STAND DENSITY AND CANOPY GAPS

Boris Zeide[1]

Abstract—Estimation of stand density is based on a relationship between number of trees and their average diameter in fully stocked stands. Popular measures of density (Reineke's stand density index and basal area) assume that number of trees decreases as a power function of diameter. Actually, number of trees drops faster than predicted by the power function because the number depends, in addition to tree size (diameter), on the area of gaps between tree crowns. The gaps are inevitable even in dense even-aged stands with sizeable crown overlap. Taking both factors of self-thinning (increasing tree size and gap area) into account improves estimation of stand density and clarifies several other issues.

INTRODUCTION

Competition among trees is one of the main factors determining their growth and survival. This factor, unlike many others, can be easily and often profitable controlled by thinning. The problem is to find an optimal level of competition. To tell whether it is too low or too high, we need (1) a method to assess the current level of competition in a given stand and (2) some benchmark of competition which can be linked to its optimal level. Stand density is a good proxy of many complex processes involved in competition among trees in a given stand. Foresters have done much to devise various measures of density and establish benchmarks of this variable. Still, there is plenty of room for improvement. The key point is to account for canopy gaps resulting from self-thinning. Though not as popular as basal area, stand density index is a most promising measure of density. This report will examine its advantages and disadvantages, propose a new measure of density accounting for canopy gaps, and identify normal and complete density levels.

STAND DENSITY INDEX

Reineke (1933) developed his index of density assuming that the relationship between the number of trees per unit area of fully-stocked stands and their average diameter is linear (on the log-log scale):

$$\ln N = \ln a - r \ln \frac{D}{25.4} \qquad (1)$$

In this equation, *a* is the density of fully-stocked stands, also known as normal or equilibrium density. It is measured by number of trees with a specified diameter (25.4 cm). This level of density is achieved when mortality matches the expansion of crowns, so that crown closure is supposed to remain constant. Reineke realized the relevance of this relationship to estimating density and proposed the stand density index, *S*:

$$S = N\left(\frac{D}{25.4}\right)^{r} \qquad (2)$$

This definition applies to stands with any stocking; however, parameter *r* must be found in fully-stocked stands. Reineke considered this parameter to be a constant equal to 1.605 for all species and locations. The precision he reported is curious, particularly because Reineke obtained this estimate guided by intuition rather than calculation. When MacKinney and Chaiken (1935) reanalyzed the same data using standard statistical methods, they obtained the power of 1.7070. On permanent plots established in young (average age of 20 years) loblolly pine (*Pinus taeda* L.) stands, Williams (1994, 1996) found the power of 1.5. Using mostly temporal and older plots (from 19 to 77 years) of the same species in the same region (northern Louisiana), Meyer (1942) came up with the value of 1.9.

Biological Interpretation of Reineke's Constant

The form and parameters of equations that reflect mechanisms of growth can be discussed in terms of biology, in addition to statistics. Such equations are useful not only for data description but for our understanding as well. As far as equation (1) is concerned, it can be shown that Reineke's constant is a measure of intraspecific competitive ability of trees, called self-tolerance by analogy with tolerance (Zeide 1985). Tolerant species utilize light of lower intensity and other resources more fully than do intolerants, and their canopies are denser. Therefore, they survive better in mixed stands than do intolerants of the same crown class and age. Tolerance is the interspecific competitive ability of trees.

Albeit tolerance predicts the success in competition with other species, it tells little about the ability of trees to coexist with conspecifics. In pure stands, the capacity of tolerant species to withstand shade is counterbalanced by their denser canopies, just as higher light requirements of intolerant species are matched by their sparser canopies. Light utilization and canopy density work in opposition, precluding any inference about the relationship between tolerance and mortality in pure stands. For managing plantations, we need to know a species self-tolerance, that is the ability of trees to compete with or tolerate conspecifics. Self-tolerance, and not tolerance, is relevant for determining optimal planting density, thinning intensity, and other activities in pure stands.

A sensible measure of self-tolerance is the proportion of trees, *-dN/N*, eliminated by a certain increase in average diameter, *dD/D*:

$$\text{Self-tolerance} = \frac{-dN/N}{dD/D} \qquad (3)$$

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[1] Professor of Forestry, School of Forest Resources, University of Arkansas at Monticello, Monticello, AR 71656-3468.

