), were obtained from July to October in 1989 and from April to October in 1990, 1991 and 1992. The first installation was terminated in 1992 and the second one was installed at the same site to assure the site conditions and preparation were as uniform as possible. In the second installation, groundline diameters and total heights were recorded annually over 5 years. After termination of the second installation in October 2003, data from 32 plots (2 installations \times 16 plots) were available. Measurements of the first installation were collected at approximately 30-day intervals while those of the second installation were collected at one-year intervals. Therefore, to make data consistent between the two installations, only the measurements recorded at the end of each growing season were used in this study. The data of the two installations were combined for further analysis. Quadratic mean groundline diameter, average dominant seedling height, numbers of seedlings per unit area and BA at groundline (BA_g) per unit area were computed.

3.2 Carrying capacity estimation

Maximum stand BA that is sustainable over a period of time can be regarded as a measure of carrying capacity. MSDR measures can be converted to BA per unit area to obtain estimates of maximum stand BA carrying capacity. Estimates from the various MSDR measures were compared with estimates from an equation fitted to the maximum stand BA observed on the operational spacing trial plots using the Chapman-Richards growth equation.

3.2.1 Maximum stand BA

Chapman-Richards (C-R) growth equation (Richards 1959, Chapman 1961) is a generalization of Von Bertalanffy's (1938) model. The C-R growth equation has been used in BA growth studies (e.g.: Radtke and Burkhardt 1999, Gyawali and Burkhardt 2015).

The maximum stand BA observed on the spacing trial plots was estimated by fitting the C-R equation using a nonlinear quantile regression (nlqr) method proposed by Koenker and Park (1996).

$$G_{max} = \gamma_1 \cdot (1 - e^{\gamma_2 \cdot t})^{\gamma_3} \quad (15)$$

where

G_{max} = maximum stand BA (m²/ha)

t = stand age (yr)

$\gamma_1, \gamma_2, \gamma_3$ = Chapman-Richards coefficients.

In Eq. 15, the coefficient γ_1 represents the asymptote of the maximum stand BA trajectory, the coefficient γ_2 represents the rate of growth and γ_3 is a shape coefficient. The nlqr process was implemented in the quantreg package in R.

3.2.2 Implied maximum stand BA

The definition of BA per unit area is as following:

$$G = N \cdot \bar{D}_q^2 \cdot g \quad (16)$$

where

G = stand BA (m²/ha)

\bar{D}_q = quadratic mean diameter (cm)

N = number of trees per hectare

g = a constant, equal to $\pi/40000 \approx 0.00007854$.

Three diameter-based MSDR measures were chosen: Reineke's STR (Reineke 1933), C-D rule (Kira, et al. 1953), and Nilson's sparsity index (Nilson 2006). Each of the measures were converted to BA per unit area to obtain estimates of maximum stand BA carrying capacity, denoted implied maximum stand BA.

For Reineke's STR, N is a function of \bar{D}_q (Eq. 1), denoted $N(\bar{D}_q)$. The implied maximum stand BA can be obtained by calculating N in Eq. 16 from $N(\bar{D}_q)$ in Reineke's STR, namely:

$$G_{R \max} = (e^a \cdot \bar{D}_q^b) \cdot \bar{D}_q^2 \cdot g = e^a \cdot \bar{D}_q^{b+2} \cdot g \quad (17)$$

where

$G_{R \max}$ = Implied maximum stand BA computed from Reineke's STR

; other symbols have been defined above.

For the C-D rule, Sterba (1987) showed that stand BA can be computed from Eq. 4, that is:

$$G_{CD} = N \cdot \left(\frac{1}{\alpha_0 \cdot \bar{H}_d^{\alpha_1} \cdot N + \beta_0 \cdot \bar{H}_d^{\beta_1}} \right)^2 \cdot g \quad (18)$$

where

G_{CD} = Implied stand BA computed from C-D rule

; other symbols have been defined above. Further, Sterba (1987) set the first derivative dG_{CD}/dN equal to zero and solved the equation to get the implied maximum stand BA:

$$G_{CD \max} = \frac{\bar{H}_d^{-(\alpha_1 + \beta_1)}}{4 \cdot \alpha_0 \cdot \beta_0} \cdot g \quad (19)$$

where

$G_{CD \max}$ = Implied maximum stand BA computed from C-D rule

For Nilson's sparsity index, the calculation of implied maximum stand BA is similar to Reineke's STR, that is:

$$G_{N \max} = \left(\frac{100}{c_0 + c_1 \cdot \bar{D}_q} \right)^2 \cdot \bar{D}_q^2 \cdot g \quad (20)$$

where

$G_{N \max}$ = Implied maximum stand BA computed from Nilson's sparsity index

; other symbols have been defined above. A list of formulas for computing implied maximum stand BA from three MSDR measures is shown in Table 1.

Reineke's STR was estimated with quantile regression (quantile=0.99), as were the C-D rule coefficients (quantile=0.99) and Nilson's sparsity index (quantile=0.01) using the package `quantreg` in R.

Table 1 Equations of implied maximum stand BA computed from diameter-based MSDR measures. (N =number of trees per ha; \bar{D}_q =quadratic mean diameter (cm); \bar{H}_d =mean dominant tree height (m); G =basal area (m²/ha); G_{max} =maximum stand BA (m²/ha); e =exponential constant; g = a constant, equal to $\pi \backslash 40000 \approx 0.00007854$; other symbols= coefficients)

	Number of trees per ha (N)	Implied Max. BA
Reineke's STR	$N = e^a \cdot \bar{D}_q^b$	$G_{R\ max} = e^a \cdot \bar{D}_q^{b+2} \cdot g$
C-D rule	$N = \frac{\bar{D}_q^{-1} - \beta_0 \cdot \bar{H}_d^{\beta_1}}{\alpha_0 \cdot \bar{H}_d^{\alpha_1}}$	$G_{CD\ max} = \frac{\bar{H}_d^{-(\alpha_1+\beta_1)}}{4 \cdot \alpha_0 \cdot \beta_0} \cdot g$
Nilson's sparsity index	$N = \left(\frac{100}{c_0 + c_1 \cdot \bar{D}_q} \right)^2$	$G_{N\ max} = \left(\frac{100}{c_0 + c_1 \cdot \bar{D}_q} \right)^2 \cdot \bar{D}_q^2 \cdot g$

3.3 Effect of different physiographic regions on carrying capacity

To evaluate the effect of physiographic regions on carrying capacity, the dataset of the operational spacing plots was divided into two sub-datasets: Piedmont and Coastal Plain, with six blocks in each region. The coefficients of three MSDR measures were estimated for each region by methods previously described. Reineke's assumption of a constant slope was examined and compared on the basis of stand BA carrying capacity. In addition, the occurrence of self-thinning among different planting density was determined in each region.

3.3.1 Full and reduced model of Reineke's STR

The full model is based on the assumption of different slopes between the two regions. An indicator variable (x_r) and an interaction term ($\text{Ln}\bar{D}_q \cdot x_r$) are added in Reineke's equation (Eq. 1), that is:

$$\text{Ln}N = a + b \cdot \text{Ln}\bar{D}_q + c \cdot x_r + d \cdot (\text{Ln}\bar{D}_q \cdot x_r) \quad (21)$$

where

Ln = natural logarithm

N = number of trees per hectare

\bar{D}_q = quadratic mean diameter (cm)

x_r = 1, if plots in the Piedmont; 0, if plots in the Coastal Plain

a, b, c, d = coefficients.

The reduced model is assumed to have a common slope for the two regions (i.e.: no interaction term). The equation form is:

$$\text{LnN} = a' + b' \cdot \text{Ln}\bar{D}_q + c' \cdot x_r \quad (22)$$

where

a', b', c' = coefficients

; other symbols are the same as those in Eq. 21. Two hypotheses are examined:

- (I) H_0 : The assumption of a common slope between two regions is valid.
 H_a : The assumption of a common slope between two regions isn't valid
- (II) H_0 : The self-thinning lines between two regions aren't different
 H_a : The self-thinning lines between two regions are different

3.3.2 Occurrence of self-thinning

VanderSchaaf and Burkhart (2008) developed a reduced segmented regression model to project diameter-density trajectory on a log-log scale, that is,

$$\text{LnN} = d_1 \cdot S_1 + \left(d_1 + d_2 \cdot [\text{Ln}\bar{D}_q - T]^2 \right) \cdot S_2 \quad (23)$$

where

S_1, S_2 = indicator variables for stand dynamics

T = joint point

d_1, d_2 = coefficients.

$S_1 = 1$ if the stand is within the density-independent mortality stage and 0 otherwise; $S_2 = 1$ if the stand is within the competition-induced mortality stage and 0 otherwise. T is $\text{Ln}\bar{D}_q$ at occurrence of self-thinning. The corresponding cumulative mortality was determined. The equation of cumulative mortality is:

$$M = \frac{N_0 - N_t}{N_0} \cdot 100\% \quad (24)$$

where

M = cumulative mortality (%)

N_0 = initial planting density (stems/ha)

N_t = number of trees per hectare at age t .

3.4 Stand Competition in the miniature scale spacing trial

Three diameter-based MSDR measures were used and the occurrence of self-thinning was calculated to describe the behavior of stand competition in the miniature scale spacing trial. The method of estimation of coefficients in the MSDR measures is the same as that used for the operational spacing trial. The trends of diameter-density trajectories and BA-age trajectories were examined and compared with those of the operational spacing trial.

Chapter 4

Results and Discussion

4.1 Carrying capacity estimation

4.1.1 Maximum stand BA

An estimate of maximum stand BA of 63.2 (m²/ha) was obtained from the C-R equation coefficient γ_1 (Eq. 15). By age 18, the maximum stand BA was estimated at 58.2 (m²/ha). The C-R equation was fitted with the data in four square plots separately (1.2 × 1.2, 1.8 × 1.8, 2.4 × 2.4, 3.6 × 3.6 m) at the 0.99 quantile to examine the effect of initial planting density on the maximum stand BA. The trend of maximum stand BA growth at each square plot was similar to that of the overall maximum stand BA growth. As shown in Fig. 4, maximum stand BA was larger at the higher initial planting densities (i.e.: narrow spacings) than that at the lower initial planting densities (i.e.: wide spacings). At age 18, the maximum stand BA for the 1.2 × 1.2 m plot (i.e.: 6727 trees/ha) was about double that for the 3.6 × 3.6 m plot (i.e.:747 trees/ha). Higher total BA production was produced at higher initial planting density plots. This phenomenon was also found by Amateis and Burkhart (2012), who indicated that the high initial planting density plots yielded more total volume/ biomass per unit area. By comparing the maximum stand BA in four square plots, we see that the overall maximum stand BA trajectory was closest to the maximum stand BA trajectory at the 1.2 × 1.2 m plot (the closest spacing plot). Two trajectories became closer with an increase of age while the maximum stand BA at the 1.2 × 1.2 m plots remained higher than the overall maximum stand BA through age 18.

However, when the stand age was extended to years 25 and the same fitting procedure was implemented, it showed that the estimate of overall maximum stand BA at age 25 would

drop to near 55 (m^2/ha), which was lower than the maximum stand BA discussed above (Fig. 5). A similar pattern of lower stand BA was found in the 1.8×1.8 m spacing while for the 1.2×1.2 m, 2.4×2.4 m and 3.6×3.6 m spacings, the maximum stand BA estimated at age 25 was higher than that at age 18. One possible explanation of this phenomenon is that disturbances damaged some highly productive plots, which dragged down the overall cumulative stand BA after age 20. Another possibility is that the close spacing plots over shot carrying capacity at the early stage and subsequent intraspecific competition caused a rapid decline of cumulative stand BA. Notably, as shown in Fig. 5, the second explanation isn't consistent with findings in the 1.2×1.2 m spacing, which exhibited non-decreasing maximum stand BA trajectory through age 25. However, in fact, the cumulative mortality in the 1.2×1.2 m spacing was more than 80% at age 25 and more than half of the plots collapsed after age 18. In other words, the data after age 18 had little or even no influence on the fitted curve. In Fig. 5, there were no data points along with the fitted curve after age 18. In short,

Thus, in this study, the confounding effect of these uncontrollable factors would make the estimates obtained after age 20 unreliable for representing the overall stand BA carrying capacity for loblolly pine. That is, stand age close to 20 could be an appropriate timing to determine the overall stand BA carrying capacity. The timing of BA decline was consistent with Buford's report (1991), whose data were from a loblolly pine randomized block spacing experiment. Buford (1991) indicated that at age 20, the closest spacing began to fall below the others in BA per hectare. Also, Matney and Sullivan (1982) found that at high density plots, stand BA peaked between the ages of 15 and 20 for loblolly pine. Furthermore, from Fig. 5, it showed that the maximum stand BA trajectory of each plot wouldn't converge at age 25, which was different from the average stand BA trajectory reported by Antón-Fernández, et al. (2012) using the same

dataset. It still followed that higher total BA production was produced at higher initial planting density plots.

