Self-thinning

Introduction

Self-thinning is the natural process whereby numbers of trees per unit area decrease as average tree size increases over time. It is a process intrinsic not only to oak forests but to all forest and plant communities whose composition and structure are influenced by competition for growing space. Whereas self-thinning is a process, the term stand density refers to various expressions of the absolute or relative amounts of an attribute of tree populations (e.g. numbers of trees or stand basal area) per unit land area. As might be expected, the two concepts are closely connected. Together, they rank among the most important concepts in forest ecology and silviculture.

Self-thinning

The principle of *self-thinning* is most easily described by the temporal changes that occur in the numbers of trees in undisturbed even-aged stands. However, self-thinning also occurs in uneven-aged stands. According to this principle, the finite growing space of a stand is occupied by progressively fewer trees as average tree size increases with stand age. Trees at a competitive disadvantage die from crowding and suppression as stands approach a limiting number of trees of a given average size that can coexist within an area. As stands reach the stem exclusion stage of development (Chapter 5), tree crowns expand to fill the available growing space. Crown expansion continues until an upper limit of tree crowding is reached. Thereafter, stands follow a relatively predictable course of density-dependent tree mortality as numbers of trees per unit area decrease with increasing average tree size. It is generally assumed that the combined effects of crown expansion and tree mortality are compensatory so that canopy closure is always maintained except in the presence of 'irregular' mortality. The latter may be caused by such factors as air pollution, high winds, flooding, epidemic insect and disease outbreaks, and other factors.

Reineke's model

Reineke's model for defining average maximum stand density expresses the negative relation between number of trees per unit area and average stand diameter in undisturbed, even-aged stands (Reineke, 1933). Plotting the logarithm of number of trees over the logarithm of mean stand diameter produces a straight line. The relation is given by:

$$\log(N) = a' + b[\log(D)], \tag{6.1}$$

where N is number of trees per unit area, D is the diameter (dbh) of the average tree, and a' and b are constants for a given species or group of species, where the constant b defines the slope of the line. The non-linear analogue of Equation 6.1 is given by:

$$N = aD^b \tag{6.2}$$

The relation has often been used to describe the average maximum limits of stand density and, by extension, to provide a relative measure or index of stand density (Reineke, 1933). Similar models of self-thinning based on the relation between numbers of trees and tree height are used in European forestry. Such models can be empirically derived by regression analysis and other statistical methods (Weller, 1987b) using data from temporary or permanent field plots from undisturbed stands encompassing a wide range of average stand diameters within a given forest type. Data from permanent plots with repeated measurements are preferred because periodic mortality is actually observed, which reduces assumptions about the self-thinning process (Zeide, 1987). Stands selected to define a line or limit of average maximum stand density should be at or near the upper limits of stand density with respect to their average diameter. The resulting line showing number of trees per acre by mean stand dbh is sometimes interpreted as a *self-thinning line*, or line of 100% relative density (Fig. 6.1). The line provides a useful definition of the upper limits of stand density because the number of trees per unit area and mean dbh are highly correlated.

Reineke (1933) postulated that the coefficient *b*, which determines the slope of the self-thinning line (Equations 6.1 and 6.2), assumes a value close to -1.605 for all tree species. For even-aged, upland oak forests in the eastern United States dominated by white, black, scarlet and chestnut oaks, the estimated slope coefficient was -1.5 based on temporary plot data from undisturbed stands ranging in site index from 50 to 80 ft (Fig. 6.1). Data from permanent plots in similar oak stands in the Central Hardwood Region produced a self-thinning line with a slope coefficient of _1.57 (Fig. 6.1).

