1 **Estimation of Carrying Capacity in Loblolly Pine (*Pinus taeda* L.)**

2
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6

7 **Abstract**

8 For plant populations, carrying capacity is the maximum number or biomass of a species that can
9 be sustained under finite site resources on a long-term basis. This study was aimed at estimating
10 the carrying capacity in planted stands of loblolly pine. Maximum stand basal area (BA) that can
11 be sustained over a long period of time can be regarded as a measure of carrying capacity. To
12 quantify and project stand BA carrying capacity, one approach is to use the estimate from a fitted
13 cumulative BA-age equation; another approach is to obtain BA estimates implied by maximum
14 size-density relationships (MSDRs), denoted implied maximum stand BA. The efficacy of three
15 diameter-based MSDR measures: Reineke's self-thinning rule, competition-density rule and
16 Nilson's sparsity index, were evaluated. Estimates from these three MSDR measures were
17 compared with estimates from the Chapman-Richards (C-R) equation fitted to the maximum
18 stand BA observed on plots from spacing trials. The spacing trials, established in two
19 physiographic regions (Piedmont and Coastal Plain) in the southeastern United States, and at two

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different scales (operational and miniature) were examined to provide an empirical basis for potential carrying capacity of loblolly pine.

Results showed that 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. All three MSDR measures provided similar estimates of stand BA carrying capacity, with Nilson's sparsity index yielding the most stable and reliable estimate. The potential stand BA carrying capacity between the two physiographic regions was significantly different. The maximum stand BA associated with planting density developed similarly at the operational and miniature scales.

Keywords: stand basal area, Reineke's self-thinning rule, competition-density index, Nilson's sparsity index, physiographic regions, miniature scale trial (microcosm)

1. Introduction

Carrying capacity can be regarded as the maximum population size or biomass of a species that a certain environment can support given finite resources (Helms 1998 , p.25). The concept of carrying capacity contains two meanings: a measure of environmental productivity and a description of equilibrial population density (Dewar 1984). Carrying capacity illustrates how environmental factors constrain the size of populations that can safely be attained; populations tend to stabilize at or fluctuate around these limits (Price 1999). In forestry, stockability, or stocking capacity (DeBell, et al. 1989, Hall 1983), shares similar concepts with carrying capacity. Stand stocking, which is a relative term, refers to the adequacy of a given stand density to meet desired management objectives (Bickford, et al. 1957). Stand carrying capacity can also be referred to as the maximum possible stocking of trees that a stand can sustain over a long term. Stand carrying capacity among physiographic regions may vary (Hasenauer, et al. 1994), depending on the resource and sink functions of the environment (e.g: solar radiation, nutrients availability, decomposition rate) (Durham 1991, Harms, et al. 1994), physical environmental limits (e.g: growing space), and the stand species and age composition (e.g: mixed stands, multiaged stands).

Stand basal area (BA), the sum of cross-sectional areas of all stem diameters at breast height in a unit area, is an informative measure of stand density and a satisfactory expression of stocking levels and stand carrying capacity (Bickford, et al. 1957, Burkhart and Tomé 2012, p.175-177) because it integrates the effect of both diameter and number of trees in a stand. Estimates from a fitted cumulative BA-age equation can be used to quantify stand BA carrying capacity, or, alternatively, BA estimates implied by maximum size-density relationships (MSDRs), denoted implied maximum stand BA, can be derived.

1.1 Maximum size-density relationship (MSDR) and its measures

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. Many MSDR measures have been developed by incorporating different size variables, such as average dominant tree height (Hart 1926), quadratic mean diameter (Reineke 1933), and plant weight (Yoda, et al. 1963). By comparing the MSDR measures of three different size variables derived from a common formulated structure, Burkhardt (2013) indicated while the differences aren’t large due to the choice of tree size variable, quadratic mean diameter proved most informative and was well ground in theory. Zeide (1987, 1995) argued that stem diameter is highly correlated to tree crown size, which is the vital stand size variable representing crowding of trees. Accordingly, implied stand BA carrying capacity of three diameter-based MSDR measures, Reineke’s self-thinning rule (STR) (Reineke 1933), competition-density (C-D) rule (Kira, et al. 1953) and Nilson’s sparsity index (Nilson 2006), was evaluated and compared in this study. The 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 (Vospernik and Sterba 2014, Zeide 2010).