Hasenauer, et al. (1997) reported that the maximum stand BA was 48.7 (m²/ha) for 186 unthinned plots in operational plantings of loblolly pine in the southeastern US, which was lower than the stand BA carrying capacity obtained in our study. However, the stand BA was measured between the ages of 20-37 and the initial planting density ranged from 667 to 2520 (trees/ha). Also, the operational plantings contained some hardwood stems, which may account for the lower maximum stand BA for pine. The lower maximum stand BA obtained by Hasenauer, et al. (1997) was close to our result in the wider spacing plots (2.4 × 2.4 m and 3.6 × 3.6 m) at age 25. Notably, in addition to the maximum stand BA, the mean stand BA of Hasenauer, et al. (1997) was lower than that in this spacing trial at age 25 (obtained from the same dataset by Antón-Fernández, et al. 2012). Bailey and Ware (1983) reported maximum stand BA of 58.7 (m²/ha) for 352 natural even-aged loblolly pine plots in Georgia, which was close to what we obtained. However, in their study, only 20 % of plots were unthinned, whose stand age ranged from 18 to 103. Williams (1996) reported a maximum stand BA in northern Louisiana of 42.7 (m²/ha). The maximum stand BA was close to the wider spacing plots in this study. For a further comparison of the stand BA carrying capacity for loblolly pine, some assumptions need to be made because most studies reported only the average stand BA instead of the maximum stand BA. If we assume: (I) the stand BA follows a normal distribution; (II) the variance ($\hat{\sigma}^2$) of the distribution is a constant for loblolly pine; (III) The mean stand BA is 47 (m²/ha) at age 18 (obtained from the same dataset by Antón-Fernández, et al. 2012), then the variance ($\hat{\sigma}^2$) would be:

$$\hat{\sigma} = \frac{|G_{\max} - \bar{G}|}{Z_{0.99}} = \frac{|58.2 - 47|}{2.33} = 4.8 \quad (25)$$

where

\bar{G} = mean stand BA (m^2/ha)

G_{max} = maximum stand BA (m^2/ha)

$Z_{0.99}$ = the 99th quantile in a standard normal distribution.

Harms, et al. (2000) observed that the mean stand BA of the 1.8×1.8 m unthinned spacings in South Carolina was near 43.2 (m^2/ha) at age 20. Based on our assumptions, the maximum stand BA (quantile=0.99) would be approximate to 54.4 (m^2/ha), which was close to our result from the 1.8×1.8 m spacing. However, Harms, et al. (2000) indicated that the mean stand BA of the 1.8×1.8 m unthinned spacings in Hawaii was 63.9 (m^2/ha) at age 20 and increased to 103.1 (m^2/ha) at age 34. It meant that the stand BA carrying capacity in Hawaii was 196% more than that in the southeastern US. Similarly, Cardoso, et al. (2013) reported that in southern Brazil, the mean stand BA for loblolly pine reached 58.7 (m^2/ha) at age 12. Therefore, plantations in different regions had different maximum stand BA. One possible explanation is that the nutrient (nitrogen levels) or water availability was different among regions. The effect of physiographic regions on the stand BA carrying capacity will be discussed in detail later.

In short, an initial planting density experiment was helpful to examine the effect of planting density on the maximum stand BA. The stands with high initial planting density (e.g.: 1.2×1.2 m spacing) approached the stand BA carrying capacity sooner than the stands with lower initial planting density (e.g.: 2.4×2.4 m spacing). The stand BA carrying capacity varies among different regions. This suggested that the stand BA carrying capacity could be estimated from high initial planting density stands in a relatively short period of time so that the risk of damages and the costs of experiments could be reduced.

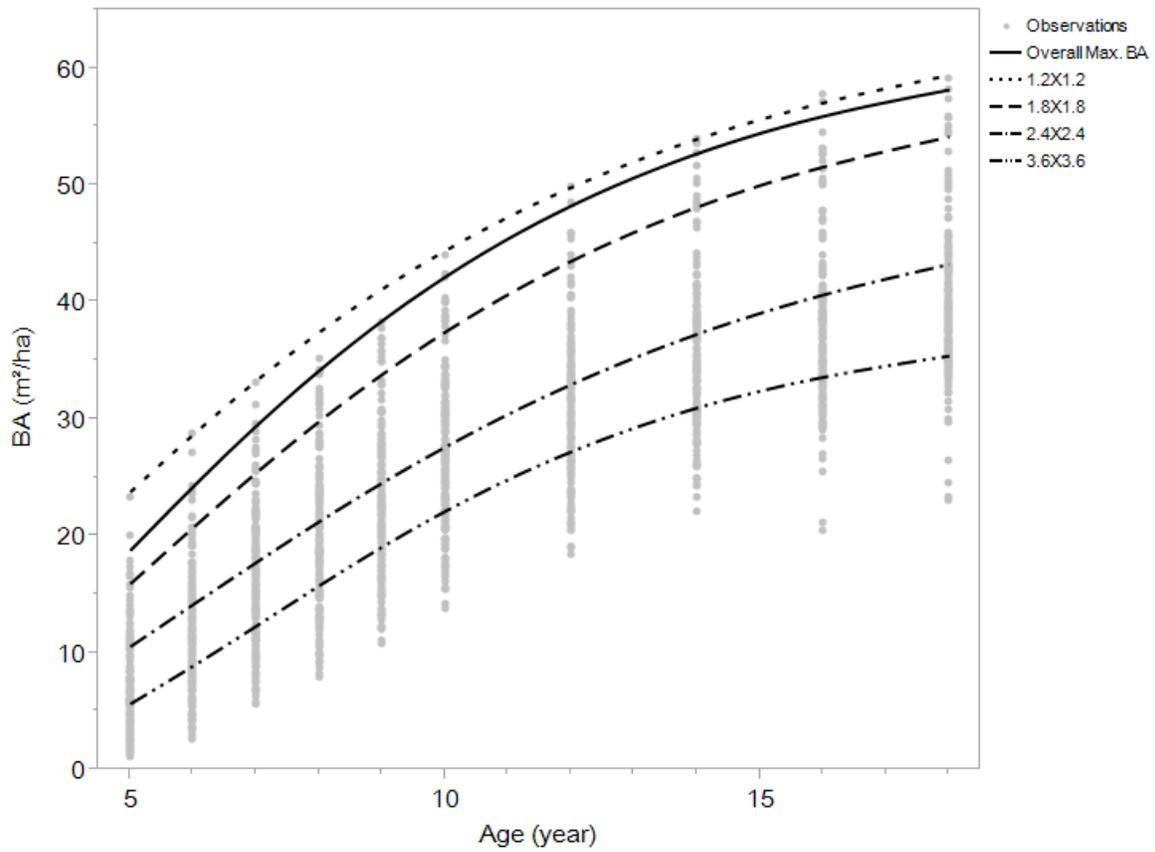


Figure 4 Maximum stand BA at different initial planting density through age 18. The trajectories were fitted by Chapman-Richards equation using quantile regression (quantile=0.99).

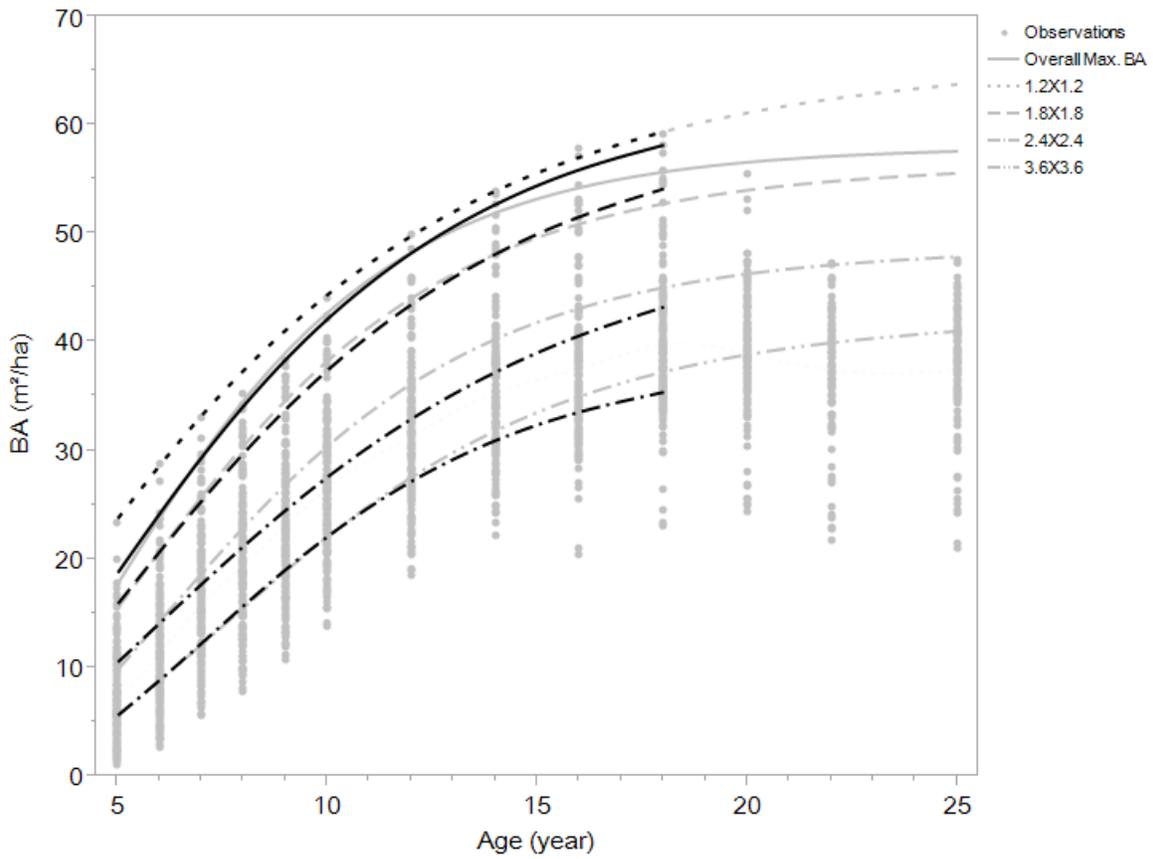


Figure 5 Comparison of maximum stand BA fitted from two stand ages intervals, ages 5-18 and 5-25. The trajectories were fitted by Chapman-Richards equation using quantile regression (quantile=0.99).

4.1.2 Implied maximum stand BA

The implied maximum stand BA at age 18 was estimated at 61.5, 61.5, and 55.3 (m²/ha) from Reineke's STR, C-D rule, and Nilson's sparsity index, respectively (Fig. 6). The coefficients of each MSDR measure are shown in Table 2. In Figs. 7 and 8, the measurements at ages 16-18 were close to the MSDR lines, which implied that the stands in this age interval have reached the maximum stand density (i.e.: stand BA carrying capacity). $G_{R\ max}$ and $G_{CD\ max}$ were consistently higher than the maximum stand BA obtained from the C-R equation (G_{max}) through age 18. $G_{N\ max}$ was higher than G_{max} at the early stage while it became lower than G_{max} since age 15 (Fig. 6). The difference between implied maximum stand BA (i.e.: $G_{R\ max}$, $G_{CD\ max}$ and $G_{N\ max}$) and G_{max} was relatively small after age 12 because the coefficients of the MSDR measures were estimated from the measurements only at the 99th quantile, which were in the ages 12-18 range (Figs. 7 and 8).