Over time, stands lying below the self-thinning line will grow and move towards the line. On approaching the self-thinning line, stand development trajectories converge with the self-thinning line. Stand development then proceeds along the line from upper left (younger stands) to lower right (older stands) (Fig. 6.1). However, density-dependent mortality does not occur among trees with equal probability; it is concentrated among the suppressed trees. The overall rate of mortality thus is greatest during the stem exclusion stage of stand development, which is when a large proportion of trees succumb to suppression.
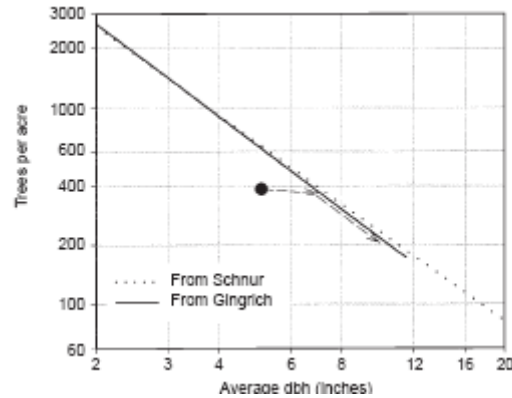
Fig. 6.1. Self-thinning lines (lines of average maximum stand density) for even-aged upland oak forests in the eastern United States based on the Reineke model. The dotted line is derived from Schnur's (1937) stand table for mixed upland oak stands widely distributed across the eastern United States. The solid line is derived from Gingrich's (1971) stand table for mixed upland oak stands in the Central Hardwood Region. The arrow from a hypothetical disturbed stand represented by the dot on the graph illustrates a typical trajectory of convergence with the Gingrich-based self-thinning line. Trajectories of stands below the self-thinning line generally move slightly downward from left to right. The downward trend results from competition-induced mortality, which occurs even in stands below average maximum density. After convergence with the self-thinning line and in the absence of further disturbance, the trajectory continues along the self-thinning line. The slope coefficient for the Schnur-based self-thinning line is -1.50 and for the Gingrich-based line is -1.57.

The _3/2 rule

Another approach to defining the self-thinning line is based on the relation between average total plant biomass and number of plants per unit area in single-species populations undergoing density-dependent mortality (Yoda *et al.*, 1963). The power function model, similar to Equation 6.2, is used to describe the relation. However, in this case the model expresses the relation between average plant dry weight (biomass), w, and number of plants per unit area (N) such that:

$$w = aN^b \qquad\qquad [6.3]$$

where a and b are usually estimated by regression from experimental data or field observations. Alternatively, the relation can be expressed as total plant weight (W) per unit area by:

$$W = a'N^{b'} \qquad\qquad [6.4]$$

The _3/2 power relation is displayed with N on the horizontal axis, in contrast to Reineke's model, where N is displayed on the vertical axis. Self-thinning for the _3/2 power relation thus graphically proceeds from lower right (younger stands) to upper left (older stands) along the self-thinning line (Fig. 6.2).
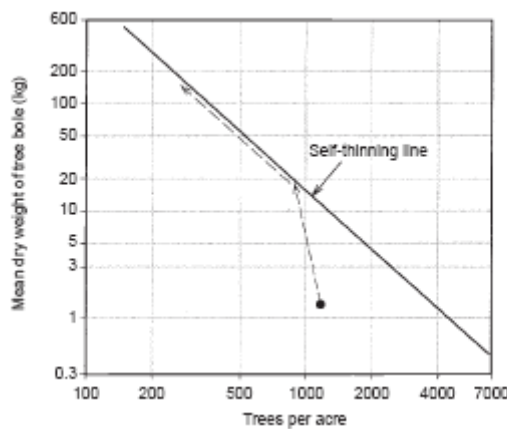
Fig. 6.2. A self-thinning line (line of average maximum stand density) for normally stocked even-aged upland oak forests in the eastern United States based on the relation between average dry weight of tree bole (inside bark) and number of trees per acre. The relation is conceptually similar to Reineke's model (Fig. 6.1), but differs in format. The arrow from a hypothetical disturbed stand represented by the dot on the graph illustrates a possible trajectory of convergence with the self-thinning line. As stand biomass increases and the number of trees per acre decreases over time, the stand trajectory moves upward and to the left along the self-thinning line. (Adapted from Schnur 1937)

Numerous studies have shown that b, the slope coefficient in Equation 6.3, approximates -1.5 (and equivalently, $b' = -0.5$ in Equation 6.4) for many plant species including herbs, shrubs and trees (Yoda *et al.*, 1963; Harper, 1977; Miyanishi *et al.*, 1979; White, 1985; Weller, 1987a). The relation consequently has become known variously as the '-3/2 power law of self-thinning', the 'self-thinning rule' and the '-3/2 rule'. However, the relation is herein referred to as a rule rather than a law because of its demonstrated lack of generality (Sprugel, 1984; Weller, 1987a; Zeide, 1987; Norberg, 1988; Lonsdale,1990) and the absence of a supporting theory (Hutchings, 1983). Discrepancies between observed slope values and -1.5 nevertheless have been interpreted as experimental error because of the coefficient's presumed generality (Miyanishi *et al.*, 1979; White, 1981). The rule also is purported to be independent of environmental factors (Yoda *et al.*, 1963; White and Harper, 1970), and to be applicable to species mixtures as well as single-species stands (Westoby, 1984; White, 1985).