1.2 Microcosms

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. 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, saving travel time to plot sites and security costs (Amateis, et al. 2003b).

Some microcosms have been used for forest soil nutrients and tree physiology studies (e.g: Davis, et al. 2007) while other microcosms have been designed for forest growth research (e.g: Smith and Hann 1984). An example is the loblolly pine miniature scale spacing trial installed on the Virginia Tech campus. This miniature scale spacing trial, 1/16 of an operational scale spacing trial previously established, has proven a useful experimental tool to simulate stand development (Amateis, et al. 2003a, 2003b, Russell, et al. 2009, Sharma, et al. 2007).

The purpose of this investigation was to estimate the stand BA carrying capacity in loblolly pine. Specifically, we evaluated the efficacy of three diameter-based MSDR measures for estimating stand BA carrying capacity among various physiographic regions and at different experimental scales. Further, we explicitly explored the effect of physiographic regions and experimental scales on the behavior of MSDRs and stand BA carrying capacity in order to provide a comprehensive view of potential stand density and stockings.

2. Materials and methods

2.1 Spacing trials

2.1.1 Operational scale trial

Limiting density is an important concept that can be addressed through spacing trials that incorporate with a wide range of initial planting densities. Measurements were obtained from a loblolly pine spacing trial that employed the plaid nonsystematic design from Lin and Morse (1975). The experiment was established at four locations in 1983: two in the upper Coastal Plain and two in the Piedmont.¹ Three nearly contiguous and compact factorial blocks were established at each site. In each block, a spacing factor (F) of 1.2 m 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 (1F×1F, 1.5F×1.5F, 2F×2F, 3F×3F), and 12 rectangular plots (1F×1.5F, 1F×2F, 1F×3F, 1.5F×1F, 1.5F×2F, 1.5F×3F, 2F×1F, 2F×1.5F, 2F×3F, 3F×1F, 3F×1.5F, 3F×2F). 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. A common open-pollinated family was planted at both Coastal Plain sites and a different open-pollinated family was employed at both Piedmont sites. Other than controlling competing vegetation with chemical herbicides in the first three years, no other management treatments were applied. A summary of field procedures can be found in Amateis and Burkhart (2012).

Groundline diameter (GLD) was measured at ages 1–5 and diameter at breast height (DBH) was recorded annually for ages 5–25. Total height was measured annually for ages 1–10 and biennially for ages 12–25. Each tree was examined for signs of disease or damage and assigned a

¹ A description of the physiographic regions in the southern US can be found in Wear and Greis (2012).

vigor code (dead, good, disease or insect damage, herbicide damage, other damage). Due to the damage of plots by ice storms, insect infestation or other serious disturbances after age 18, only the measurements from ages 5–18 were used for analyses. Quadratic mean diameter, average dominant tree height, numbers of trees per unit area, BA per unit area were computed.

2.1.2 Miniature scale trial

A miniature scale trial, or microcosm, was established in the spring of 1989 and again 1998. The experimental design was the same as the operational scale trial while the spacing factor (F) was 7.6 cm, that is, 1/16 of the operational scale trial. 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 recorded at the end of each growing season were combined for analyses in this study. 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.

