

A REEVALUATION OF THE $-3/2$ POWER RULE OF PLANT SELF-THINNING¹

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Abstract. The self-thinning rule predicts that for a crowded even-aged plant population a log-log plot of average plant mass vs. plant density will reveal a straight “self-thinning” line of slope $-3/2$. The rule is supported by examples from many individual populations, and by the existence of an interspecific relationship that yields a line of slope $-3/2$ in a log-log plot displaying average mass and density data from many populations of different species. I examined and reanalyzed the evidence to evaluate the strength of support for this widely accepted rule.

Some problems in fitting thinning lines and testing agreement with the rule have no truly satisfactory solution, but three improvements on commonly used methods were made: the analysis related stand biomass density to plant density because the alternative of relating average plant mass to plant density is statistically invalid; principal components analysis was used rather than regression, because regression relies on unrealistic assumptions about errors in the data; and statistical tests of hypotheses were used to interpret the results.

The results of this reanalysis were that 19 of 63 individual-population data sets previously cited in support of the thinning rule actually showed no significant correlation between stand biomass density and plant density, and 20 gave thinning slopes significantly different ($P < .05$) from the thinning rule prediction. Four other analyses provided additional evidence against a single quantitative thinning rule for all plants: slopes of the thinning lines were more variable than currently accepted, differed significantly among plant groups, were significantly correlated with shade tolerance in forest trees, and differed among stands of the same species. The same results held for the intercepts of self-thinning lines.

Despite the failure of the thinning rule for individual populations, the combined data for all populations are still consistent with an interspecific relationship of slope $-3/2$; therefore, the existence of the interspecific relationship does not necessarily support the within-population thinning rule. The within-population and interspecific relationships are apparently different phenomena that may arise from different constraints, so the two relationships should be tested and explained separately.

Key words: average mass–density relationship; biomass–density relationship; interspecific mass–density relationship; plant competition; plant population dynamics; self-thinning; Yoda’s law; $-3/2$ power law.

INTRODUCTION

The self-thinning rule (also called the $-3/2$ power rule or Yoda’s law) describes a relationship between size and density in even-aged plant populations that are crowded but actively growing. If competition from other populations and crowding-independent stresses (drought, fire, disease, etc.) are absent, mortality or “thinning” is caused by competition within the population, hence the term “self-thinning.” Yoda et al. (1963) observed a general relationship among successive measurements of a stand after the start of self-thinning: when the logarithm of average mass is plotted

against the logarithm of plant density, the points form a straight “self-thinning line” of the form $\log \bar{m} = \gamma \log N + \log K$, where \bar{m} is average individual mass (in grams), N is plant density (in individuals per square metre), $\gamma = -3/2$, and K is a constant. Since $\bar{m} = B/N$, (where B is stand biomass density or yield in grams per square metre), this equation is equivalent to $\log B = \beta \log N + \log K$, with $\beta = -1/2$ (note that $\beta = \gamma + 1$). Westoby (1984) gives a recent review of the derivation and interpretation of these equations.

Two lines of evidence support this relationship as an ecological “rule” or “law” governing even-aged plant populations. First, the slopes of many reported thinning lines are near $\gamma = -3/2$, including data from monospecific populations ranging in size from small herbs to large trees (Yoda et al. 1963, White and Harper 1970, White 1980). Westoby (1984) and Weller (1985)

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give references to additional corroborative examples. White (1980) presented thinning slopes between $\gamma = -1.8$ and $\gamma = -1.3$ as examples of the same quantitative rule, and this range is considered remarkably invariant (Watkinson 1980, Furnas 1981, Lonsdale and Watkinson 1982, Hutchings 1983). White (1980) and Gorham (1979) have been widely cited as firmly establishing the generality of the $-3/2$ power rule (Hutchings 1979, Dirzo and Harper 1980, Watkinson 1980, Furnas 1981, White 1981, Lonsdale and Watkinson 1982, 1983, Westoby and Howell 1982, Dean and Long 1985).

The other major evidence for the self-thinning rule is the existence of an interspecific average mass–density relationship of slope $-3/2$ that is observed when data from stands of many species are plotted on a single plot of $\log \bar{m}$ vs. $\log N$, either as individual mature stands (Gorham 1979) or single-species self-thinning lines (White 1980). The data form a band of slope $-3/2$ that applies over seven orders of magnitude of plant density and 10 orders of magnitude of average mass (Westoby 1984, Westoby and Howell 1986). The upper boundary line of the band separates possible combinations of average mass and density from impossible combinations and has been called the “ultimate thinning line” (Hutchings 1979, Cousens and Hutchings 1983). Because the interspecific relationship exists despite large differences in shape and growth form among species, it has been interpreted as evidence that the Yoda model for intraspecific thinning also applies to interspecific size–density relationships (Gorham 1979), that the self-thinning rule applies over a wide range of plant types and growth forms (Gorham 1979, White 1980, 1981, Westoby 1981, Malmberg and Smith 1982), or that the same thinning law applies to all plant species (Hutchings and Budd 1981a, Hutchings 1983). Even plants such as clonal perennial herbs and seaweeds, which do not trace a $-3/2$ thinning line through time, are thought to obey the law because density and average mass are still limited by the ultimate thinning line (Hutchings 1979, Cousens and Hutchings 1983).