The -3/2 rule can be interpreted geometrically. The rule assumes that plant weight, w, is proportional ( ) to plant volume, v, which in turn is proportional to any linear plant dimension on which volume depends raised to the third power:

$$v \quad w = aN^b \qquad\qquad\qquad [6.5]$$

If we select crown diameter (Cd) as a linear dimension of interest, then (Cd) $\quad aN^b$. To conceptualize the relation geometrically, it is convenient to consider (Cd) proportional to a cylinder representing the 'exclusive space' of a tree (Norberg, 1988). Then (Cd), which is proportional to the cylinder's cross-sectional area, can be used to represent crown area. Further, the cylinder's height is assumed proportional to crown diameter. This three-dimensional space conceptually envelopes the tree, extending downward from the top of the crown to its corresponding 'exclusive ground area' and into its soil space. The volume of exclusive space also can be viewed as a hexagonal column, which conceptually allows for symmetrical packing of trees without producing crown overlap or unoccupied area as in circular crown areas (Fig. 6.3). The explanatory value of this simplified geometric view and its relation to the -3/2 rule is apparent from the geometric relation between the volume of a cylinder and its diameter (i.e. volume is equal to the cylinder's squared diameter raised to the 3/2 power). Note that this relation only holds when the cylinder's height is proportional to its diameter.

To satisfy the geometric analogy for the -3/2 power rule, the thinning-rule model must provide a measure of Cd^2. Such a measure is given by N, the number of trees per unit area (Equation 6.3). Because the reciprocal of N represents the area occupied by the average tree, N is related to crown area and thus crown diameter (Cd^2). For every unit increase in crown area, the exclusive space (volume) of a tree increases by 3/2. So, given a finite amount of growing space, the number of trees (N) in that space must decrease at a rate of -3/2 per unit increase in crown area. To conform to this geometric model, however, a tree must maintain the same height-to-diameter ratio during self-thinning (Fig. 6.3). Accordingly, the various tree structures, including bole and crown, must remain proportionately similar during self-thinning (Yoda *et al.*, 1963). Such constancy of proportions is known as *isometry* or *geometric similarity* (McMahon and Bonner, 1983; Norberg, 1988).
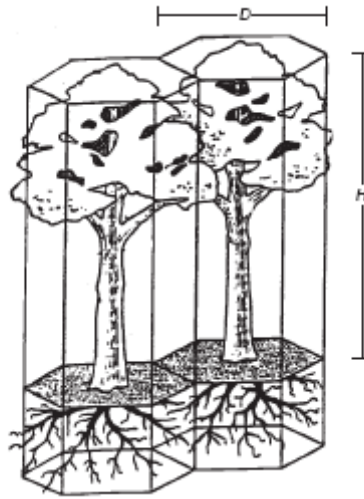
Fig. 6.3. The 'exclusive space' of closely packed trees. *D* is the diameter of the 'exclusive ground area' associated with each tree's crown area and *H* is tree height. The thinning rule theory implies that the ratio of *D:H* remains constant throughout stand development. (Redrawn from Norberg, 1988, with permission from the University of Chicago).

Under the -3/2 power rule, coefficient *b* (Equation 6.3) is assumed to be -3/2 for all species. In contrast, coefficient *a* varies among species and determines the intercept (or elevation) of the thinning lines. This coefficient has been termed the 'packing constant' (Norberg, 1988) because it reflects the proportion of space occupied by plant biomass and the average plant biomass per unit of ground area. Coefficient *a* thus increases with increasing density, or packing, of plant parts within a tree's exclusive space. Coefficient *a* also has been theorized to be related to the mass of mechanical tissue (bolewood in the case of trees) required to support a unit area of canopy (Givnish, 1986).