2.2 Intensively managed plantation (IMP) plots

With only two replicates of the operational scale spacing trial in the Piedmont and Coastal Plain physiographic provinces, we utilized additional data from permanent sample plots in plantations in the two regions to contrast and compare results from the experimental plantings. In total, 170 permanent plots were established in 3–8-year-old intensively managed plantations (IMPs) across the natural loblolly pine growing regions (Piedmont, Atlantic Coastal Plain and Gulf Coastal Plain) during the period 1996–2000 (Amateis, et al. 2006). The plantations selected for plot installations were representative of current management and silviculture practice at the time; the locations of IMPs are shown in Russell, et al. (2012). The initial planting densities in IMP plots ranged from 1125–2250 trees/ha and the measurements were recorded at establishment and on a 2-year cycle subsequently. Each IMP installation received site preparation, fertilization and vegetation control suitable for sites as needed and were planted with genetically improved stock. Three kinds of vigor codes (live, dead, and thinned) were collected at each measurement. For each dead tree, the cause of death (lightening, disease or insects or others) was recorded. To ensure stands were in the self-thinning phase, unthinned plots with Reineke's SDI equal or greater than 750 trees/ha in the Piedmont and Atlantic Coastal Plain were selected for comparison with the results from the spacing trials.

154 2.3 Three diameter-based MSDR measures

155 2.3.1 Reineke's self-thinning rule (STR)

156 Reineke's STR (Reineke 1933) describes a linear relationship between maximum stand density
157 (N) and quadratic mean diameter ($\bar{D}_q$) on a log-log scale in fully stocked even-aged stands. That
158 is,

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

159 where Ln = natural logarithm; a, b = coefficients.

160 Reineke proposed a stand density index (SDI) for estimating and comparing the degree of
161 stocking in even-aged stands. SDI is defined as the number of trees per unit area when quadratic
162 mean diameter is equal to 25.4 cm (Eq.2). Reineke's SDI is expressed in the form

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

163 where in metric units N = number of trees per ha; $\bar{D}_q$ = quadratic mean diameter in cm; and all
164 symbols remain as previously defined.

165 2.3.2 Competition-density (C-D) rule

166 Similar to Reineke's STR, a logistic form of the C-D rule was introduced for describing trees
167 competition and thinning behavior (Kira, et al. 1953, Shinozaki and Kira 1956, Tadaki 1963).

168 For a given dominant tree height, quadratic mean diameter ($\bar{D}_q$) increased with decreasing
169 number of trees per unit area. The C-D expression can be shown as a four-parameter equation:

$$\bar{D}_q = \frac{1}{\alpha_0 \cdot \bar{H}_d^{\alpha_1} \cdot N + \beta_0 \cdot \bar{H}_d^{\beta_1}} \quad (3)$$

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

Theoretically, the coefficients of the C-D rule and Reineke's STR are algebraically interchangeable. The mathematical derivations were shown in Sterba (1987). Vospernik and Sterba (2014) indicated that the four-parameter C-D equation could be reduced to a three-parameter equation (Eq. 4) by substituting one parameter β_1 with the slope (b) in Reineke's STR.

$$\bar{D}_q = \frac{1}{\alpha_0 \cdot \bar{H}_d^{\alpha_1} \cdot N + \beta_0 \cdot \bar{H}_d^{-\frac{\alpha_1}{0.605}}} \quad (4)$$

2.3.3 Nilson's sparsity index

Nilson's sparsity index (Nilson 2006) focuses on the average distance between trees. Nilson (2006) assumed a linear relationship between stand sparsity (L) and quadratic mean diameter ($\bar{D}_q$), that is,

$$L = \sqrt{\frac{10000}{N}} \quad (5)$$

$$L = c_0 + c_1 \cdot \bar{D}_q \quad (6)$$

where $c_0, c_1 =$ Nilson's coefficients.

For a given species, each stand will approach the MSDR line on the L-D plane.

2.4 Stand carrying capacity estimation

2.4.1 Maximum stand BA

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):

$$G_{max} = \gamma_1 \cdot (1 - e^{\gamma_2 \cdot t})^{\gamma_3} \quad (7)$$

186 where G_{max} = maximum stand BA (m^2/ha); t = stand age (yr); $\gamma_1, \gamma_2, \gamma_3$ = C-R coefficients.