Table 2 Coefficients of MSDR measures (Reineke's STR, C-D rule and Nilson's sparsity index)

MSDR measures	Reineke's STR (a,b)	C-D rule ($\alpha_0, \alpha_1, \beta_0, \beta_1$)	Nilson's sparsity index (c_0, c_1)
Coefficients	(12.035, -1.455)	($2.23 \times 10^{-6}, 0.525,$ 0.562, -1.019)	(0.176, 0.108)

As shown in Fig. 6, compared to $G_{R\ max}$ or $G_{CD\ max}$, $G_{N\ max}$ estimated by Nilson's sparsity index was stable and constant after age 12. For Reineke's STR (Eq. 17), $G_{R\ max}$ was proportional to \bar{D}_q^{b+2} . The coefficient (b) was -1.455 (i.e.: $b + 2 > 0$) so $G_{R\ max}$ was non-

decreasing and divergent. For the C-D rule (Eq. 19), $G_{CD\ max}$ was proportional to $\bar{H}_d^{-(\alpha_1+\beta_1)}$. The sum of coefficients ($\alpha_1 + \beta_1$) was less than zero (i.e.: $-(\alpha_1 + \beta_1) > 0$) so $G_{CD\ max}$ was also non-decreasing and divergent. For Nilson's sparsity index (Eq. 20),

$$G_{N\ max} \propto \left(\frac{\bar{D}_q}{c_0 + c_1 \cdot \bar{D}_q} \right)^2 = \left(\frac{1}{\frac{c_0}{\bar{D}_q} + c_1} \right)^2 \quad (26)$$

where all symbols have been defined in Chapter 3. Equation 26 implied that if \bar{D}_q increased to infinity, $G_{N\ max}$ would converge to a constant. Thus, due to the structure of the equation, the trend of $G_{N\ max}$ becomes horizontal since age 12, which was different from those of $G_{R\ max}$ and $G_{CD\ max}$ in Fig. 6.

In addition, the trends of $G_{R\ max}$ and $G_{CD\ max}$ were similar to that of G_{max} . The curves of $G_{R\ max}$ and $G_{CD\ max}$ merged at age 18, which is close to the maximum stand BA in 1.2×1.2 m spacing. Notably, $G_{R\ max}$ was a function of quadratic mean diameter (Eq. 17) while the $G_{CD\ max}$ was a function of dominant tree height (Eq. 19). This result implied that either diameter or tree height can be used to estimate the stand BA carrying capacity. Furthermore, if the BA-age plane was transformed to LnN-LnD plane (Fig. 7), the MSDR lines estimated by C-D rule and Reineke's STR were close and similar, whose slope and intercept were (-1.52, 12.26) and (-1.45, 12.04), respectively. Thus, in this study, it would be reasonable to assume Reineke's STR and the C-D rule are interchangeable when projecting stand BA carrying capacity for loblolly pine. A similar pattern for Norway spruce was reported by Vospernik and Sterba (2014). They suggested that if Reineke's STR and the C-D rule are fitted from the same dataset and if both rules are set equal at potential density, both relationships are valid for characterizing potential density. Huber, et al. (2014) also indicated both rules were adequate for estimation of maximum stand BA for

Norway spruce and silver fir. The results in this study supported Vospernik and Sterba's (2014) conclusion, while, in this study, the assumption of same slope between Reineke's STR and the C-D rule was not imposed to estimate the stand BA carrying capacity. Further, Vospernik and Sterba (2014) indicated a large number of plots was required for fitting the four-parameter C-D equation while our results showed that the number of plots (192 plots) in this study was adequate for estimating coefficients of the C-D rule. Specifically, we suggest that a wide range of initial planting densities and physiographic regions (discussed in next section) could be another important factors to ensure consistency between Reineke's STR and the C-D rule.

Comparing $G_{R\ max}$ with $G_{N\ max}$ on the BA- \bar{D}_q plane (Fig. 9) shows that both $G_{R\ max}$ and $G_{N\ max}$ cannot represent the maximum BA before \bar{D}_q increases to 10 cm. However, Reineke's STR overestimated the maximum stand BA when the quadratic mean diameter became larger whereas the maximum stand BA estimated by Nilson's sparsity index approached an asymptote with an increase of diameter. The nondecreasing nature of $G_{R\ max}$ made Reineke's STR unsuitable for projecting the stand BA carrying capacity across a wide range of quadratic mean diameters.

Overall, we suggest that Nilson's sparsity index is preferred for estimating stand BA carrying capacity. As mentioned above, one of the advantages is that $G_{N\ max}$ was more stable than $G_{R\ max}$ and $G_{CD\ max}$. Another advantage is that unlike the C-D rule, only two independent variables, number of trees per unit area and quadratic mean diameter, were needed to estimate $G_{N\ max}$. Indeed, although the implied maximum stand BA was slightly higher or lower than G_{max} , the difference 5.6% was acceptable. In addition, MSDR measures can provide more information of stand dynamics than a single BA-age curve.

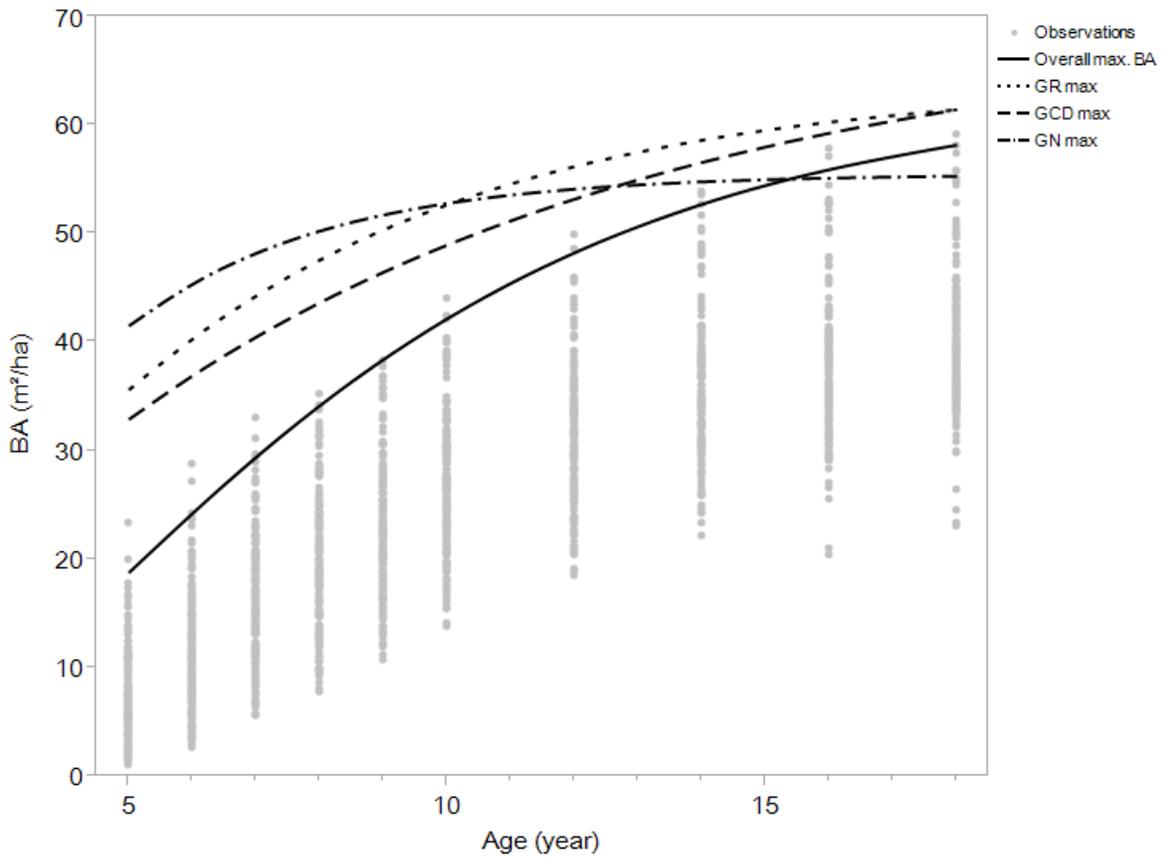


Figure 6 Implied maximum stand BA trajectories. The overall maximum stand BA was estimated by the C-R equation. The implied maximum stand BAs ($G_R max$, $G_{CD} max$ and $G_N max$) were estimated by Reineke's STR, C-D rule and Nilson's sparsity index, respectively.

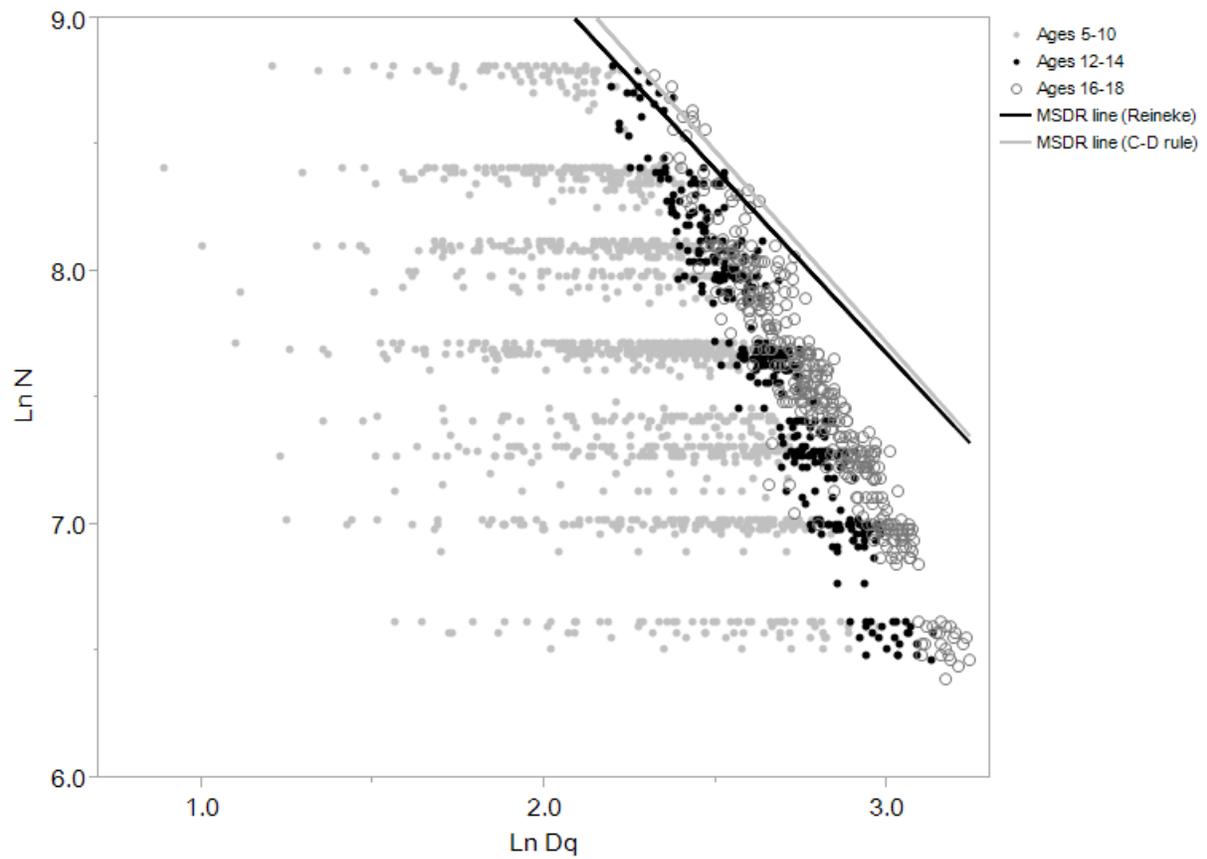


Figure 7 Size-density relationship plot with the MS DR lines (self-thinning lines) estimated by Reineke's STR and the C-D rule.