Relation between Reineke's model and the _3/2 rule

The diameter of a tree raised to some power between 2 and 3 equals its volume. For many species, the value of the exponent has been shown to be near 2.5 (Yoda *et al.*, 1963). Reineke's model and the -3/2 rule therefore are related by the approximate relation between average tree volume, *v*, and tree diameter, *D*, where

$$v = D^{2.5} \qquad\qquad\qquad [6.6]$$

From Equation 6.2 it then follows that

$$D^{2.5} \quad N^{2.5/b} \qquad\qquad\qquad [6.7]$$

When *b* = -1.605 in Equation 6.1 (Reineke's postulated constant), the relation becomes:

$$v = N^{-1.56} \qquad\qquad\qquad [6.8]$$

where the exponent approximates -3/2 (Zeide, 1985). In postulating a constant of -1.605, Reineke was implying, intentionally or not, that the relation between a tree's growing space and its diameter is *not* constant (i.e. not isometric). To be consistent with the assumption of constancy of tree proportions (isometry) inherent in the -3/2 power rule, the Reineke model must assume a slope constant of -2.

Oak forests and the _3/2 rule

Knowledge of the limiting relation between numbers of trees and volume per tree in oak stands is silviculturally useful. The relation can be used as a standard against which other stands can be measured. The -3/2 power rule attempts to describe this limiting relation in general terms for a wide range of plant communities. But to what extent do oak forests conform to the -3/2 power rule?

Evaluation of the rule can be divided into two questions. First, does the mathematical form of the model (i.e. the power function) adequately express the relation? Second, is the slope coefficient of -3/2 universally *Self-thinning and* applicable? If the answer to the first question is no, then the second becomes irrelevant. However, rejection of -3/2 as a universal slope coefficient does not, by itself, negate the utility of the model form.

Evaluating conformance of oak forests to the -3/2 power rule is complicated by three factors. First, oak yield tables are the only comprehensive sources of information. But yield tables seldom report total tree biomass or volume; most yield tables include only bole volume, which must substitute for bole biomass. Moreover, even if bole mass were measured directly, it is unlikely to be a constant fraction of total tree mass (Sprugel, 1984). Although information on the allocation of biomass to below- and above-ground portions of oaks is sketchy, there is evidence that allocation varies greatly with site quality and between trees of coppice and non-coppice origin (Canadell and Rodà, 1991). Second, most oak stands are comprised of a mixture of species. This confounds the effects of competition within and among species, which have fundamentally different explanations in relation to the thinning rule (Zeide, 1985; Norberg, 1988; Weller, 1989). Variation in wood density among species can also introduce error into coefficient estimates. Third, yield tables available to evaluate self-thinning relations for oak have been smoothed by hand-fit curves or other unspecified methodologies. As such, they represent models, not data (Weller, 1987a). This obscures variation in the original data and may introduce other possible errors (Lonsdale, 1990).

Despite these problems, it may be of interest to evaluate the -3/2 rule in relation to existing yield tables. Based on three oak yield tables for the midwestern and eastern United States, the line representing the relation between bole volume and number of trees produced slope coefficients that ranged from -1.7 to -2.2 (Fig. 6.4). Those estimates were based on substituting bole volume for w in Equation 6.3. The yield table values fit the power function with negligible error (Fig. 6.4), which indicates that their developers deemed this function to adequately describe the self-thinning line.