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The smaller the ratio, the fewer trees succumb with the same increase of diameter, and therefore, the more self-tolerant is the species. On the other hand, by differentiating Reineke's relationship [equation (1)], we obtain the following expression for *r*:

$$r = \frac{-dN / N}{dD / D} \tag{4}$$

The identity of (3) and (4) indicates that *r* is a measure of self-tolerance. Having this measure, we can compare ranking of tree species with respect to their self-tolerance and tolerance. For southern pines, the relationship is reversed: the least tolerant longleaf pine (*Pinus palustris* Mill.) was found to be the most self-tolerant, while the most tolerant slash pine (*P. elliottii* Engelm.), for which *r* is 25 percent greater, the least self-tolerant (Zeide 1985). This means that when average diameter in fully stocked stands of slash pine increases by 1 percent, they loose 25 percent more trees than do longleaf pine stands.

Doubts About Reineke's Index

Reineke's index is described in mensuration textbooks, sometimes used by researchers, but seldom by practicing foresters. The Forestry Handbook (Wenger 1984) mentions the index in passing and does not even define it. The acceptance of Reineke's index was hampered by the lack of biological interpretation and empirical faults. The "statistical basis" for the relationship advanced by Reineke is questionable and not altogether relevant; it is his belief that "stands of all ages on all sites have essentially the same characteristic frequency-curve form" (Reineke 1933). Many researchers noticed that number of trees drops faster than follows from the power function of diameter (Briegleb 1952; Meyer 1938, 1942; Spurr 1952; Zeide 1995). For this reason, Meyer (1938) used a curved-down (on the log scale) line. Wahlenberg's (1960) corrections of stand density index exhibit a similar downward trend.

A thorough, though not entirely consistent, examination of Reineke's index was done by Spurr (1952). While acknowledging that the correlation of stand density index with age is much lower than that of basal area, he still concluded that "since basal area is apparently fully as satisfactory as stand-density index in most cases, because it is simply obtained, and since it is a finite value in comparison to stand-density index which is an approximate value, it is to be preferred as a measure of density" (Spurr 1952).

Spurr's view was endorsed by the committee on stocking of the Society of American Foresters which, after 8 years of deliberation, found that Reineke's index changes with tree size and age and decided that the index "does not appear to be a good measure of density" (Bickford and others 1957). This tendency to dismiss what may be the most significant American contribution to forest science persists until present. The leading textbook of forest mensuration, published 50 years after Spurr's book, echoes his opinion and even his words: "in most cases BA [basal area] is fully as satisfactory as stand-density index, and because it is more simply obtained, it is preferred as a measure of density" (Avery and Burkhart 2002). It may be that Reineke's index is not a good measure of density, but it is the best we have. At least it does not lead to the confusion between overstocked and understocked stands of the same species as basal area does. However, the relationship between the number of trees and diameter may be not as simple as Reineke believed.

TWO CAUSES OF SELF-THINNING

Natural mortality (self-thinning) is caused by two factors: increase of tree size [represented by diameter in equation (1)] and decrease of tolerance, which leads to the accumulation of the area of gaps between tree crowns. To understand why gaps are inevitable, even in dense stands with a sizeable overlap of crowns, let us consider the dynamics of canopy closure.

Canopy Closure in Fully Stocked Stands

Canopy closure is a compromise between two opposing processes: lateral growth of crowns, which increases horizontal closure and mortality of trees, which diminishes it. The following arguments suggest that, after crown closure at about the time when height growth peaks, the second process predominates, and the area of gaps builds up with age and tree size: (1) As trees grow older and taller, they allocate an increasing proportion of their resources to support and maintain the crown. Unable to invest as much resource to adapt to deficiency of light as do younger trees, each year trees become less tolerant to shade; (2) with age, the size of a gap created by a fallen tree increases, while the ability of neighboring trees to close the gap decreases. Although the same factors (increased size of dying trees and decreased growth of their neighbors) reduce mortality, due to declining tolerance (and self-tolerance), canopy closure diminishes; (3) when other factors are equal, the ratio of average crown length to crown width increases with diminishing canopy closure. A sample across many forest stands shows that crown length increases faster than crown width (Zeide 1991); and (4) seed production increases with age and tree size, and it is of selective advantage for older trees not to choke their progeny but loosen the canopy and provide light for advance regeneration.

The first process of crown enlargement is not purely physical. Its effect is determined by the level of tolerance or, in pure stands, of self-tolerance of a species. The second process of gap accumulation results from the change of this level. Our understanding of density and stand dynamics in general will benefit from assessing each process (increasing average crown size and diminishing closure) separately.