Plant ecologists have attributed great theoretical and practical importance to the self-thinning rule, variously praising it as the best documented generalization (White 1981) and most general principle (Westoby 1981) of plant demography; a central concept of population dynamics that may link ecosystem function with evolutionary demography (Westoby 1981, 1984); a uniquely precise mathematical formulation in a science where most generalities are qualitative, not quantitative (Hutchings and Budd 1981a); a scientific law (Yoda et al. 1963, Dirzo and Harper 1980, Lonsdale and Watkinson 1982, Malmberg and Smith 1982, Hutchings 1983); or even the only law in plant ecology (Harper, cited in Hutchings 1983). McIntosh (1980) agreed that, if substantiated, a self-thinning law could well be the first basic law demonstrated for ecology.

In addition to applying to monospecific populations, the rule is thought to govern even-aged two-species

mixtures (White and Harper 1970, Bazzaz and Harper 1976, Malmberg and Smith 1982), many-species mixtures (White 1980, 1981), and possibly even animal populations (Furnas 1981, Wethey 1983, Begon 1986). The rule has been used to compare relative ages or fertilities of populations growing at different sites (Yoda et al. 1963, Barkham 1978) or to draw inferences about the important causes of mortality in a population (Barkham 1978, Schlesinger 1978). As a management tool, the rule is considered useful in forestry (see Yoda et al. 1963, Drew and Flewelling 1977, 1979, and Japanese papers cited therein) and other applications requiring predictions of the limits of biomass production for a given species at any plant density (Hutchings 1983).

Any relationship proposed as an ecological law or important inferential or management tool should be thoroughly and carefully validated. Toward that end, I present an examination of the evidence for the self-thinning rule to determine if it supports acceptance of the relationship as a rule or law. I consider some troubling statistical problems with existing evidence for the rule, and attempt to alleviate these problems in analyzing biomass–density data sets to accomplish three objectives: describe the ranges of variation for thinning slope and intercept, statistically evaluate the constancy within the plant kingdom of the predicted thinning slope $\gamma = -3/2$ (or $\beta = -1/2$), and determine whether or not the interspecific size–density relationship necessarily supports the within-population self-thinning rule.

SOME PROBLEMS WITH THE EVIDENCE FOR THE SELF-THINNING RULE

There are important analytical problems at each of four steps in fitting a self-thinning line: (1) selecting the points to be used, (2) choosing between the $\log \bar{m}$ – $\log N$ or $\log B$ – $\log N$ formulations of the rule, (3) estimating the slope of the thinning line, and (4) comparing the fitted slope to the value predicted by the self-thinning rule. Because these problems may diminish the strength of the evidence for the self-thinning rule, they must be fully discussed before examining the existing evidence for the rule.

Selecting points for fitting the self-thinning line

The need to edit the data to select points for fitting the self-thinning line arises because the thinning line is an asymptotic constraint that acts only when stands are sufficiently crowded. To estimate the slope and position of a thinning line using linear statistics, it is necessary to eliminate data points from populations that are not undergoing crowding-dependent mortality: young populations that have not yet reached the thinning line, stands understocked because of poor establishment or crowding-independent mortality, and senescent stands (Mohler et al. 1978). Failure to eliminate such points will bias the thinning line estimates (Mohler et al. 1978), but when the data are confounded by

biological variability and measurement errors, recognition and elimination of irrelevant points is difficult. Since there is usually no a priori estimate of thinning line position, decisions to eliminate data points must be made a posteriori (Westoby and Howell 1982, Westoby 1984). One method of identifying irrelevant points is visual inspection of $\log \bar{m}$ - $\log B$ plots. More objective, nonvisual criteria for identifying spurious points have been proposed (Mohler et al. 1978, Hutchings and Budd 1981b, Westoby 1984), but these methods are unproven and postdate the major compendia of data supporting the rule. Editing data prior to hypothesis testing should be suspect because it reduces the objectivity of the analysis, but there is presently no general alternative to editing before fitting the thinning line. Furthermore, as shown in the next section, the opportunities for subjectivity and error inherent in data editing are greatly increased when $\log \bar{m}$ - $\log N$ plots are used.

Choosing the best mathematical representation

The data analyst must also decide whether to fit a relationship between average mass and plant density or a relationship between stand biomass density and plant density. Although these two forms of the self-thinning rule are mathematically equivalent, they are not statistically equivalent. The $\log B$ - $\log N$ formulation is the correct choice because the $\log \bar{m}$ - $\log N$ alternative suffers from two major limitations. First, changes in average plant mass can be misleading because average size increases through two processes: growth of living plants and elimination of small plants. Therefore, the average size of the stand increases more rapidly than the sizes of individuals composing it (Bruce and Schumacher 1950), and average mass increases when small individuals die, even if the survivors do not actually grow (Westoby and Brown 1980, Westoby 1984). However, stand biomass density increases only through growth and always decreases with mortality, so a correlation of $\log B$ with $\log N$ is more clearly interpretable and focuses attention on the extent to which mortality permits a more-than-compensatory increase in the size of the survivors.