The tenuous conclusions from the above empirical evidence indicate that self-thinning lines in oak forests: (i) show varying proximity to the theoretical -3/2 slope; and (ii) are nominally, if not statistically, more negative than -3/2. Other investigators have concluded that self-thinning lines based on yield tables are likely to have slopes steeper than -3/2 because only portions of trees (boles) are represented, and because they include only trees above some minimum size (Harper, 1977; Lonsdale, 1990). The latter factor may explain, in part, why the yield tables for the Connecticut oak stands (Fig. 6.4C), limited to stems 2 inches dbh and larger, produce a steeper thinning line than either the upland oak or the Wisconsin yield tables, which included stems 0.6 inch dbh and larger (Fig. 6.4A and B).
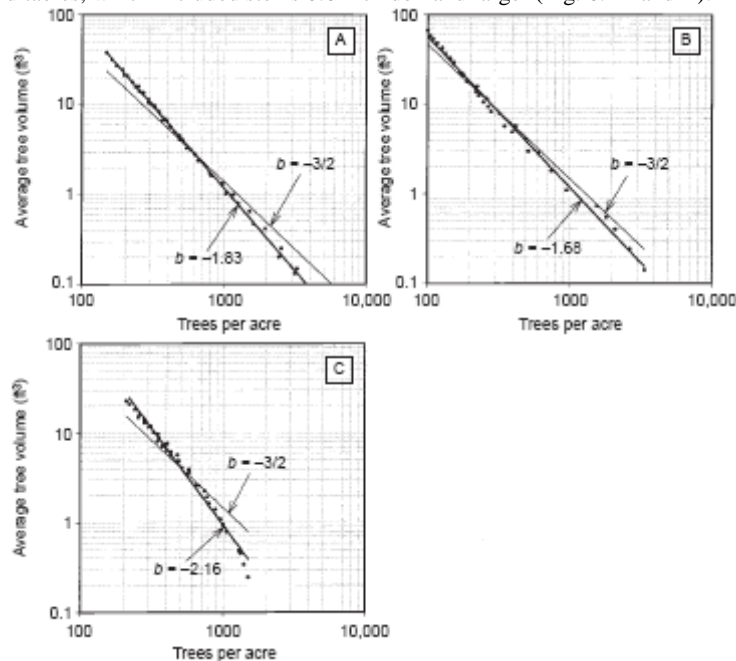

Fig. 6.4. Self-thinning lines for oak stands derived from published yield tables compared to the -3/2 thinning rule line. (A) From yield tables for even-aged upland oak stands in the central and eastern states. (From Schnur, 1937.) (B) From yield tables for mixed hardwood stands dominated by northern red oak in southwestern Wisconsin. (From Gevorkiantz and Scholz, 1948.) (C) From yield tables for mixed oak stands in Connecticut. (From Frothingham, 1912.) Heavy lines are fit by linear regression to table values (shown by dots); b is the slope coefficient. Each regression fit is based on the model:
$\log_{10}(v) = a + \log_{10}[b(N)]$
where v is the volume of the average trees, N is stand density (trees acre^{-1} and $\log_{10}$ is the logarithm to the base 10. Regression estimates are averaged across the site classes given in each yield table.

More recent data based on permanent plot data from unthinned upland oak stands representing three site classes in the oak–hickory region produced self-thinning lines that were quite different from those derived from earlier yield tables (Gingrich, 1971).The newer data suggest that each site class produces a separate concave downward curve when both axes are transformed to logarithmic scale (Fig. 6.5). This pattern is consistent with those derived from Douglas-fir yield tables based on long-term observations from permanent sample plots (Curtis, 1982; Zeide, 1987). However, it is possible that at least part of the concave pattern could be caused by incomplete utilization of growing space in younger oak stands (e.g. stands with less than 500 ft^3 per acre of volume and more than 1200 trees per acre in Fig. 6.5).

Yield tables for English oak stands in England also show that the self-thinning line plotted on log–log scale does not form a straight line. The slope coefficient for fully stocked stands up to 100 years old is -1.48, which approximates to the hypothetical value of -3/2 (White and Harper, 1970). However, in stands between 100 and 150 years old, the coefficient shifts to -1. This shift indicates that bole volume per unit of ground area remains constant for English oak with continued tree growth and self-thinning (Harper, 1977; Norberg, 1988). Accordingly, the volume of bolewood lost to mortality would be compensated by the gap-filling of survivors. A slope of -1 also could indicate stagnating height growth in old stands, or root competition and soil physical constraints on root expansion (Norberg, 1988).

The emerging evidence from permanent plot data collectively indicates that the thinning line as expressed by the -3/2 thinning rule does not form a straight line over the life of a stand. If we accept that evidence, the power function equation generally, and thus the -3/2 slope coefficient specifically, cannot realistically describe self-thinning in oak stands. Moreover, there is evidence that the relation is not independent of site effects (Zeide, 1987).