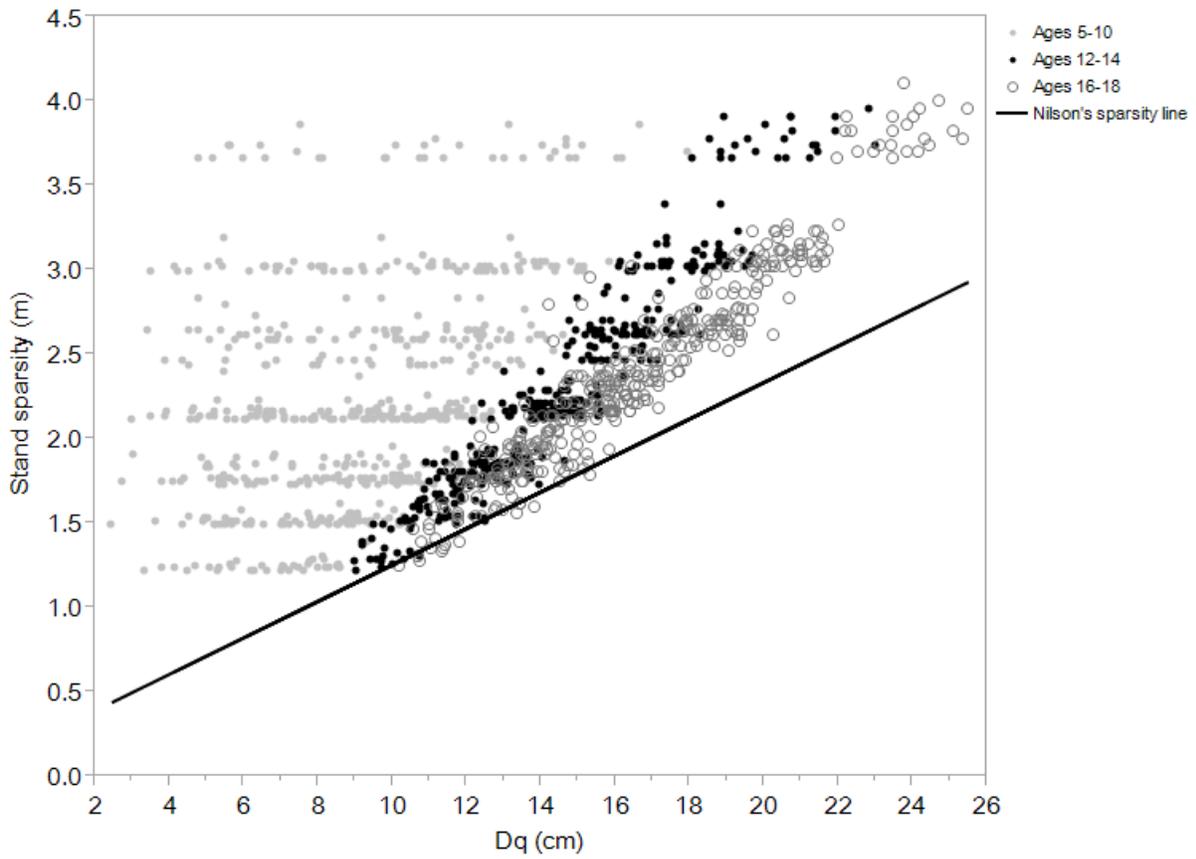


Figure 8 Stand sparsity-quadratic mean diameter plot with the MSDR line estimated by Nilson's sparsity index.

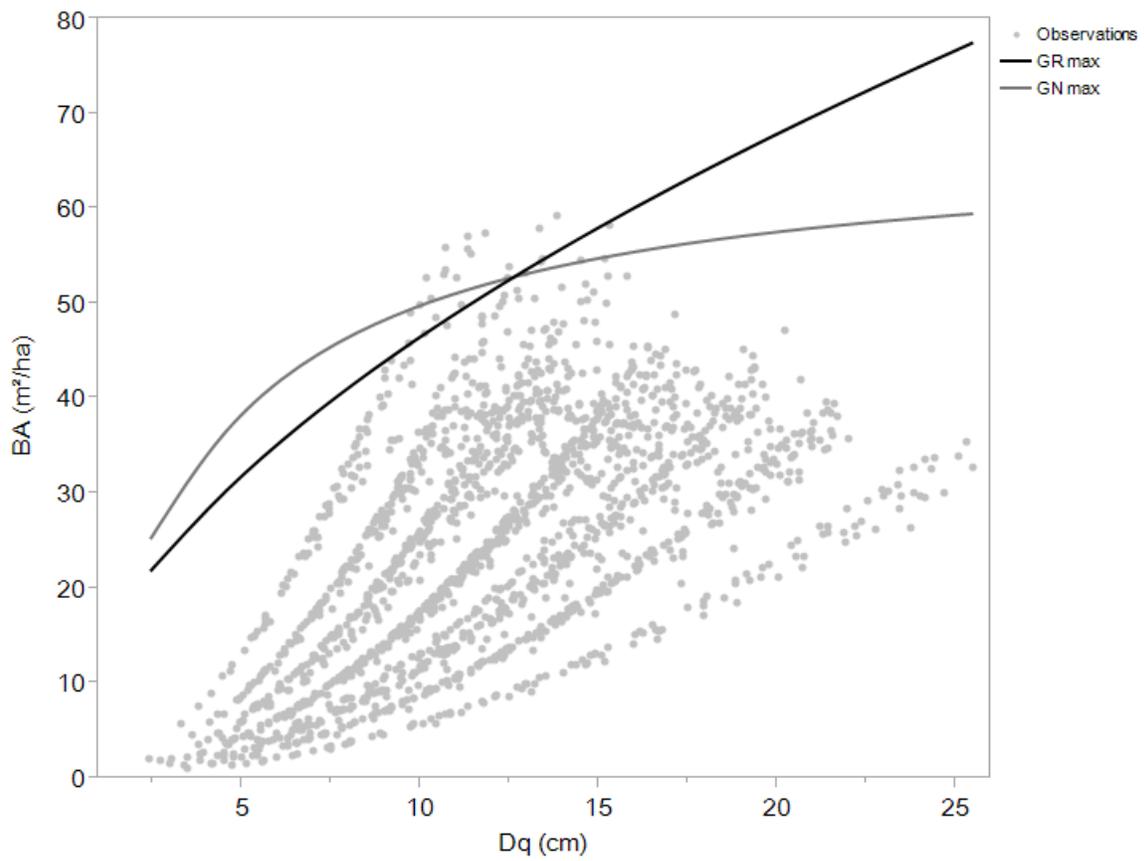


Figure 9 Comparison of the implied maximum stand BAs ($G_{R\ max}$ and $G_{N\ max}$) estimated by Reineke's STR and Nilson's sparsity index on the BA-quadratic mean diameter plot.

4.2 Effect of physiographic regions on carrying capacity

4.2.1 Reineke's self-thinning line

For the full model, the slope and intercept of Reineke's self-thinning (MSDR) line in the Piedmont and the Coastal Plain were (-1.468, 12.134) and (-1.623, 12.286), respectively. For the reduced model, the common slope was -1.518 with intercepts for the Piedmont and the Coastal Plain of 12.259 and 12.015, respectively. Figs. 10 and 11 show that the MSDR line in the Piedmont fitted by either the full model or the reduced model was higher than that in the Coastal Plain. The maximum stand BA implied by either model showed the same pattern (Fig. 12). However, the interaction term ($\text{Ln}\bar{D}_q \cdot x_r$) in the full model wasn't statistically significant (p-value = 0.12753). Thus, for the first hypothesis, the null hypothesis can't be rejected. The assumption of a common slope proposed by Reineke (1933) is valid in this study. For the second hypothesis, the intercepts for the two regions were significantly different (p-value < 0.001). The difference of intercepts represents the effect of physiographic regions¹. It is suggested that the reduced models can be used to estimate the MSDR line and the maximum stand BA in the two regions.

The maximum Reineke's SDI in the Piedmont of 1614 (trees/ha) or 1554 (trees/ha) was higher than that in the Coastal Plain, which was 1136 (trees/ha) or 1218 (trees/ha), estimated by the full model and reduced model, respectively. The difference of maximum SDI between the two regions was larger when the full model was implemented. However, for either model, the estimated maximum SDI in the Piedmont is considerably higher than the widely accepted

¹ In this study, the effect of genetic variation on growth wasn't considered because it was based on the assumption that the seed sources chosen for each region were most suitable and adaptable to the environmental and climatic conditions of the Piedmont or the Coastal Plain.

maximum SDI (around 1100 trees/ha) for loblolly pine. The high maximum SDI estimated in the Piedmont is mainly driven by the very high planting density and there are few data points at quadratic mean diameter equal to 25.4 cm (i.e: $\text{Ln}\bar{D}_q = 3.23$). Thus, in both regions, the stand age was extended to years 25 and the same fitting procedure was implemented. It showed that the estimate of maximum SDI in the Piedmont dropped to 1486 (trees/ha) or 1298 (trees/ha) and that in the Coastal Plain, it declined to 1015 (trees/ha) or 1022 (trees/ha), obtained from the full model and reduced model, respectively. Although the estimated maximum SDI in the Piedmont is still larger than 1000 trees/ha, Figs. 10 and 11 show that the MSDR line estimated by the reduced model is much closer to the cloud of data, which should be a more reasonable and reliable estimate of the maximum SDI in both regions. Also, the intercepts for the two regions were significantly different (p-value <0.001) (Fig. 14). Further, the maximum stand BA converted by the reduced model using the data before age 25 was near the upper boundary of the stand BA (Fig. 12). In this analysis, the reduced model of Reineke's STR stabilized the estimate of the MSDR line and the maximum stand BA in both regions. However, due to the collapse of some stands in the Piedmont after age 18, only a few data points were available for fitting Reineke's STR. Therefore, to examine the effect of physiographic regions on maximum SDI, more data in both regions might be needed for further analysis. For simplicity, the reduced model using data before age 18 is denoted model (18); the other reduced model using data before age 25 is denoted model (25).

The reduced segmented regression model developed by VanderSchaaf and Burkhart (2008) was used to fit the data in four square plots separately (1.2×1.2 , 1.8×1.8 , 2.4×2.4 , 3.6×3.6 m) to examine the effect of initial planting density in each physiographic region. The cumulative mortality was also calculated. The coefficients of the segmented regression are

listed in Table 3 and the cumulative mortality-age trajectories are shown in Fig. 13. Overall, the percentage of the maximum SDI at T was highest at the closest spacing and was lowest at the widest spacing. The closer spacings had higher cumulative mortality than the wider spacings. Although the effect of initial planting density for the two regions was similar, the stand dynamics in the Piedmont and the Coastal Plain were different at a given initial planting density (Fig. 14). In the Piedmont, only the close spacings surpassed the MSDR line. Self-thinning in the 1.2×1.2 m spacing started at 60% of maximum SDI while the occurrence of self-thinning in the other plots was initiated below 50% of maximum SDI. For the four square spacings in the Piedmont, the cumulative mortality was lower than 30%. However, most of stands in the Coastal Plain approached the MSDR line. Except the 3.6×3.6 m spacing, the self-thinning occurred at 50-70% of the maximum SDI. The cumulative mortality in the wider spacings was low and close to that in the Piedmont while the mortality in the closer spacings was more than 40%. The higher cumulative mortality in the Coastal Plain resulted in the lower stand BA carrying capacity. Furthermore, Fig. 14 shows that at the early stage, the growth of stands in the Coastal Plain was faster than those in the Piedmont. In the Coastal Plain, number of trees per hectare declined rapidly after the stands surpassed the MSDR line while in the Piedmont, the stands sustained larger quadratic mean diameter trees for a given initial planting density.

In short, results suggested that the reduced model of Reineke's STR is appropriate for estimating MSDR lines and maximum stand BA. If management objectives focus on total biomass production (e.g.: pulpwood), the closer spacings in the Coastal Plain can accumulate stand volume in a short period of time (shorter rotation age) while thye total production is less than the closer spacings in the Piedmont. For solidwood products (e.g.: saw timber), the wider spacings are suggested and the effect of physiographic regions is relatively small in this study.

Table 3 Coefficients of the segmented regression developed by VanderSchaaf and Burkhart (2008) among four square spacings in the Piedmont and in the Coastal Plain.