The second shortcoming of the $\log \bar{m}$ - $\log N$ analysis is more serious and damaging to the case for the self-thinning rule: the analysis is statistically invalid, gives biased results, and leads to unjustified conclusions. To understand why, consider the methods used to measure biomass. Stand biomass is often measured directly by harvesting all the plants in a stand and weighing them as a single group. Even when each individual is weighed (or individual masses estimated from a relationship between mass and some plant dimension), stand biomass is still estimated directly as the sum of the individual masses. Average plant mass is then derived from the original measurements (Mook and van der Toorn 1982) by dividing stand biomass by the number of plants. In general, there are "serious drawbacks" in analyzing such derived ratios (Sokal and Rohlf 1981),

but these problems are particularly acute when the ratio is correlated with one of the variables from which it was derived. Such an analysis gives correlations that have been variously called "spurious" (Pearson 1897, as cited in Snedecor and Cochran 1956), "artificial" (Riggs 1963), and "forced" (Gold 1977).

A high correlation between $\log \bar{m}$ and $\log N$ is both unsurprising and uninterpretable because $\log N$ is typically used to calculate $\log \bar{m}$. This is most easily seen in the special case when the original measurements of $\log B$ and $\log N$ are truly unrelated (i.e., statistically independent). Because average mass is calculated from the equation $\log \bar{m} = \log B - \log N$, $\log \bar{m}$ is a function of $\log N$ even though $\log B$ is not. The variance of $\log \bar{m}$ is $\text{Var}(\log B) + \text{Var}(\log N) - 2 \text{Cov}(\log B, \log N)$ (Snedecor and Cochran 1956), which reduces to $\text{Var}(\log B) + \text{Var}(\log N)$ because the covariance of unrelated variables is zero. Thus, the variance of $\log \bar{m}$ is higher than the variance of $\log B$, and all of the additional variation is attributable to $\log N$. Since $\log N$ explains more of the variance in $\log \bar{m}$ than in $\log B$, the correlation between $\log \bar{m}$ and $\log N$ is higher and more likely to be significant than the correlation between $\log B$ and $\log N$. Furthermore, the original variation among the $\log B$ data that could not be explained by $\log N$ may now be hidden by the portion of the variation in $\log \bar{m}$ that is directly, but trivially, related to $\log N$. Although mathematically real, the improvement in the $\log \bar{m}$ - $\log N$ relationship over the $\log B$ - $\log N$ relationship does not represent an increase in information and can be very misleading to the unwary (Gold 1977).

The deceptive effects of this data transformation are also present in simple plots of the data. This is important because self-thinning data must be edited to remove spurious points before fitting a thinning line. Since plots of the data are important tools for recognizing such points, a transformation that yields plots with artificially enhanced linear trends and hidden variation will cause inappropriate point selections. In the most extreme case, the distorted $\log \bar{m}$ - $\log N$ plot may suggest a linear relationship when none was present in the original $\log B$ - $\log N$ data. More subtle errors arise when a real size-density correlation exists, but points that are not associated with the constraint of the thinning line are mistakenly included in fitting the thinning line.

A few examples will illustrate how the deceptive effects of transforming stand biomass to average mass pervade the evidence for the self-thinning rule. Additional examples are given in Weller (1985). In the first example, the $\log \bar{m}$ - $\log N$ plot (Fig. 1A) from a study of *Trifolium pratense* (Black 1960) shows an apparent linear trend and high correlation between $\log \bar{m}$ and $\log N$ among nine data points thought to form a thinning line in agreement with the self-thinning rule (White and Harper 1970). However, the untransformed $\log B$ - $\log N$ plot (Fig. 1B) shows the true situation: there is no significant negative correlation between $\log B$ and $\log N$, and time trajectories of stands cut steeply across