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

190 2.4.2 Implied maximum stand BA

191 The definition of stand BA is as following:

$$G = N \cdot \bar{D}_q^2 \cdot g \quad (8)$$

192 where G = stand BA (m^2/ha); $\bar{D}_q$ = quadratic mean diameter (cm); N = number of trees per ha;

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

194 Three MSDR measures (Reineke's STR, C-D rule and Nilson's sparsity index) were converted to
195 stand BA to obtain estimates of stand BA carrying capacity. For Reineke's STR, N is a function
196 of $\bar{D}_q$ (Eq. 1), denoted $N(\bar{D}_q)$. The implied maximum stand BA can be obtained by calculating N
197 in Eq. 8 from $N(\bar{D}_q)$ in Reineke's STR, namely:

$$G_{Rmax} = (e^a \cdot \bar{D}_q^b) \cdot \bar{D}_q^2 \cdot g = e^a \cdot \bar{D}_q^{b+2} \cdot g \quad (9)$$

198 where G_{Rmax} = implied maximum stand BA computed from Reineke's STR.

199 For the C-D rule, Sterba (1987) showed that stand BA can be computed from Eq. 3, that is:

$$G_{CD} = N \cdot \left(\frac{1}{\alpha_0 \cdot \bar{H}_d^{\alpha_1} \cdot N + \beta_0 \cdot \bar{H}_d^{\beta_1}} \right)^2 \cdot g \quad (10)$$

200 where G_{CD} = implied stand BA computed from C-D rule. Further, Sterba (1987) set the first

201 derivative dG_{CD}/dN equal to zero and solved the equation to get the implied maximum stand BA:

$$G_{CD\ max} = \frac{\bar{H}_d^{-(\alpha_1+\beta_1)}}{4 \cdot \alpha_0 \cdot \beta_0} \cdot g \quad (11)$$

202 where $G_{CD\ max}$ = implied maximum stand BA computed from C-D rule.

203 For Nilson's sparsity index, the calculation of implied maximum stand BA is similar to

204 Reineke's STR, that is:

$$G_{N\ max} = \left(\frac{100}{c_0 + c_1 \cdot \bar{D}_q} \right)^2 \cdot \bar{D}_q^2 \cdot g \quad (12)$$

205 where $G_{N\ max}$ = implied maximum stand BA computed from Nilson's sparsity index.

206 A list of formulas for computing implied maximum stand BA from three MSDR measures is

207 shown in Table 1. Reineke's STR was estimated with quantile regression (quantile=0.99), as

208 were the C-D rule coefficients (quantile=0.99) and Nilson's sparsity index (quantile=0.01), using

209 the package quantreg in R.

210 Table 1 Equations of implied maximum stand BA computed from diameter-based MSDR
 211 measures. (N=number of trees per ha; $\bar{D}_q$ =quadratic mean diameter (cm); $\bar{H}_d$ =mean dominant
 212 tree height (m); G=basal area (m²/ha); G_{max} =maximum stand BA (m²/ha); e=exponential
 213 constant; g = a constant, equal to $\pi/40000 \approx 0.00007854$; 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	$N = \left(\frac{100}{c_0 + c_1 \cdot \bar{D}_q} \right)^2$	$G_{N\ max} = \left(\frac{100}{c_0 + c_1 \cdot \bar{D}_q} \right)^2 \cdot \bar{D}_q^2 \cdot g$

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215 2.5 Effect of physiographic regions on stand carrying capacity

216 For both the operational scale spacing trial and the IMP plots, data were divided into two regions:

217 Piedmont and Atlantic Coastal Plain. The coefficients of three MSDR measures were estimated

for each region by methods described in “2.4 Stand carrying capacity estimation”. For estimation of Reineke’s STR, preliminary results showed that the assumption of a constant slope was valid in this study. Thus, the model is assumed to have a common slope for the two regions and an indicator variable (x_r) was added in Reineke’s equation (Eq. 1), that is:

$$\ln N = a + b \cdot \ln \bar{D}_q + c \cdot x_r \quad (13)$$

where $x_r = 1$, if plot is in the Piedmont; 0, if plot is in the Coastal Plain; a, b, c = coefficients; other symbols are the same as Eq. 1. Whether or not the self-thinning lines of the two regions are different was tested by evaluating the statistical significance of the coefficient “ c ” in Eq. 13.