Piedmont	d_1	d_2	T	% of max. SDI at T model (18)	% of max. SDI at T model (25)
1.2 × 1.2 m	8.797	-1.383	2.029	68	61
1.8 × 1.8 m	7.959	-1.195	2.292	44	42
2.4 × 2.4 m	7.411	-0.5612	2.452	32	32
3.6 × 3.6 m	6.591	-1.204	2.976	32	36
Coastal Plain					
1.2 × 1.2 m	8.782	-2.622	1.958	77	68
1.8 × 1.8 m	7.974	-4.243	2.443	72	71
2.4 × 2.4 m	7.400	-1.492	2.637	54	56
3.6 × 3.6 m	6.592	-0.2131	2.570	22	22

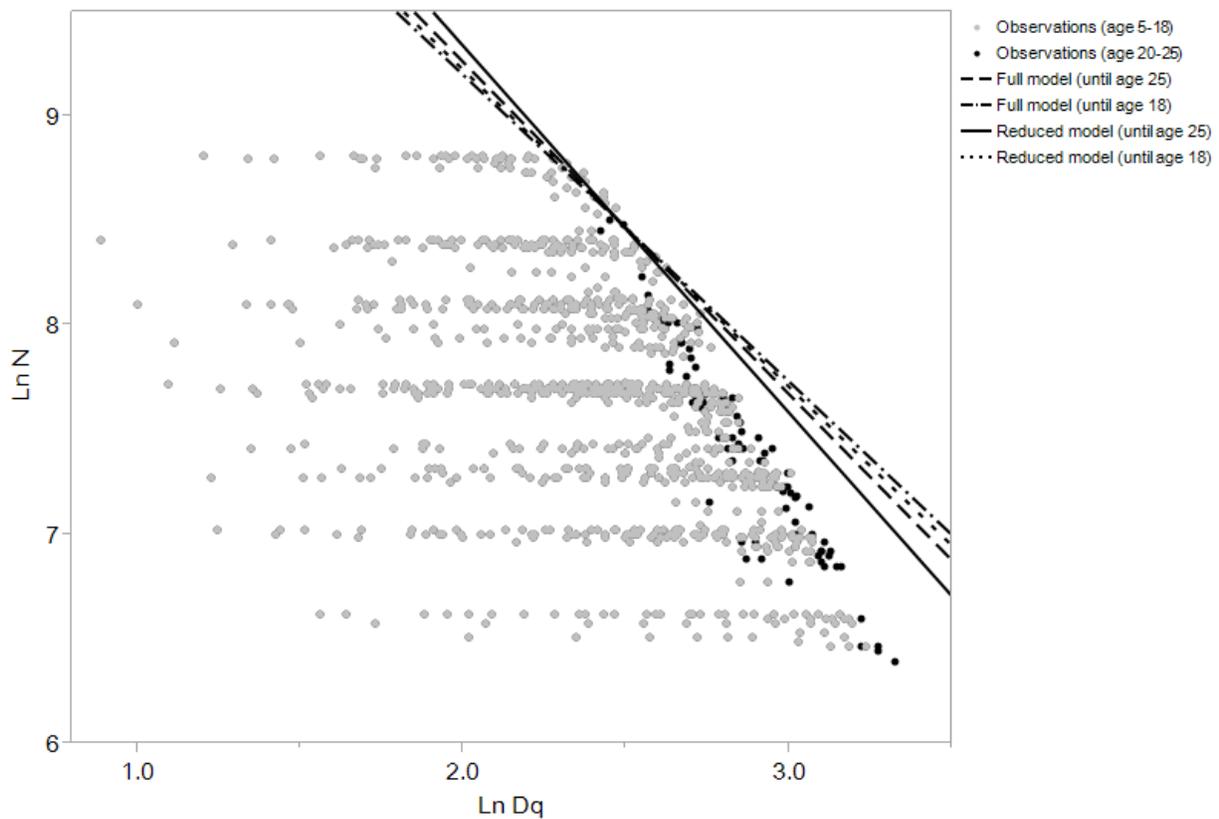


Figure 10 Comparison of the MSDR lines in the Piedmont. The MSDR lines were separately estimated by the full model (Eq. 21) and the reduced model (Eq. 22) using two datasets (before age 18 and before age 25).

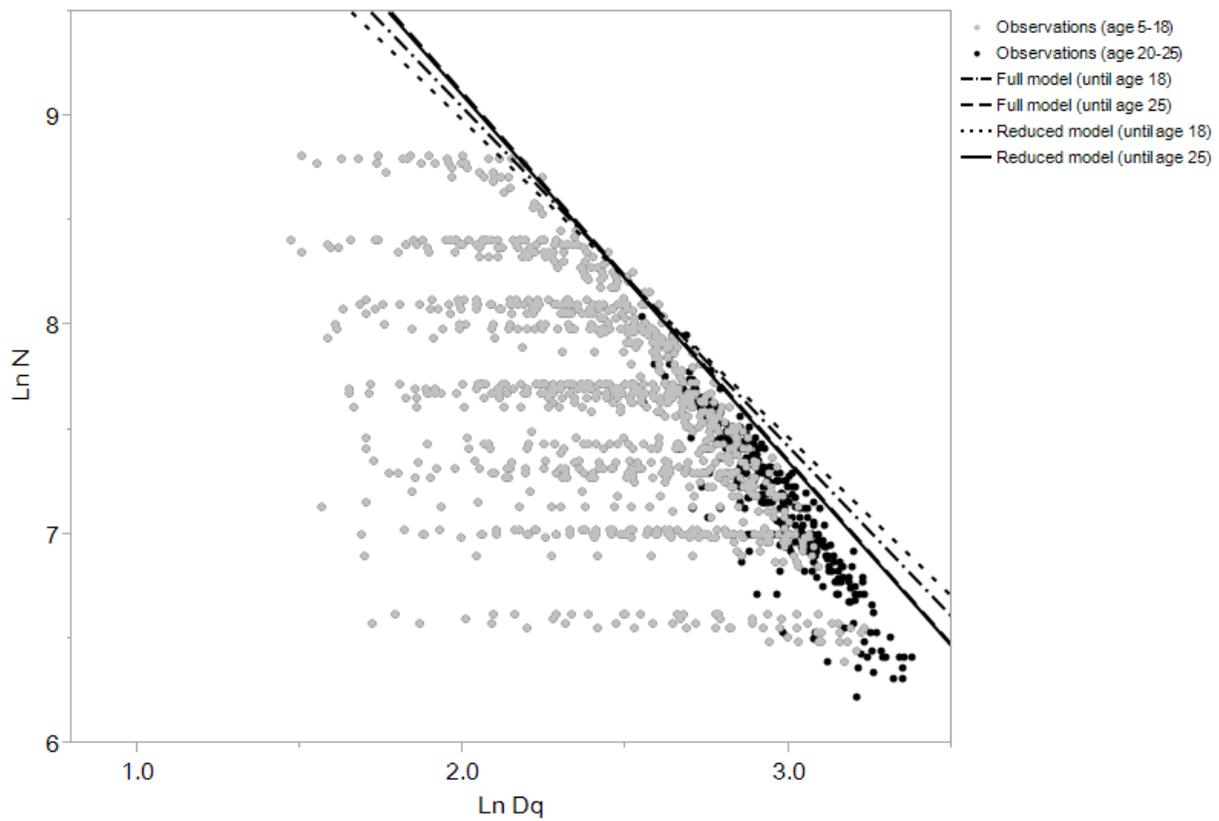


Figure 11 Comparison of the MSDR lines in the Coastal Plain. The MSDR lines were separately estimated by the full model (Eq. 21) and the reduced model (Eq. 22) using two datasets (before age 18 and before age 25).

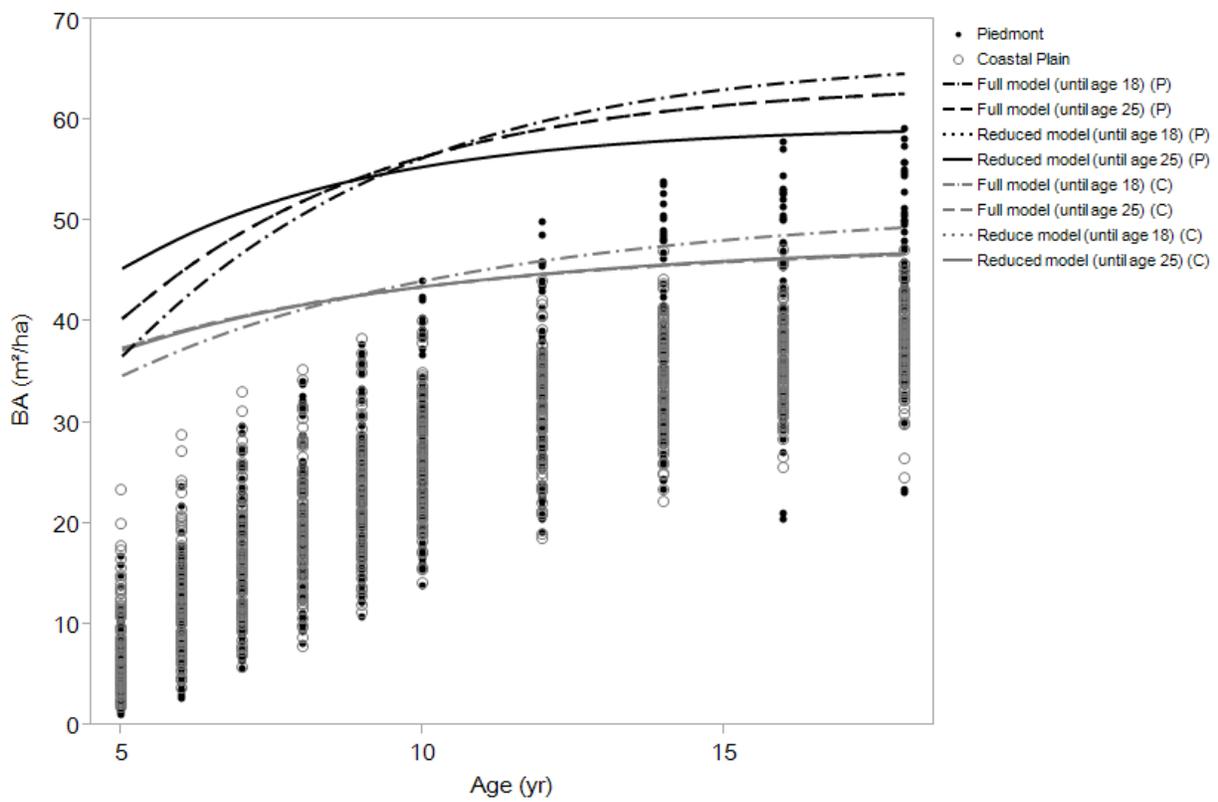


Figure 12 Comparison of the maximum stand BA in the Piedmont and in the Coastal Plain. The implied maximum stand BA ($G_{R\ max}$) was separately fitted by the full model (Eq. 21) and the reduced model (Eq. 22) using two datasets (before age 18 and before age 25).