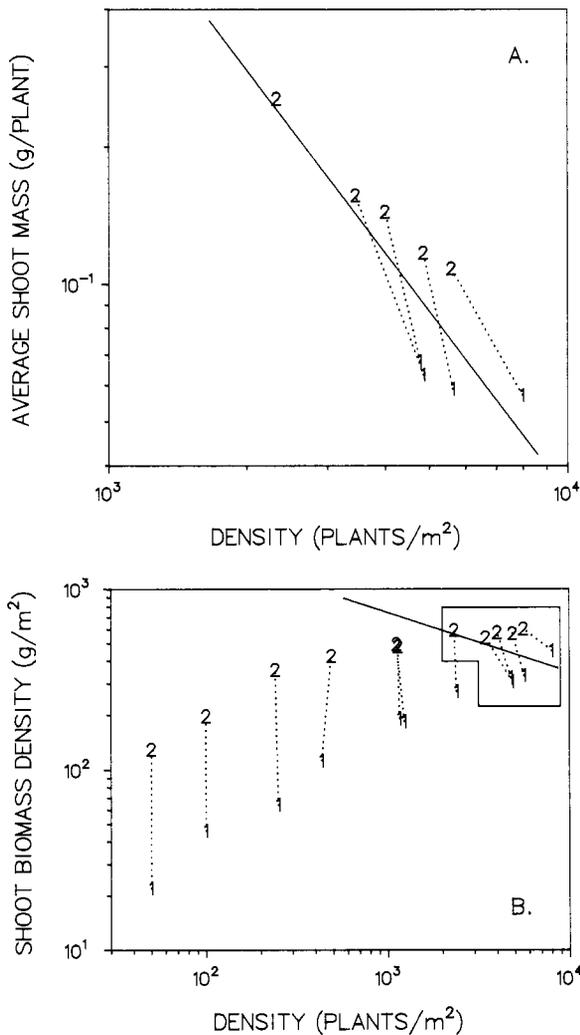


FIG. 1. A spurious reported self-thinning line. White and Harper (1970) fit the solid regression line $\log \bar{m} = -1.33 \log N + 3.86$ ($n = 9$, $r^2 = 0.76$) to data for *Trifolium pratense* (Black 1960). (A) is a plot of the nine points in the $\log \bar{m}$ - $\log N$ plane. Dotted lines represent time trajectories for particular treatments. In the $\log B$ - $\log N$ plot (B), the nine points are boxed in and other points omitted by White and Harper are also shown. For the nine $\log B$ - $\log N$ points, $r^2 = 0.14$ and $P = .33$.

the proposed thinning line rather than approaching it asymptotically.

The second example is a less extreme case, in which a linear trend is present but the $\log \bar{m}$ - $\log N$ plot (Fig. 2A) gives a distorted impression of which points lie along the constraining line. The $\log B$ - $\log N$ plot (Fig. 2B) of the data (on *Chenopodium album*; Yoda et al. 1963) shows an apparent linear constraint that can be estimated by fitting a line through 13 of the data points (those indicated as squares in Fig. 2B). The remaining 14 points are distant from the constraint and should probably be removed before curve fitting, but this is hidden in the $\log \bar{m}$ - $\log N$ plot, where the extraneous

data points fall in line with the others. Fitting a thinning line through all 27 data points by a principal components analysis (PCA) of $\log \bar{m}$ against $\log N$ gives a thinning slope of $\gamma = -1.33$ (95% CL: $[-1.53, -1.16]$), while the 13 points actually near the constraint in the $\log B$ - $\log N$ plot give the PCA slope $\beta = -0.41$ (95% CL: $[-0.48, -0.33]$). The confidence limits show that $\beta = -0.41$ differs from the thinning rule at the 95% confidence level, while $\gamma = -1.33$ does not. The distorted $\log \bar{m}$ - $\log N$ plot changes the selection of relevant points, the estimated thinning slope, and the results of a statistical test of the self-thinning rule.

The transformation can artificially straighten data that actually define a curved path in the $\log B$ - $\log N$ plane. The straight lines in the $\log \bar{m}$ - $\log N$ plane of Fig. 3A (on *Fagopyrum esculentum*; Furnas 1981) seem to fit the data reasonably well, but the $\log B$ - $\log N$ plot (Fig. 3B) reveals the true curvature and the inadequacy of the straight line model. This effect is particularly important when examining data sets containing juvenile or senescent stands, for which the data often curve gradually toward or away from the thinning line.

A final example shows how the $\log \bar{m}$ - $\log N$ plot can lead to questionable interpretations of experiments. In an evaluation of the effects of site fertility on the self-thinning trajectory, five plots of *Erigeron canadensis* received different fertilizer applications in a ratio of 5:4:3:2:1 before seeds were planted on 21 October 1955 (Yoda et al. 1963). The plots were followed over six harvests spaced between 7 November 1955 and 25 June 1956. The conclusion that the position of the thinning trajectory was insensitive to soil fertility (Yoda et al. 1963, White and Harper 1970) seems justified from the $\log \bar{m}$ - $\log N$ plot (Fig. 4A). The five treatments seem to follow the same path through the plane, and the large differences in fertility to have affected only the rate of progress along the common trajectory. However, the $\log B$ - $\log N$ plot (Fig. 4B) suggests a possible alternative interpretation. Initially, the populations seem to follow very different trajectories, but the differences gradually disappear and are gone around the fourth harvest, ≈ 4.5 mo after planting. Perhaps the fertilizer applications actually did change the position of the thinning trajectory, and the treatments converged on a common path only after several months of leaching and plant uptake eliminated the large initial differences in plot fertility.