Digging for more information of stand density, cumulative mortality was determined as:

$$M = \frac{N_0 - N_t}{N_0} \cdot 100\% \quad (14)$$

where M = cumulative mortality (%); N_0 = initial planting density (stems/ha); N_t = number of trees per ha at age t .

In addition, the tree form factor, height:diameter (H:D) ratio incorporating diameter at breast height (D) with tree height (H) was calculated. The t-test was used to compare the difference of means of H:D ratios between two physiographic regions.

2.6 Behavior of MSDRs and stand BA carrying capacity at two experimental scales

Three MSDR measures were estimated and converted to maximum stand BA_g for the miniature scale trial. The method of estimation of coefficients in the MSDR measures was the same as that used for the operational scale spacing trial. To compare the behavior of stand competition between two scales of spacing trials, a reduced segmented regression model developed by VanderSchaaf and Burkhart (2008) was used to project a diameter-density trajectory:

$$\text{LnN} = d_1 \cdot S_1 + (d_1 + d_2 \cdot [\text{Ln}\bar{D}_q - T]^2) \cdot S_2 \quad (15)$$

where $S_1 = 1$ 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, and $d_1, d_2 =$ coefficients.

3. Results and discussion

3.1 Estimates of stand carrying capacity

An estimate of maximum stand BA of 63.2 (m^2/ha) was obtained from the C-R equation coefficient γ_1 (Eq. 7). By age 18, the maximum stand BA was estimated at 58.2 (m^2/ha). Bailey and Ware (1983) reported maximum stand BA of 58.7 (m^2/ha) for 352 natural even-aged loblolly pine plots (20% were unthinned) in Georgia, which was close to what we obtained. Hasenauer, et al. (1997) reported maximum stand BA of 48.7 (m^2/ha) for 186 unthinned plots in operational plantings of loblolly pine without genetic improvement or intensive silvicultural treatments in the southeastern US, which was lower than the stand BA carrying capacity in this study. Their measurements were obtained between the ages of 20–37 and the initial planting density ranged from 667 to 2520 (trees/ha), which was lower than the spacing trials in this study. Also, the operational plantings contained some hardwood stems, which may account for the lower maximum stand BA for pine.

By contrast, Harms, et al. (2000) indicated that the “average” 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. The “average” stand BA in Hawaii is close to the “maximum” stand BA in this study. Similarly, in southern Brazil, the average stand BA for loblolly pine reached 58.7 (m^2/ha) at age 12 reported by Cardoso, et al. (2013), which is higher than the maximum stand BA at age 18 in

this study. These results imply that, for a given species, stand BA carrying capacity can be different among regions, including areas outside the species native range.

The implied maximum stand BA at age 18 in this study was estimated at 61.5, 61.5, and 55.3 (m^2/ha) from Reineke's STR, C-D rule, and Nilson's sparsity index, respectively. As shown in Fig. 1, $G_{R\ max}$ 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} after age 15. The difference between implied maximum stand BAs (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 (Table 2) were estimated from the measurements only at the 99th quantile, which were in the ages 12-18 range.