Augmenting Reineke's Relationship

If number of trees is a function of two predictors instead of one, it is natural to add to equation (1) a module describing the diminishing crown closure. This module would unload the power of diameter (parameter *r*) from representing the change in closure, in addition to tree size. To construct such a module we need to select its form and a driving variable. The observations that the number of trees falls faster than the power function suggest the exponential form. Because tolerance decreases with increasing age and tree size, either of these variables can be used to drive the module of canopy closure. Thus, the relationship between number of trees and average diameter in fully stocked stands can be written as:

$$\ln N = \ln a - b \ln \frac{D}{25.4} - c(D - 25.4) \tag{5}$$

where *a* is normal stand density, *b* is the rate of tree mortality caused by the increase in crown size, and *c* is the mortality rate due to diminishing canopy closure. Accordingly, stand density index is:

$$S = N\left(\frac{D}{25.4}\right)^{b} e^{c(D-25.4)} \tag{6}$$

As does Reineke's index, equation (6) defines stand density as the number of trees per unit area with $D = 25.4$ cm (this is why 25.4 is subtracted from *D* in the closure module). This definition applies to any even-aged stand though, as with Reineke's parameter *r*, parameters *b* and *c* have to be found in fully stocked stands. The definition [equation (6)] does not impose canopy gaps. If canopy closure is complete, *c* would be 0 and equation (6) would be reduced to equation (2). Equation (5) explains why steeper slopes are observed in older stands with larger diameters [1.9 reported by Meyer (1942) as compared with 1.5 found in younger stands observed by Williams (1994, 1996)]. When number of trees is approximated by a power function of diameter [equation (1)], parameter *r* increases with diameter because it equals:

$$r = b + \frac{c(D-25.4)}{\ln\frac{D}{25.4}} \tag{7}$$

DATA

Equations (1) and (5) were fitted to the data from one of the oldest active thinning and pruning studies of loblolly pine located near Monticello in southeastern Arkansas. This study was established on 40 plots in a fully stocked ($S = 629$) 12-year-old plantation. Site index is 20 m (base 25 years). Five control plots were added at age 27. Reineke's slope for these control plots and 40 plot measurements before thinning was $r = 1.61 \pm 0.06$ ($R^2 = 0.95$, average number of trees per ha = 1,015). The height of even-digit upper stem diameters was measured by a Zeiss Teletop (lately by a Criterion 400). As a result, we have reliable estimates of total and merchantable volumes obtained using Grosenbaugh's height accumulation method. Tree diameters have been measured 11 times, the last time at age 43, which exceeds the rotation age for intensively managed loblolly pine plantations. A more detailed history of the study, description of methods, and the complete set of these data can be found on: http://www.afrc.uamont.edu/growthyield/montthinprun/index.html. The unmanaged plots of these data can be used to fit equation (5), though the small number of observations (70, of which 40 are at age 12) would make it difficult to obtain needed precision. A convincing way to check Reineke's parameter is to use his data. Such data were obtained by digitizing Reineke's (1933) Figure 7 B-E that depicts the number of trees and average diameter of fully stocked stands of southern pines. The stands were measured once and, as Reineke indicates, those with larger diameters may be on poorer sites.

RESULTS

The values of parameter *b* obtained by fitting equation (5), using SAS Proc Model, to the unmanaged plots of the Monticello study are 1.3-1.4 (table 1). However, the insufficient number of points (70) makes the error so large as to preclude any definite conclusion. The results from Reineke's data for southern pines are more certain (table 2) and allow one to conclude that: (1) Parameters *b's* are consistently lower than *r's*, which shows that gaps indeed increase with average diameter and, therefore, age; (2) as do Reineke's parameters, *b's* change with species and can serve as a measure of their self-tolerance; (3) both the Monticello and Reineke's data suggest that for loblolly pine $b = 1.35$; (4) similarity of these estimates (and those obtained by the growth approach below) justifies fixing this parameter to obtain more precise estimates of parameter *c* for the Monticello data (table 1); (5) the thinning rates of the canopy closure module (*c's*) are virtually identical for the studied southern pines and do not appear to be related to self-tolerance; and (6) the smaller value of *c* (0.0125) for the Monticello data may be a result of constant and relatively high site quality. It is likely that this parameter (but not *b*) is larger for poorer sites where usually canopy is less dense. This connection is supported by Reineke's data with its greater *c* (0.017) and by the site quality which decreases with stand diameter.