The $\log B$ - $\log N$ plot also indicates a thinning line whose slope is very different from the expected value of $\beta = -1/2$, because the $\log B$ - $\log N$ plot reveals a fact obscured in the $\log \bar{m}$ - $\log N$ plot: all five treatments lost biomass between harvests 2 and 3, which were taken during the winter. The simultaneous decline of both biomass density and plant density over this interval suggests that winter conditions caused crowding-independent mortality. Data from these harvests should be excluded when fitting the thinning line because the use of data from populations suffering crowding-in-

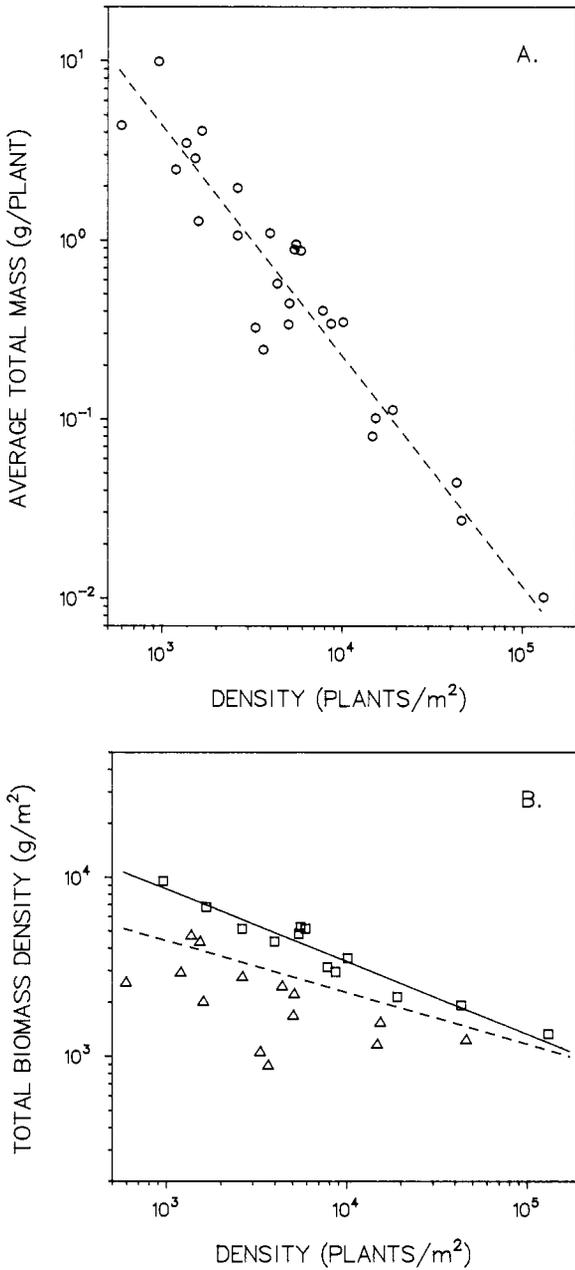


FIG. 2. Potential bias in data editing in the $\log \bar{m}$ - $\log N$ plane. Data are for *Chenopodium album* (Yoda et al. 1963). In the $\log \bar{m}$ - $\log N$ plot (A) all 27 data points appear to follow a common linear trend (---). The equation of this line, estimated from PCA of $\log \bar{m}$ and $\log N$, is $\log \bar{m} = -1.33 \log N + 3.94$ ($r^2 = 0.90$, $P < .0001$; 95% CI for β : $[-1.53, -1.16]$). In the $\log B$ - $\log N$ plot (B), an apparent linear constraint is evident; however, many data points fall relatively far from the constraining line (triangles). A new (—) PCA line through the 13 points (\square) closer to the border of the constrained region is $\log B = -0.41 \log N + 5.15$ ($r^2 = 0.93$, $P < .0001$; 95% CI for β : $[-0.48, -0.33]$).

dependent mortality gives biased thinning line estimates (Mohler et al. 1978, Westoby 1984). PCA analysis of harvests 4 through 6 gives a thinning slope of $\beta = -1.04$, which is statistically different from the hypothesized value $\beta = -1/2$ ($P < .0001$).

Most of the evidence for the self-thinning rule has been analyzed in $\log \bar{m}$ - $\log N$ form, since only Westoby and his colleagues, Mook and van der Toorn (1982), and Zeide (1985) have used the $\log B$ - $\log N$ formulation. Most studies may, then, suffer from one or more of the problems illustrated in the preceding examples: the points selected for analysis may not be the best