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 (Fig. 1). For Reineke's STR (Eq. 9), $G_{R\ max}$ 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. 11), $G_{CD\ max}$ 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. 12), maximum stand BA is

$$G_{N\ max} \propto \left(\frac{\bar{D}_q}{c_0 + c_1 \cdot \bar{D}_q} \right)^2 = \left(\frac{1}{\frac{c_0}{\bar{D}_q} + c_1} \right)^2 \quad (16)$$

Eq. 16 implies that if $\bar{D}_q$ increases to infinity, $G_{N\ max}$ converges to a constant. Thus, due to the structure of the equation, the trend of $G_{N\ max}$ becomes horizontal after age 12, which was different from trends of $G_{R\ max}$ and $G_{CD\ max}$ in Fig. 1.

In addition, the curves of $G_{R\ max}$ and $G_{CD\ max}$ merged at age 18. $G_{R\ max}$ was a function of quadratic mean diameter (Eq. 9) while the $G_{CD\ max}$ was a function of dominant tree height (Eq. 11). This result implied that either diameter or tree height can be used to estimate the stand BA carrying capacity. 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; our results showed that the number of plots (192 plots) in this study was adequate for estimating coefficients of the C-D rule.

Nilson's sparsity index is preferred for estimating stand BA carrying capacity. As mentioned above, one of the advantages is that $G_{N\ max}$ is 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, are needed to estimate $G_{N\ max}$. For fitting, Nilson's sparsity index, unlike Reineke's STR, doesn't require a logarithm transformation, thus avoiding transformation bias for predictions.

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

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

Figure 1 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.

3.2 Effect of physiographic regions on stand carrying capacity

Figs. 2a and 2b show that the MSDR lines between the two regions were significantly different ($p\text{-value} < 0.001$, $\alpha = 0.05$). The maximum stand BA or MSDR line in the Piedmont was higher than that in the Coastal Plain regardless of using data from the operational scale spacing trial or the IMP plots. For the operational scale spacing trial, by age 18, the maximum stand BA in the Piedmont and in the Coastal Plain were estimated at $59.2 \text{ (m}^2/\text{ha)}$ and $47.1 \text{ (m}^2/\text{ha)}$, respectively. These results are contrary to analyses by Hasenauer, et al. (1994) which showed the Atlantic Coastal Plain having the highest level of “stockability,” followed by the Piedmont as second highest and the Gulf Coastal Plain as lowest when using permanent plot data from operational plantings that were not genetically improved and were not managed with intensive silvicultural treatments

The implied maximum stand BA was similar to the maximum stand BA obtained by the C-R equation in both the Piedmont and the Coastal Plain (Fig. 3). Three MSDR measures reflected the difference of stand BA carrying capacity between regions while Reineke’s STR and Nilson’s sparsity index performed better than the C-D rule.

In this study, the site index in the Piedmont was lower than that in the Coastal Plain, which implied the site quality in the Piedmont was poorer. However, the results showed that the stand BA carrying capacity was greater in the Piedmont. Higher site quality did not guarantee higher BA yields. Two factors are involved in BA yields: tree diameter growth and tree mortality levels. A sharp decline of live trees caused the lower stand BA carrying capacity in the Coastal Plain. Tree mortality levels in the Coastal Plain were twice to three times higher than that in the Piedmont for both the operational scale spacing trials and the IMP plots (Figs. 4a and 4b). In the

325 operational scale spacing trial, the difference of tree mortality levels between the two regions
326 increased with the increase of planting density.

327 By examining the vigor code of each individual, only a small portion of trees suffered from
328 insect or disease damage in both regions. Trees at the operational scale spacing trial damaged by
329 insects, diseases, herbicides or other factors accounted for 3% and 8% of total trees in the
330 Piedmont and Coastal Plain, respectively; for the IMP plots, 10% and 23% of dead trees in the
331 Piedmont and Coastal Plain were damaged by insects or diseases. Other damages caused by fire,
332 lightening, wind or ice storm were not observed. Although the percentage of damaged trees was
333 greater in the Coastal Plain, more than 75% of trees didn't suffer from natural disturbances. The
334 difference of tree mortality levels between the two regions doesn't appear to be mainly and only
335 driven by natural disturbances in this study. The lower stand carrying capacity in the Coastal
336 Plain may be caused by other factors.