Table 1— Parameters of equation (5, log-transformed and untransformed) fitted to the unmanaged plots of the Monticello study

Predicted variable	*a*	*b*	*c*	R^2
lnN	619 ± 21	1.40 ± 0.55	0.011 ± 0.024	0.944
N	629 ± 23	1.31 ± 0.62	0.014 ± 0.029	0.948
lnNN	629 ± 15	1.31 ± 0.39	0.014 ± 0.018	0.945
				0.949
		Fixed b = 1.35		
lnN	621 ± 11	1.35	0.013 ± 0.002	0.945
N	629 ± 18	1.35	0.012 ± 0.003	0.949
lnNN	629 ± 9	1.35	0.012 ± 0.002	0.946
				0.950

R^2 = proportion of explained variance. Number of observations = 70

DISCUSSION

Quantifying Stand Characteristics

The proposed relationship between a number of trees and their diameter in fully stocked stands [equation (5)] clarifies self-thinning and leads to more precise definitions for several stand characteristics.

Maximum Density Index

Equation (5) accounts for the two self-thinning processes explicitly and allow us to reconstruct maximum index. Although in equation (5) *a* is the same as in (1), equation (5) contains another constant factor: *exp(*25.4*c)*. Actually, gap accumulation starts with $D = 0$ and not $D = 25.4$. Maximum stand density index, S_{max} is equal to the product of normal density index *a* and *exp(*25.4*c)*:

$$S_{\max} = ae^{25.4c} \tag{8}$$

This equation provides two density benchmarks: normal (with natural gaps) density, *a*, and complete (without gaps) density S_{max}.

Table 2—Comparison of parameters of equations (1) and (5) calculated using Reineke's (1933) data for southern pines.

Pine species	*N*	*r*	*a*	*b*	*c*
Loblolly	127	1.72 ± 0.04	729 ± 17	1.35 ± 0.21	0.017 ± 0.009
Longleaf	191	1.46 ± 0.04	649 ± 21	1.23 ± 0.19	0.015 ± 0.012
Shortleaf	179	1.98 ± 0.03	740 ± 12	1.71 ± 0.15	0.015 ± 0.008
Slash	121	1.87 ± 0.05	712 ± 18	1.58 ± 0.23	0.017 ± 0.013

N = number of temporary fully stocked plots.

Equation (5) explained 85-94 percent of variance, which was about 0.2 percent more than the proportion explained by equation (1).

Canopy Closure and Gap Proportion in Fully Stocked Stands

In normal stands described by equation (5) maximum density cannot be attained because it is diminished by the term *exp(-cD)*, which is the proportion of canopy closure. The complementary gap proportion is:

$$Gap\ proportion = 1 - e^{-cD} \tag{9}$$

For stands with $D = 10$ cm, it is 0.12 (if $c = 0.0125$), while for $D = 40$ cm the proportion is 0.39.

Maximum Stand Diameter

Decreasing self-tolerance and gap accumulation makes inevitable the decomposition of even-aged stands. Although stand decomposition is a continuous process, there is a moment when density of trees drops below a point where they stop competing with each other. Beyond this moment, the even-aged stand does not exist. What remains are lone trees that do not affect each other. Average diameter at this moment can be called maximum stand diameter. It is easy to detect this transition from separate trees to a stand, when density increases in young plantations with different spacing until trees start competing with each other and their diameter increment declines. This level of density has been documented in many spacing trials. For loblolly pine, it is equal to $S_{min} = 135$. This minimum level of stand density index was calculated using the above definition [equation (6)] with $b = 1.35$ and $c = 0.0125$] as the average of 11 paired indices (immediately before and after the onset of competition) from 4 different sources, including the pioneering Correlated Curve Trend study conducted in South Africa (Craib 1947).

Canopy closure [*exp(-cD)*] can be viewed as the ratio of the actual and maximum density indices. When the actual index $S = S_{min}$, the ratio equals:

$$\frac{S_{\min}}{S_{\max}} = \frac{135}{629e^{0.3175}} = e^{-cD_{\max}} \tag{10}$$

Hence, $D_{max} = 149$ cm.

Self-tolerance

Equations (3) and (4) identified *r* as a measure of self-tolerance. This neat result may be too simple. As does tolerance (Zeide 1985), self-tolerance is likely to decrease with age and tree size rather than stay constant. Having an improved relationship between a number of trees and diameter [equation (5)], we can differentiate it with respect to diameter and redefine self-tolerance as $b + cD$.

This measure can be improved by reversing it, so that high values correspond to high self-tolerance and by setting its minimum (absence of self-tolerance) to 0. This can be done by dividing the maximum value ($b + cD_{max}$) by the actual value and subtracting 1:

$$Self - tolerance = \frac{c(D_{\max} - D)}{b + cD} \tag{11}$$

In one number this measure captures three parameters of growth and survival.