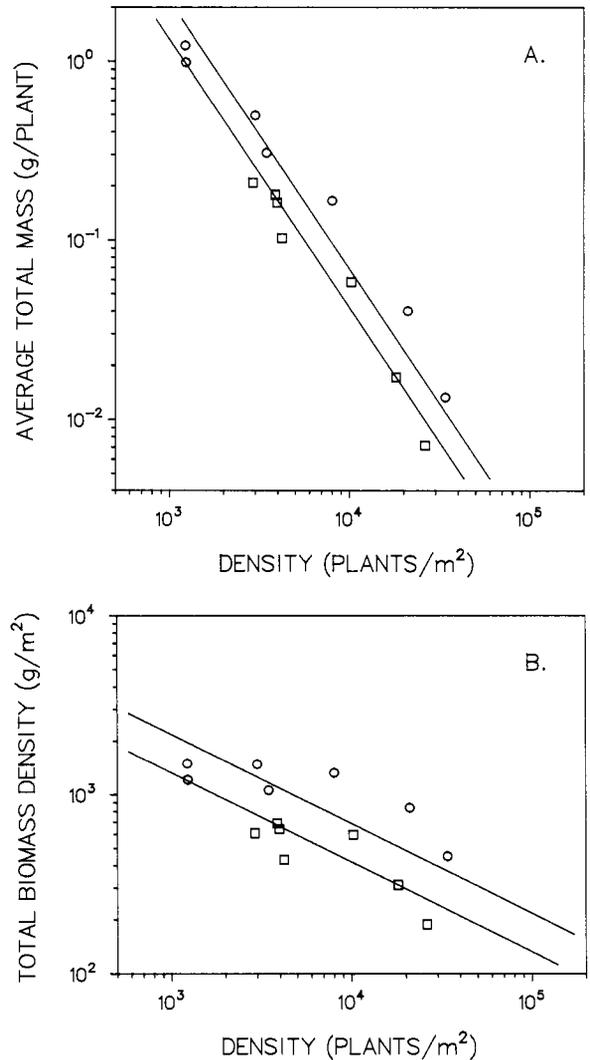


FIG. 3. Example of deceptive straightening of curves in the $\log \bar{m}$ - $\log N$ plane. Data are from an experiment with *Fagopyrum esculentum* where population \circ received five times as much fertilizer as population \square (Furnas 1981). Both trajectories appear reasonably linear in the $\log \bar{m}$ - $\log N$ plot (A), and the two lines $\log \bar{m} = -1.50 \log N + 4.837$ and $\log \bar{m} = -1.50 \log N + 4.622$ reported by Furnas seem to fit the data well. Both trajectories are seen to be curved in the $\log B$ - $\log N$ plot (B).

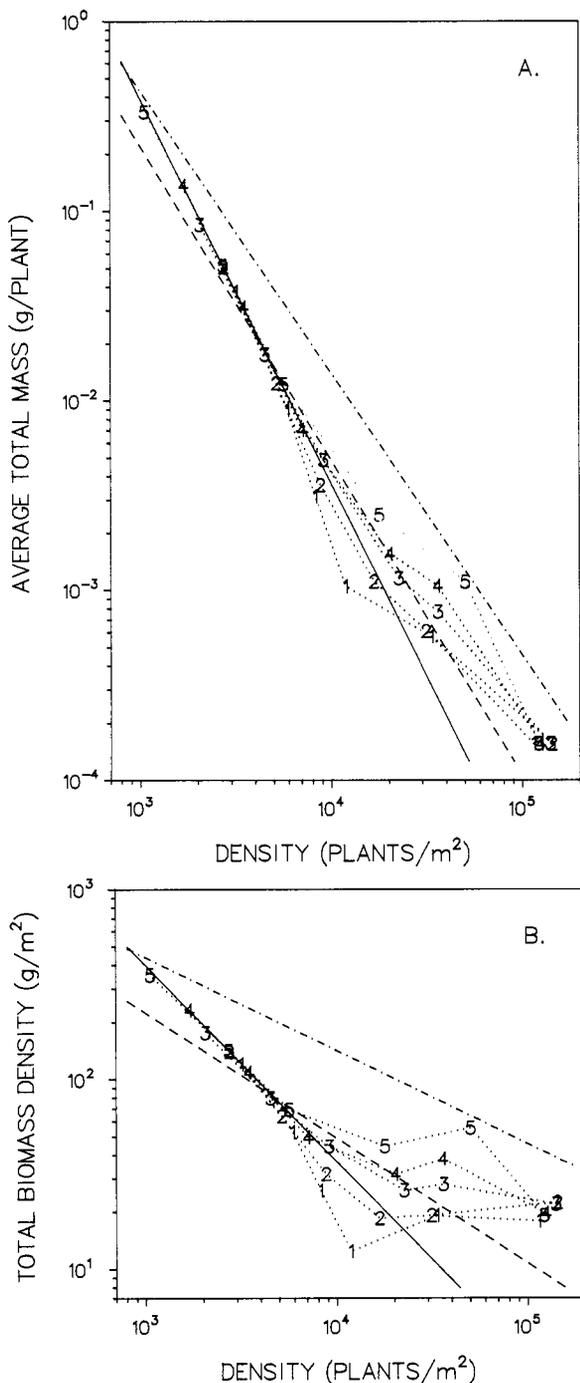


FIG. 4. Potential misinterpretations of experimental results due to deceptive effects of the $\log \bar{m}$ - $\log N$ plot. Numbers marking data points (*Erigeron canadensis*; Yoda et al. 1963) indicate the relative amount of fertilizer applied in the ratio 5:4:3:2:1 before planting. Dotted lines (\cdots) sequentially connect points from six harvests and represent time trajectories for particular treatments. Yoda et al. concluded that the data agree with a slope of $\gamma = -1.5$ ($-\cdot-$), and White (1980) fit the regression line $\log \bar{m} = -1.66 \log N + 4.31$ ($-\cdot-\cdot-$). The present study fit the PCA line ($---$) ($\log B = -1.04 \log N + 5.70$ ($r^2 = 0.99$, $P < .0001$; 95% CI for slope: $[-1.12, -0.96]$). (A) $\log \bar{m}$ - $\log N$ plot. (B) $\log B$ - $\log N$ plot.

choices, the correlations are inflated, spurious relationships may have been created and interpreted, and the interpretations of the effects of experimental treatments and environmental factors may be biased.