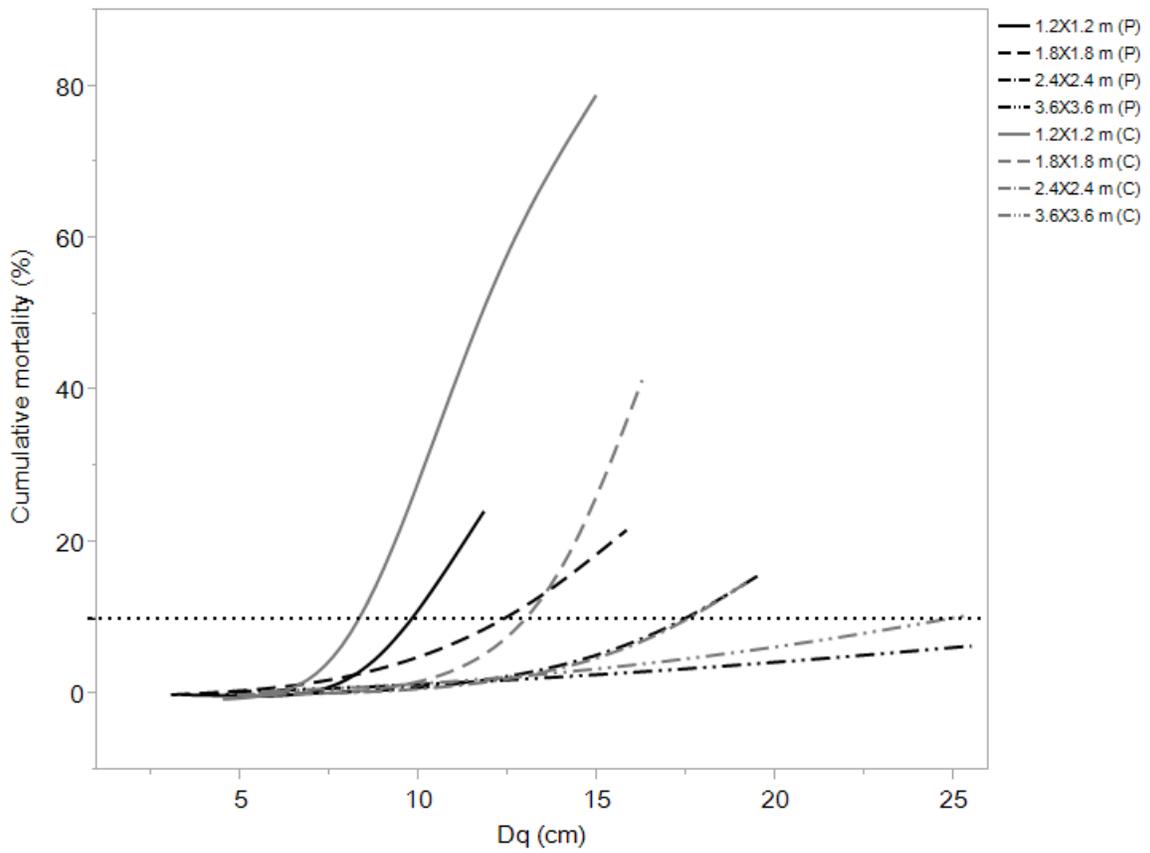


Figure 13 Comparison of the cumulative mortality among four square spacings in the Piedmont and in the Coastal Plain.

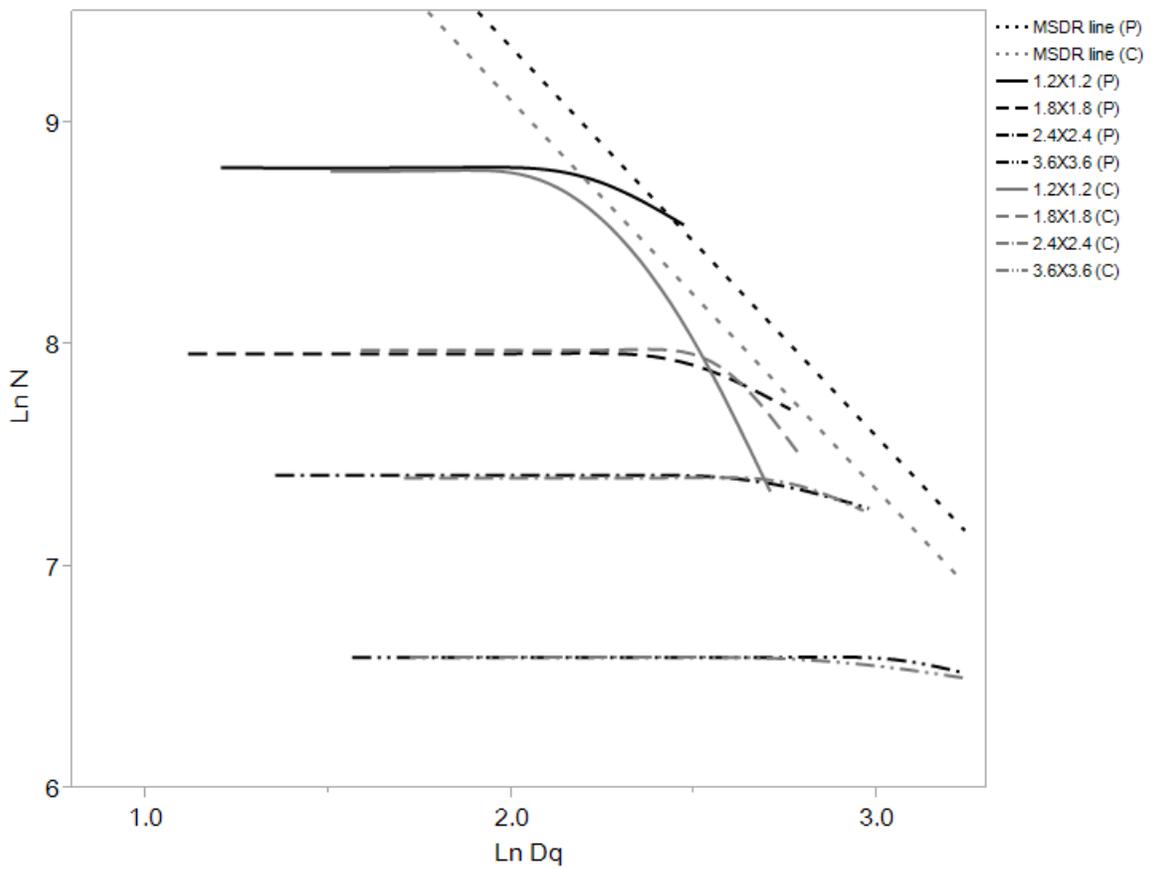


Figure 14 Comparison of the diameter-density trajectories among four square spacings in the Piedmont and in the Coastal Plain. MSDR lines were obtained from the reduced model, model (25). The intercepts of MSDR lines between the two regions were significantly different (p -value < 0.001).

4.2.2 Maximum stand BA

The maximum stand BA of 63.3 (m²/ha) in the Piedmont obtained from the C-R equation's coefficient γ_1 (Eq. 15) was higher than that of 48.3 (m²/ha) in the Coastal Plain. By age 18, the maximum stand BA in the Piedmont and in the Coastal Plain were estimated at 59.2 (m²/ha) and 47.1 (m²/ha), respectively. In the Piedmont, the $G_{CD\ max}$ and $G_{N\ max}$ were close to the maximum stand BA at age 18. The $G_{R\ max}$ estimated by model (18) was higher but the $G_{R\ max}$ estimated by model (25) was close to the $G_{CD\ max}$ and $G_{N\ max}$; in the Coastal Plain, the implied maximum stand BA ($G_{R\ max}$, $G_{CD\ max}$ and $G_{N\ max}$) was close to the maximum stand BA (Fig. 15).

The trend of the implied maximum stand BA in each region was similar to the overall trend when using the whole dataset. As discussed in section 4.1.2, due to the structure of equations, the curves of $G_{R\ max}$ and $G_{CD\ max}$ were non-decreasing and divergent while the curve of $G_{N\ max}$ was asymptotic. However, in the Piedmont or the Coastal Plain, the curves of $G_{R\ max}$ and $G_{CD\ max}$ didn't converge at age 18. This implies that the maximum stand BA estimated by Reineke's STR and the C-D rule were not consistent in both regions, especially when the model (18) was used to calculate $G_{R\ max}$. This result was different from the finding using the whole dataset (including Piedmont and Coastal Plain). Compared to Reineke's STR, the C-D rule is relatively stable when estimating the maximum stand BA. One possible explanation is that the C-D rule composed of three predictors— number of trees per unit area, quadratic mean diameter, and dominant tree height— can explain more variation of the outcomes than Reineke's STR, which contains two predictors only. A disadvantage of the C-D rule is that there are four coefficients in the model and a nonlinear fitting procedure is needed.

When compared to the other MSDR estimates, $G_{N\ max}$ was the closest implied maximum stand BA to the maximum stand BA obtained by the C-R equation both in the Piedmont and in the Coastal Plain. $G_{N\ max}$ can reliably reflect the effect of physiographic regions on the maximum stand BA although the dataset was divided. In other words, if the dataset isn't large, Nilson's sparsity index may be more useful than Reineke's STR or the C-D rule for projecting maximum stand BA. Further, Nilson's sparsity index is a linear equation and contains only two coefficients in the model. For fitting, Nilson's sparsity index, unlike Reineke's STR, doesn't require a logarithm transformation, which results in a transformation bias for predictions. This result supported our previous suggestion that Nilson's sparsity index is an appropriate MSDR measure to determine stand BA carrying capacity.

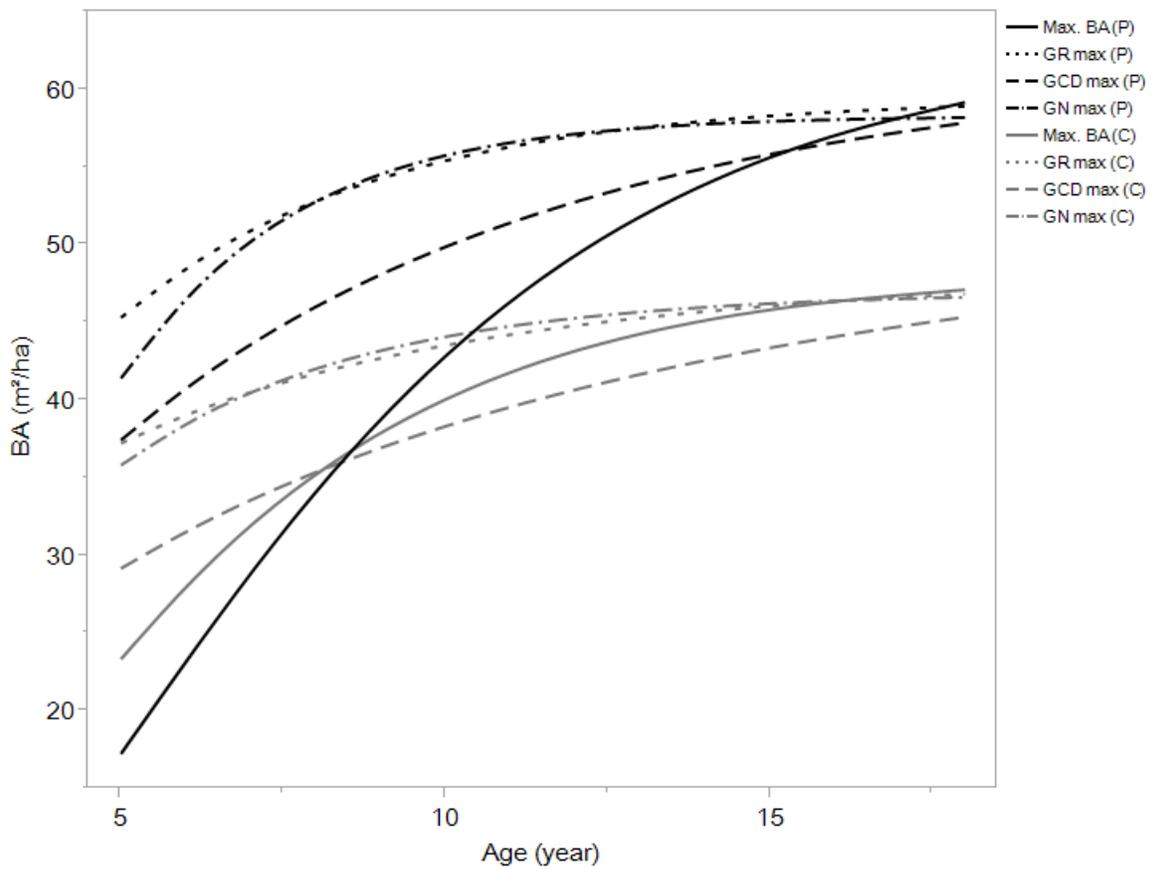


Figure 15 Comparison of the implied maximum stand BA ($G_R max$, $G_{CD} max$ and $G_N max$) and the maximum stand BA (obtained by the C-R equation) in the Piedmont and in the Coastal Plain. $G_R max$ was estimated by model (25).