Conformity of tree growth to the slope coefficient of -3/2 requires that trees maintain *geometric similarity* and constant proportions, or *isometry*, among their various components as they grow. Alternatively, *elastic similarity* occurs when tree components proportionately change with increasing tree size (*allometry*) (McMahon and Bonner, 1983).
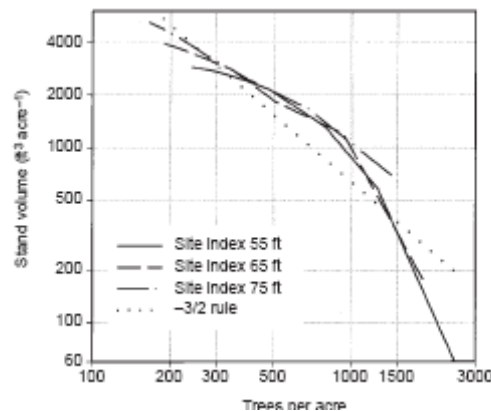

Fig. 6.5. Stand volume in relation to stand density for three site index classes in unthinned (normal) stands in upland hardwoods dominated by mixed oaks in the Central Hardwood Region. The stands represent mixtures of black, white, scarlet and chestnut oaks. The dotted line is the theoretical self-thinning line (-0.5 from Equation 6.4) assumed by the thinning rule model; other lines represent table values based on models derived from permanent plots. (Adapted from Gingrich, 1971, Table 1.)

Constant ratios among tree dimensions such as crown diameter and bole diameter in relation to changing overall tree size thus represent geometric similarity for those dimensions. For a species or species group to intrinsically conform to the -3/2 rule, ratios among tree components must remain constant (isometric) as tree size increases. A test of isometry is provided by the ratio of crown diameter to dbh in relation to changing tree size. These relations are defined by tree-area equations for oaks in stands at average maximum density. The equations indicate that the crown diameter:dbh ratio for forest-grown trees declines from about 30:1 for trees of small diameter to about 17:1 for trees of large diameter (Fig. 6.6d and e). For open-grown trees, ratios of crown diameter to dbh vary even more (Fig. 6.6a–c). In either case, small oaks have proportionately more crown area than large oaks. Such proportionate changes in tree dimensions are not consistent with geometric similarity and hence the -3/2 rule. In fact, bole diameters must increase at a proportionately faster rate than crown area (and correlatively crown mass) to prevent trees from collapsing under their own weight (McMahon, 1973). True isometry in oaks or any other tree species therefore is unlikely. Moreover, predictable changes in crown diameter :

dbh ratios, by themselves, provide an alternative basis for defining a self-thinning line and corresponding measures of relative density, as discussed later in this chapter.

Self-thinning consequently appears to be heavily influenced by tree geometry, which is continually changing to meet requirements for structural resistance to bole breakage as crown mass increases (McMahon, 1973). Moreover, trees grow with great physical plasticity to take advantage of their changing competition environment (Sorrensen-Cothern *et al.*, 1993). For example, one side of a tree crown may expand into the gap created by the death or removal of one of its neighbours, resulting in an expanded but nonsymmetrical crown. Trees that survive self-thinning acquire new resources (space, light, soil moisture and nutrients) as a consequence of spatial adjustments resulting from the death of neighbouring trees and differential growth rates among competing survivors. Associated with these newly acquired resources are changes in the allocation of growth to the various parts of trees, which thereby influence their proportions, shape and competitive relations with neighbours (Sorrensen-Cothern *et al*., 1993). The capacity of oaks to fill irregular canopy spaces, and thus their conformity to allometric growth, may be further reinforced by their upward spreading (decurrent) crowns and weak apical control of lateral branching.

Despite apparent limitations of the -3/2 self-thinning rule to describe the underlying geometric relations for trees in evenaged oak stands, the general pattern of rapidly decreasing numbers of trees with increasing mean size is well established. Self-thinning formulae such as the -3/2 rule and Reineke's model describe stand-level changes in the number of trees with increasing tree size. These formulae are useful expressions of a relatively predictable process that has practical silvicultural value for defining limits of stand density in relation to average tree size. In turn, those limits can be used as a standard or index for expressing the relative density of any other stand. This leads to the subject of stand density and how it can be measured and expressed in oak forests.

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