Fitting the self-thinning line

Estimating the equation of the thinning constraint would ideally yield a line that bounded all data points from above (Hutchings and Budd 1981a). This ideal method might also eliminate the need to delete data from uncrowded populations, thus alleviating the problems arising from data editing. Unfortunately, there are no statistical methods for fitting such a boundary, so thinning lines are fit through the data near the boundary with standard least squares techniques such as regression or PCA (Hutchings and Budd 1981a).

Linear regression is inappropriate for fitting thinning lines because both variables are subject to errors and neither is experimentally controlled, so neither can legitimately be designated as the independent variable in the regression (Mohler et al. 1978). When both variables are subject to errors, the linear structural relationship (Madansky 1959, Moran 1971, Jolicoeur 1975) gives the true slope of the bivariate relationship. Unfortunately, this method requires knowledge of the ratio of the residual variances of the two variables around the linear relationship, and this ratio is unestimable for most biological data (Ricker 1973, 1975, Sprent and Dolby 1980). Making the assumption that the residual variances are equal yields the same slope as that obtained from PCA. Although not exact, this assumption is more appropriate for thinning data than the regression assumption that one of the residual variances is zero; therefore, PCA is preferable to regression for estimating thinning slopes (Mohler et al. 1978). However, the percentage of variance explained by the first principal component (%EV) is not an appropriate measure of bivariate linear association, despite its use in many recent papers. While the coefficient of determination, r^2 , ranges from 0 to 1, %EV is never less than 50% because the first principal component always explains at least half of the total variation, even if the two variables are completely uncorrelated. Regardless of the fitting method used, r or r^2 should always be the reported measure of association since r measures the strength of linear association rather than the position of any particular line in the plane (Sprent and Dolby 1980, Sokal and Rohlf 1981).

The errors from using regression rather than PCA are small if the two variables are very highly correlated, but large errors can occur at lower correlations. For example, Mohler et al. (1978) presented an analysis in which the correlation between $\log \bar{m}$ and $\log N$ was reasonably high ($r^2 = 0.72$), yet the regression slope, $\gamma = -1.21$, was less steep than the PCA estimate, $\gamma = -1.52$. Since most thinning lines have been fit by regression (Westoby 1984), there may be an important bias toward underestimating the steepness of thinning

slopes, particularly since for many size-density correlations r^2 is well below 1 when the data are correctly analyzed in $\log B$ - $\log N$ form (Weller 1985).

Testing agreement with the self-thinning rule

Evaluation of the self-thinning rule has been hindered by the lack of an objective criterion for agreement with the rule. Slopes within the range $-1.8 \leq \gamma \leq -1.3$ have been considered examples of the same quantitative rule (White 1980); however, there is no objective basis to claim that -1.8 and -1.3 are close to -1.5 . In fact, these limits represent very different predictions about population growth. Over a 100-fold decrease in plant density, a population following a thinning line of slope $\gamma = -1.3$ will quadruple its aggregate biomass, while a population with a thinning slope of $\gamma = -1.8$ will increase its biomass 40 times. Although the two populations show qualitatively similar behavior in following linear trajectories in the \log size- \log density plane, the biomass response of one is 10 times greater than that of the other. The populations do not obey the same quantitative rule, and the range $-1.8 \leq \gamma \leq -1.3$ does not provide a satisfactory criterion for quantitative agreement with the self-thinning rule.

A statistical test of the hypothesis that an observed thinning slope is equal to the predicted value provides a more objective test of agreement with the rule. This test should be accompanied by tests of alternative hypotheses, since only data sets that can discriminate among reasonable alternatives provide convincing support for the self-thinning rule. Two alternatives are particularly relevant: the null hypothesis that no competitive effect is present, and the hypothesis that a carrying capacity keeps stand biomass density below a fixed level. If the null hypothesis is true, there will be no significant correlation between $\log B$ and $\log N$, or biomass density will actually increase with plant density. If stand biomass is fixed at a constant level, there will again be no significant relationship between $\log B$ and $\log N$. Data sets with no significant $\log B$ - $\log N$ correlation do not support the self-thinning rule or any other hypothesis about the course of plant competition, since such data do not even show that competition has occurred.