4.3 Miniature scale spacing trial

The overall trend of the maximum stand BA_g in the miniature scale trial (microcosm) (Fig. 16) was similar to the maximum stand BA curve in the operational scale trial and was especially close to that of the Piedmont (Fig. 12). Stand BA_g in the miniature scale trial was calculated from quadratic mean groundline diameter. The maximum Reineke's SDI^2 of 1529 (trees/m²) for the miniature scale trial was close to 1523³ (trees/ha) for the operational scale trial when using the whole dataset including Piedmont and Coastal Plain.

The implied maximum stand BA_g ($G_{R\ max}$, $G_{CD\ max}$ and $G_{N\ max}$) was close to the maximum stand BA_g obtained from the C-R equation. $G_{N\ max}$ remained the closest measure to the maximum stand BA. The coefficients of each MSDR measure are shown in Table 4. The preliminary analysis showed that coefficient estimates of the four parameter C-D equation did not readily converge. To stabilize the coefficients, the three parameter C-D equation suggested by Vospernik and Sterba (2014) was used. The coefficient (β_1) was replaced by the slope (b) of Reineke's STR, which was -1.569 in the miniature scale trial. The result showed that $G_{CD\ max}$ obtained from the three parameter model was slightly higher than $G_{R\ max}$ or $G_{N\ max}$. The curves of $G_{N\ max}$ and $G_{R\ max}$ converged towards the maximum stand BA_g curve near age five. As a result, for the miniature scale spacing trial, Reineke's STR and Nilson's sparsity index were more appropriate and reliable than the C-D rule to project the maximum stand BA_g .

² The quadratic mean groundline diameter of 25.4 mm was used for calculating Reineke's SDI at the miniature scale trial.

³ The maximum SDI of 1523 (trees/ha) was computed from the data before age 18. The maximum SDI was 1122 (trees/ha) by using the data before age 25.

For stand dynamics, the variation of stand BA_g in the miniature scale trial was larger than that of stand BA in the operational scale trial. Only a few plots reached the maximum stand BA_g ($80 \text{ dm}^2/\text{m}^2$) while the stand BA_g of most plots was below $50 \text{ (dm}^2/\text{m}^2)$. The coefficients of the segmented regression are listed in Table 5. The pattern of self-thinning among four square spacings in the miniature scale trial was different from the operational scale trial. In the miniature scale trial, self-thinning began from 48% to 57% of the maximum Reineke's SDI, while in the operational scale trial the occurrence of self-thinning ranged from 21% to 84% of the maximum Reineke's SDI. In other words, for the miniature scale trial, the effect of initial planting density on the occurrence of self-thinning wasn't significant when compared to VanderSchaaf and Burkhart's (2012) finding using the operational scale trial data. One possible explanation might be the scale of the trial. In this study, the miniature scale spacing trial was 1/16 of the operational scale trial. The extremely high initial planting density used for accelerating the development of stands resulted in the difference of self-thinning among spacings shrinking. Indeed, more measurements and replicates are needed for examining and comparing stand dynamics among various scales.

Furthermore, number of trees per unit area in the miniature scale trial declined quickly and sharply after self-thinning began, especially for the close spacings (Fig. 18). After age four, the cumulative mortality of four square spacings was above 60% and some of them approached 90%. Most of plots collapsed due to furious intraspecific competition⁴ (Fig. 17). The closest spacing had the highest cumulative mortality and the widest spacing had the lowest cumulative mortality. This pattern was similar to the operational scale trial.

⁴ There is no disturbance recorded during the experiment.

Notably, the data used for the above analyses were collected at one-year intervals (the end of each growing season) from both installations of the miniature scale spacing trial. For further comparison of stand BA_g dynamics, the measurements collected at 30-day intervals (during the growing seasons) in the first installation were selected. The stand BA_g of all plots was shown in Fig. 19. Stand BA_g increased rapidly during the growing seasons and slowed at the end of the growing season. The trend of stand BA_g was like a stair-step curve, which was different from the smooth asymptotic curve of maximum stand BA_g using annual measurements. By integrating seasonal measurements, the curve of cumulative height or cumulative groundline diameter had a similar pattern to stand BA_g (Avila 1993, Amateis, et al. 2003a). Rather than steadily increasing, the growth rate of stand BA varies within growing seasons. It implied that the timing of data collection during the seasons would affect estimation of maximum stand BA. Collecting measurements at the end of the growing season would be appropriate and reliable for estimating maximum stand BA. However, for more accurately describing stand behavior, the trees should be measured more than once a year. Monthly or seasonal data collection during the growing seasons is suggested. Indeed, it would be more applicable and economical at miniature scales than at operational scales.

In short, the miniature scale spacing trial exhibited the overall trend of the maximum stand BA curve in the operational scale trial. Three MSDR measures are reasonable to estimate the maximum stand BA_g but Reineke's STR and Nilson's sparsity index are best. Each spacing experienced serious intraspecific competition and the number of trees per unit area decreased rapidly within five years. The closer spacings had a higher cumulative mortality than the wider spacings. Although in this study, the maximum stand BA_g in the miniature scale trial didn't closely estimate the stand BA carrying capacity for loblolly pine on the operational scale, data

analysis and comparison showed that the maximum stand BA associated with stand density developed similarly at two scales (miniature and operational scales). The stand BA_g dynamics during the growing seasons can be used as a more accurate estimate of maximum attainable BA from miniature scale trials. Despite some challenges on data collection of diameter (Amateis, et al. 2003b), the miniature scale trial (microcosm) is an attractive option because it shortens the experiment time and reduces costs greatly.

Table 4 Coefficients of MSDR measures (Reineke's STR, C-D rule, and Nilson's sparsity index) using data from the miniature scale trial.

MSDR measures	Reineke's STR (a,b)	C-D rule ($\alpha_0, \alpha_1, \beta_0$)	Nilson's sparsity index (c_0, c_1)
Coefficients	(12.408, -1.569)	($5.19 \times 10^{-7}, 0.516, 4.136$)	(0.377, 0.085)

Table 5 Coefficients of the segmented regression among four square spacings in the miniature scale trial and in the operational scale trial.

Miniature	d_1	d_2	T	% of max. SDI at T
7.6 × 7.6 cm	8.981	-1.017	1.821	57
11.4 × 11.4 cm	8.283	-1.076	1.946	34
15.2 × 15.2 cm	7.546	-1.408	2.404	34
22.8 × 22.8 cm	6.778	-2.780	3.120	48
Operational				
1.2 × 1.2 m	8.774	-4.537	2.123	84
1.8 × 1.8 m	7.966	-2.837	2.404	56
2.4 × 2.4 m	7.405	-0.863	2.547	40
3.6 × 3.6 m	6.593	-0.236	2.660	21

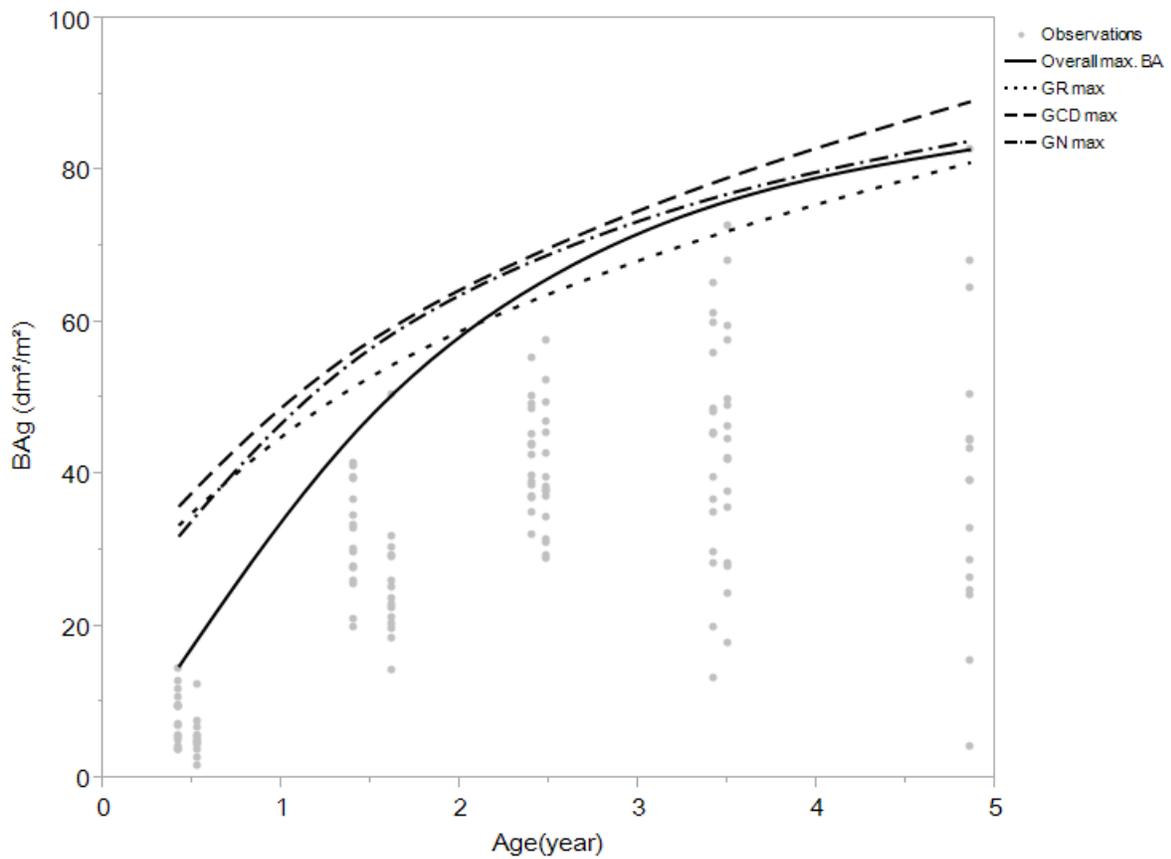


Figure 16 The implied maximum stand BA_g trajectories in the miniature scale trial. The overall maximum stand BA_g was estimated by the C-R equation. The implied maximum stand BA_g ($G_{R\ max}$, $G_{CD\ max}$ and $G_{N\ max}$) were estimated by Reineke's STR, C-D rule and Nilson's sparsity index, respectively.

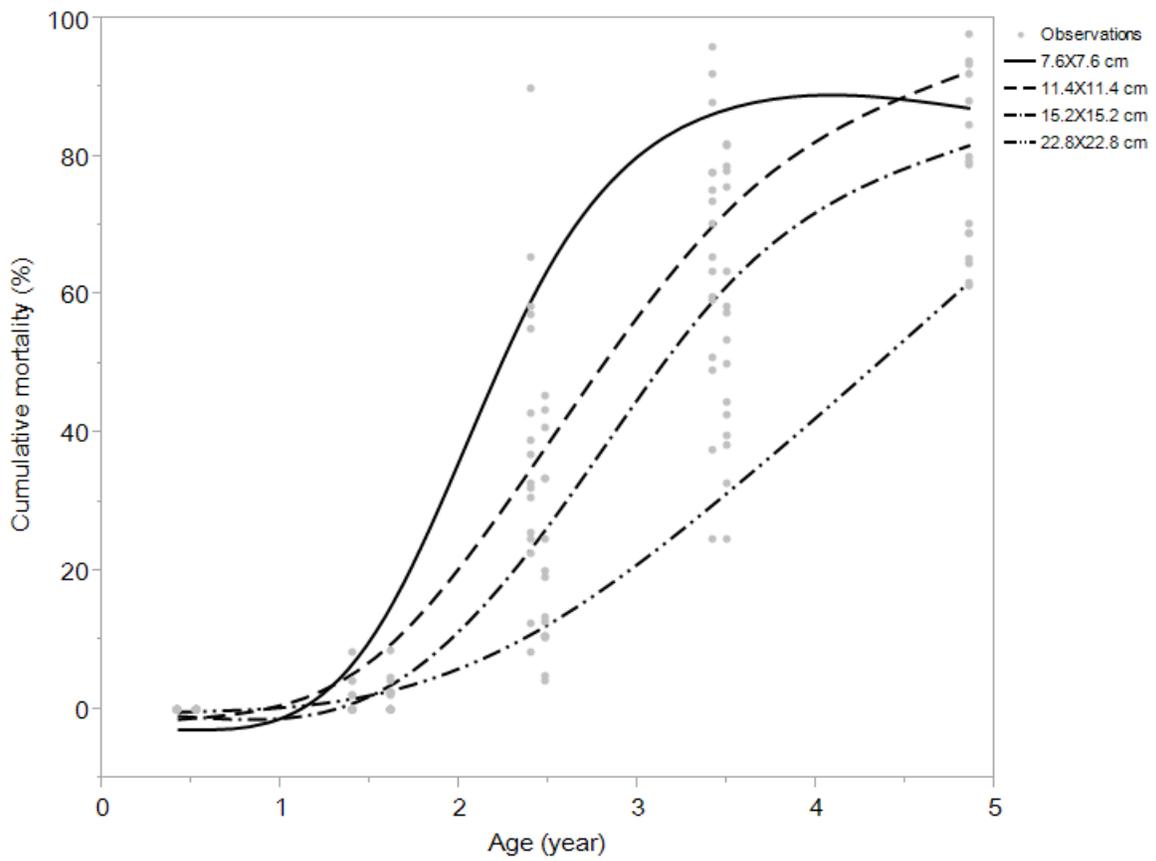


Figure 17 Comparison of the cumulative mortality among four square spacings in the miniature scale trial.