Stand Density

Stand density is supposed to describe a degree of tree crowding. A dense stand means a well stocked stand, which makes the term "stocking" redundant. Density is a relative concept; it requires two quantities for its definition: one specific to a given forest stand and the other a standard common to all stands of a given species. Stand density index defined by equation (2) or (6) cannot express density because the standard varies among species. For example, Reineke (1933) found that for red fir (*Abies magnifica* A. Murr.) it is over two times larger than for loblolly pine. Therefore, the same density index means quite a different density for the fir and the pine stands. The advantage of Reineke's index is that this standard can be expressed by a single number rather than a vector of maximal basal areas. Although Reineke (1933) did not combine actual indices with species-specific standards into a single measure, he reported the extreme values for tree species he studied.

The density of stands with complete crown closure is a suitable density standard. Now when we know how to calculate it, stand density (not index), *I*, can be defined as the ratio of the index and maximum density:

$$I = \frac{S}{S_{\max}} = \frac{N}{a}\left(\frac{D}{25.4}\right)^{b} e^{c(D-50.8)} \tag{12}$$

For loblolly pine, normal density is $I = exp(-25.4c) = 0.73$.

Why b < 2?

Scarcity of growth resources represented by stand density depends largely on the area of the crown faces of neighboring trees intercepting the chief resource, light. In Euclidean geometry area has two dimensions, and the power of stem diameter that represents the crown area in the density index should be about 2. This would be the case if crowns were solid objects completely blocking or intercepting all the light. Then the effect of density would be substantially more detrimental to growth and survival than it actually is with $b = 1.35$. This number reflects the fact that crowns are highly porous. They can be viewed as a collection of holes conducting sunlight and gases or as a multi-level hierarchy of clustered dots (pigment molecules and chloroplasts).

Euclidean geometry with its integral spatial dimensions does not work for many natural objects such as trees and their crowns. Crowns are fractals; they are hybrids of surface and volume with spatial dimensions [called by Mandelbrot (1983) “sponge dimensions”] between 2 and 3 (Zeide and Pfeifer 1991). The dimensions of their faces, named “sieve dimensions,” vary from 1 to 2. Though not yet reported in literature for loblolly pine, they can be easily calculated using photographs. Sponge and sieve dimensions are related only by an inequality; their difference is less than one (Pfeifer and Avnir 1983). For loblolly pine crowns, sponge dimension was found to be 2.3 (Zeide 1998), which means that sieve dimension might be close to the constant component of self-tolerance, $b = 1.35$.

Stand Density Index and Basal Area

Basal area has a practical advantage over stand density index; it can be easily measured by point sampling. Foresters are familiar with this measure and use it widely to select trees for thinning. Therefore, it makes sense to express practical recommendations in terms of basal area. This can be done using these formulas:

$$BA = \frac{\pi 25.4^b e^{25.4c}}{40000} D^{2-b} e^{-cD} S = \frac{D^{0.65} S}{117.62 e^{0.0125D}} \tag{13}$$

and

$$S = \frac{40000}{\pi 25.4^b e^{25.4c}} D^{b-2} e^{cD} BA = 117.62 \frac{e^{0.0125D}}{D^{0.65}} BA \tag{14}$$

Application to Other Species, Sites, and Stands

Although the improved stand density index [equation (6)] is developed for loblolly pine, it may be applicable to other species, because the main thing about the equation that is species-specific is self-tolerance, which stands behind many model parameters. This characteristic, rather than botanical name or needle length, identifies loblolly pine in the developed models. They may help to manage other species as soon as their self-tolerance is known.

In this study, self-tolerance is shown to be a function of species and diameter. It is not clear whether self-tolerance also changes with site quality. Even though sparser canopies of stands on poorer sites transmit more light, the stands may be unable to utilize it to the same extent as do those on better sites. Here again the dual nature of self-tolerance leads to the question whether an increasing amount of available light balances its decreasing utilization. If so, self-tolerance would be site-invariant.

For uneven-aged and mixed stands, stand density index can be calculated as $\Sigma\, d_i^b\, exp(c\, d_i)$, where d_i is diameter of individual trees or average diameter of trees of the same species. The parameters of the index and growth equations have to be known for each species.

The presented model may be used to estimate damage caused by insects, diseases, and other disturbances. This damage often appears as canopy gaps. In the field, it is hard to separate these from the discussed gaps resulting from decreasing self-tolerance and get unbiased assessment of damage. The established dynamics of undisturbed canopy closure permit us to do this analytically. The improved definition of stand density, and specifically normal density [parameter *a* in equation (5)], is even a more convenient standard. It captures in a single number the state of forest stands regardless of their species, age, diameter, and site.

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