337 In addition, the mean of H:D ratios was significantly higher in the Piedmont than that in the
338 Coastal Plain ($p\text{-value} < 0.001$, $\alpha = 0.05$) shown in Table 3. Compared to the Piedmont, the
339 average diameter in the Coastal Plain was higher for a given tree height; higher average diameter
340 with lower stand BA implied the number of trees per unit area was lower. In contrast, stands with
341 more "slender" trees in the Piedmont had more surviving trees and BA yield.

Figure 2 Diameter-density trajectories in the Piedmont (P) and in the Coastal Plain (C), using the data from (a) operational scale spacing trial and (b) IMP plots. The intercepts of MSDR lines between the two regions were significantly different (p -value < 0.001).

Figure 3 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 (P) and in the Coastal Plain (C) using data from the operational scale spacing trials.

Table 3 The means of H:D ratios in the Piedmont and the Coastal Plain.

The mean of H:D ratios (95% CI)	Operational scale spacing trial	IMP plots
Piedmont	78.7 (78.5, 78.9)	81.9 (81.6, 82.2)
Coastal Plain	75.0 (74.8, 75.2)	80.5 (80.1, 80.9)
p-value	<0.0001	<0.0001

Figure 4 Cumulative mortality in the Piedmont (P) and in the Coastal Plain (C), using the data from (a) operational scale spacing trial and (b) IMP plots.

3.3 Stand behavior between operational and miniature scale spacing trials

The overall trend of the maximum stand BA_g in the miniature scale spacing trial (microcosm) (Fig. 5) was similar to the maximum stand BA curve in the operational scale spacing trial (Fig. 3). The maximum Reineke's SDI^2 of 1529 (trees/m²) for the miniature scale spacing trial was close to 1523 (trees/ha) for the operational scale spacing.

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 while $G_{N\ max}$ 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 spacing 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 .

For stand dynamics, the pattern of self-thinning in the miniature scale spacing trial was similar to the operational scale spacing trial (Fig. 2a). However, as shown in Table 5, self-thinning began from 48% to 57% of the maximum Reineke's SDI in the miniature scale spacing trial, while the occurrence of self-thinning ranged from 21% to 84% of the maximum Reineke's SDI in the operational scale spacing trial. In other words, for the miniature scale spacing trial, the effect of

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

initial planting density on the occurrence of self-thinning wasn't pronounced when compared to VanderSchaaf and Burkhardt's (2012) finding using the operational scale spacing trial data. One possible explanation might be the scale of the 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.

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)	(5.19×10^{-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 5 The implied maximum stand BA_g trajectories in the miniature scale spacing trials. The overall maximum stand BA_g was estimated by the C-R equation.

Figure 6 Comparison of the diameter-density trajectories among four square spacings in the miniature scale trial.

4. Conclusions

Our study evaluated alternate approaches to estimate stand BA carrying capacity and provided enhanced understanding of plant competition and forest stand dynamics. These results can provide guidance for managers when making decisions on planting density, thinning schedules and rotation ages.

Three diameter-based MSDR measures were evaluated for estimating stand BA carrying capacity with Nilson's sparsity index providing the most stable and reliable estimate. The flexibility of $G_{N\ max}$ can be used to evaluate the effect of physiographic regions and experimental scales on stand BA carrying capacity.

Stand BA carrying capacity in loblolly pine varied among regions. In this study, stands in the Piedmont carried more BA than those in the Coastal Plain of the southeastern US. By comparison with other studies, loblolly pine planted outside its original habitats may yield more BA per unit area. To better understand carrying capacity for a given species, we suggest that plots with the same experimental design across a wide range of regions are needed.

Maximum stand BA developed similarly at operational and miniature scales. The small scale experiment (microcosm) is an attractive option because it shortens the experiment time and reduces costs greatly.

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