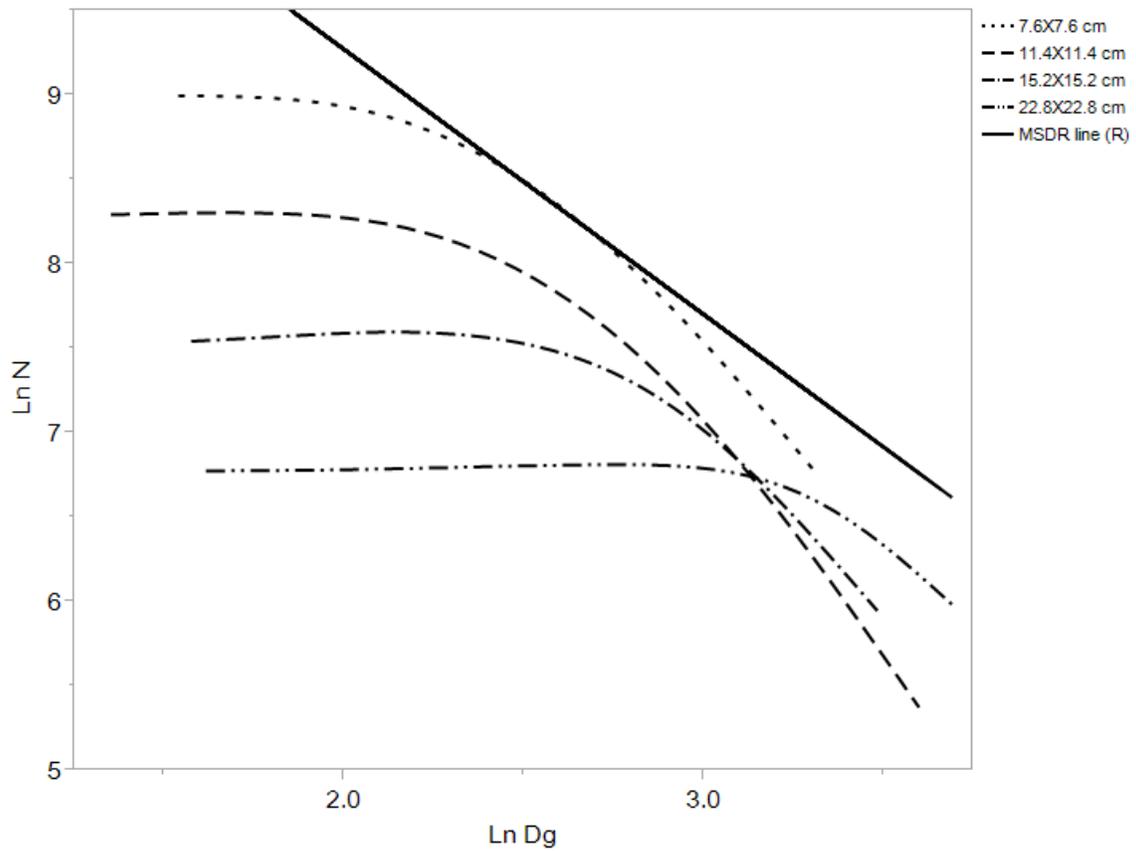


Figure 18 Comparison of the diameter-density trajectories among four square spacings in the miniature scale trial. Ln: natural logarithm; N: number of trees per m^2 ; Dg: quadratic mean groundline diameter (mm).

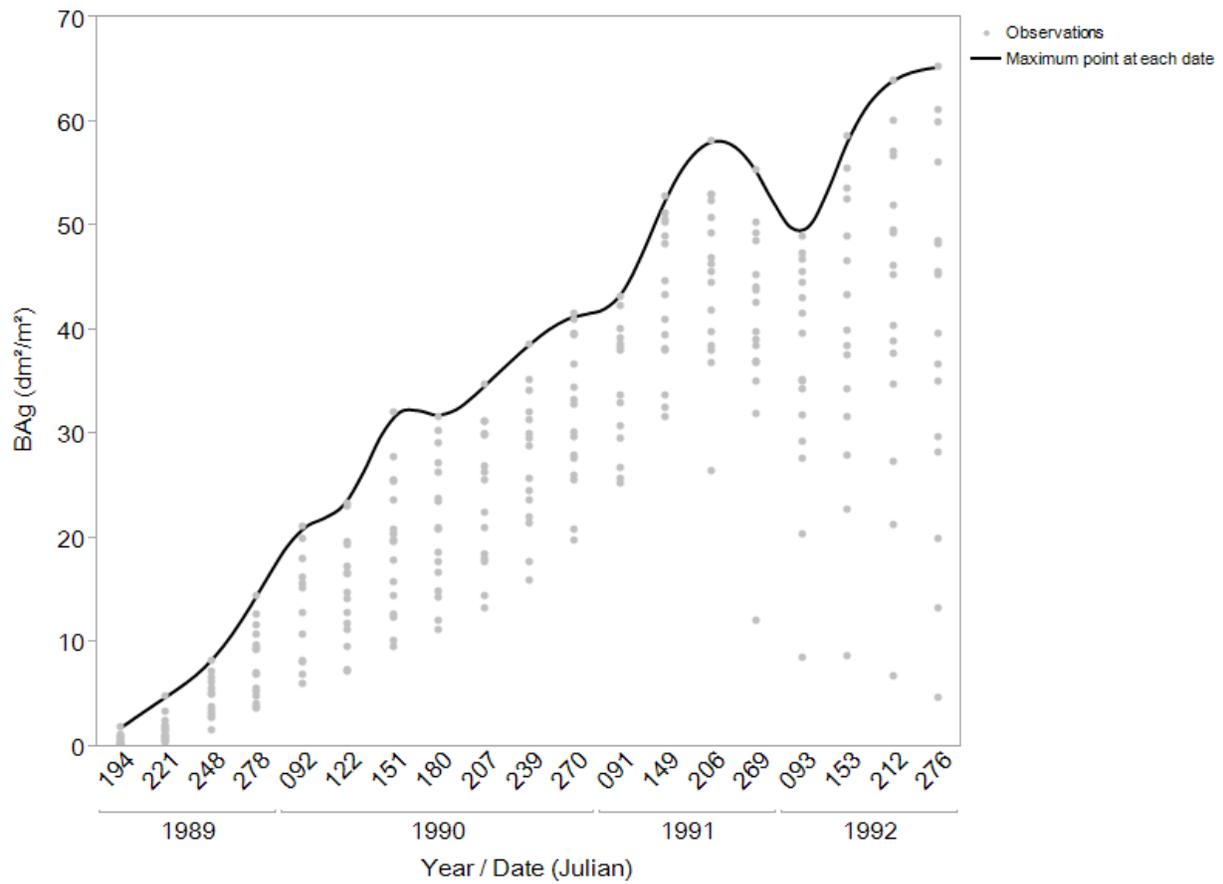


Figure 19 Measurements of stand BA_g obtained from July to October in 1989 and from April to October in 1990, 1991 and 1992.

Chapter 5

Conclusion

Stand BA carrying capacity of 63.2 (m²/ha) was obtained from the coefficient γ_1 of the C-R equation. At age 18, the maximum stand BA was estimated at 58.2 (m²/ha). In comparison of the maximum stand BA in four square plots, the overall maximum stand BA trajectory was closest to the maximum stand BA trajectory at the closest spacing. The stands with high initial planting density approached the stand BA carrying capacity sooner than the stands with lower initial planting density. Because some uncontrollable factors on long-term operational experiments can make estimates of stand BA carrying capacity unreliable for loblolly pine, it suggested that the stand BA carrying capacity could be estimated from high initial planting density stands in a relatively short period of time so that the risk of damages and the costs of experiments could be reduced.

The trend of implied maximum stand BA converted from three diameter-based MSDR measures was similar to the maximum stand BA curve obtained from the C-R equation. Although the MSDR measures are algebraically interchangeable, Nilson's sparsity index was the most stable and reliable estimate of stand BA carrying capacity. $G_{N\ max}$ was close to the maximum stand BA both at an operational scale and a miniature scale. The flexibility of $G_{N\ max}$ can illustrate the effect of physiographic regions on stand BA carrying capacity. The advantages of Nilson's sparsity index were twofold: one is that the asymptotic constraint ensures the maximum stand BA won't increase to infinity; the other is that the linear equation contains only two coefficients and no logarithm transformation is needed. Although Nilson's sparsity index hasn't been much cited in the US forestry literature, a few studies (e.g.: Zeide 2010, Gadow, et al. 2014) have pointed out the benefits of using Nilson's model, such as the consistent accuracy

on estimating self-thinning and the same dimension of two variables in the linear equation. A main disadvantage of Nilson's model is that the linear relationship between stand sparsity and quadratic mean diameter might not be valid when the residual trees can't fully occupy the canopy and mortality isn't mainly driven by intraspecific competition (Gadow and Kotze 2014).

When the effect of physiographic regions on stand BA carrying capacity was compared, the maximum stand BA of 63.3 (m²/ha) in the Piedmont was higher than that of 48.3 (m²/ha) in the Coastal Plain. By age 18, the maximum stand BA in the Piedmont and in the Coastal Plain were estimated at 59.2 (m²/ha) and 47.1 (m²/ha), respectively. The trend of the implied maximum stand BA in each region was similar to the overall trend using the whole dataset. For the self-thinning behavior, the MSDR line in the Piedmont fitted by either the full model or the reduced model was higher than that in the Coastal Plain. The maximum Reineke's SDI in the Piedmont of 1298 (trees/ha) was higher than that in the Coastal Plain, which was 1022 (trees/ha). In the Coastal Plain, number of trees per hectare declined rapidly after the stands exceed the MSDR line while in the Piedmont, the stands sustained larger quadratic mean diameter trees for a given initial planting density. Therefore, if management objectives focus on the total biomass production, the closer spacings in the Coastal Plain can accumulate stand volume in a short period of time (shorter rotation age) while the total production is less than the closer spacings in the Piedmont. For solidwood products, the wider spacings are suggested and the effect of physiographic regions is relatively small in this study.

The overall trend of the maximum stand BA_g in the miniature scale trial was similar to the maximum stand BA curve in the operational scale trial, and was especially close to that of the Piedmont. The effect of initial planting density on the occurrence of self-thinning wasn't significant at the miniature scale trial when compared to VanderSchaaf and Burkhart's (2012)

finding using the operational scale trial data. Number of trees per unit area in the miniature scale trial declined quickly and sharply after self-thinning began, especially for the close spacings. Furthermore, the trend of stand BA_g using the within-season measurements was different from that using annual measurements. Monthly data collection during the growing seasons is suggested for more accurately describing a stand behavior, especially maximum achievable stand density. Although in this study, the maximum stand BA_g in the miniature scale trial didn't closely estimate the stand BA carrying capacity for loblolly pine on the operational scale, data analysis and comparison showed that the maximum stand BA associated with stand density developed similarly at the two scales (miniature and operational scale). Indeed, the miniature scale trial (microcosm) is an attractive option because it shortens the experiment time and reduces costs greatly.

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