NEW TESTS OF THE SELF-THINNING RULE

The prevalence of some potentially serious but correctable statistical problems in the body of evidence for the self-thinning rule demands a major reanalysis of the evidence. Commonly used methods can be improved in three ways: the analysis should relate $\log B$ to $\log N$, PCA should be used rather than regression, and statistical tests of hypotheses should be used to interpret the results. I incorporated these three improvements in fitting and testing 488 relationships between biomass density and plant density. This sample includes many data sets not previously analyzed in a self-thinning context, which was important in guarding

against any a priori bias toward the self-thinning rule. Five different analyses addressed the question of constancy of thinning slopes within the plant kingdom and the agreement of observations with the self-thinning rule. (1) Statistical tests were done to check for significant relationships between $\log B$ and $\log N$ and for quantitative agreement with the self-thinning rule. (2) The frequency distributions of thinning slope and intercept were prepared, to provide a complete description of the observed variability. (3) The thinning slopes of plant groups were compared to determine if thinning line parameters vary among groups or if a single thinning rule applies to all plants. (4) The constancy of thinning line parameters with respect to a functional measure of plant performance was evaluated by testing for significant correlations of thinning slope and intercept with shade tolerance, a common forestry measure summarizing the ability of a species to regenerate in the presence of competition (Baker 1949, Harlow et al. 1978, Zeide 1985). Previous work suggests that shade-tolerant trees may have higher thinning intercepts (Westoby and Howell 1981, Lonsdale and Watkinson 1983, Dean and Long 1985) or steeper thinning slopes (Yoda et al. 1963) than intolerant trees. (5) Finally, when several thinning lines were estimated for a particular species, the results were compared to determine if thinning slope and intercept are species constants.

Sources of information

I compiled data from two classes of studies: (1) experimental and field studies (EFD) and forestry yield tables (FYD). Thirty-nine sources of EFD contained 95 data sets (see Appendix Table A1), while 51 sources of FYD contained 77 yield tables (Appendix Table A2). Some data sets gave information for several possible thinning lines, so a total of 488 biomass-density relationships were considered, 137 for EFD and 351 for FYD. To ensure comparability among studies, stand biomass values were converted to biomass densities in common units of grams per square metre, and plant densities were converted to individuals per square metre. For forestry data, stand yields in volumes of wood per unit of forest area were converted to grams per square metre by multiplying by the wood density of the species (Peattie 1950, 1953).

Fifty-six different species were represented in monospecific studies in the EFD, along with seven different two-species combinations, three multi-species mixtures, and two studies of monogeneric populations of unspecified species. The FYD considered 32 different single-species forests, two types of two-species forests, four multi-species forest types, and seven monogeneric forests of unspecified species. The multi-species stands were included because the thinning rule is thought to also apply to two-species and multi-species stands (see Introduction).

Many sources give information for stands grown un-

der different conditions of light, fertilization, site quality, initial plant density, and other factors that may affect the thinning line. Data from the different conditions could be used to estimate separate thinning lines or pooled to estimate a single line. To simplify the present analysis and to preserve comparability with the original reports, I reanalyzed the EFD with the same groupings used by the original authors, except where those authors later decided that the separate thinning lines were not different. Table A1 gives the conditions that subdivided some studies. Thinning lines were fitted separately for different site indexes in the FYD, except where the source clearly indicated that the same relationships were used to develop the tables for different site indexes. Weller (1985) gives additional details.

Methods of analysis

I examined $\log B$ - $\log N$ plots to select points for fitting thinning lines. In many cases, I did not alter the selection of points used by the original authors. However, $\log B$ - $\log N$ plots of some data sets revealed that points included in the original $\log \bar{m}$ - $\log N$ analysis were not closely associated with the potential thinning line, and these points were removed in this analysis. Selections of points were not altered when the sources gave justification for particular choices or validated their choices with field notes or mortality curves (Mohler et al. 1978, Hutchings and Budd 1981b). A complete count of the number of data sets for which my point selections differed from those of the authors is not possible because many studies did not report how many data points, or which ones, were used. Of 63 previously reported thinning trajectories, 33 indicated which points were used; I reanalyzed 24 of these with no changes in point selection.

The strength of linear association in each edited data set was measured by calculating the correlation coefficient (Sprent and Dolby 1980), and a straight line was fit by PCA (Jolicoeur 1973, 1975). Thinning intercepts, $\alpha = \log K$, were calculated from β and the mean values of $\log B$ and $\log N$ using the equation $\alpha = \bar{Y} - \beta\bar{X}$, where \bar{Y} is the average value of $\log B$ and \bar{X} is the average of $\log N$. For experimental and field data, the statistical significance of each correlation was examined by testing the null hypothesis that $\log B$ and $\log N$ were uncorrelated, and 95% confidence intervals for the PCA slopes (Jolicoeur and Heusner 1971) were used to test agreement with the value of $\beta = -\frac{1}{2}$ predicted by the self-thinning rule. With low correlation or few data, the PCA confidence limits can be imaginary, but this is correctly interpreted as the absence of a significant linear association (Jolicoeur 1973). The 95% confidence limits for the intercept were calculated by applying $\alpha = \bar{Y} - \beta\bar{X}$, to the confidence limits of β .

In the EFD, 62 data sets that did not show a significant ($P < .05$) linear association between $\log B$ and $\log N$ were removed from consideration as possible

self-thinning lines, and the fitted slopes and intercepts of these rejected data sets were omitted from all further analyses. None of these statistical tests was applied to the FYD, because yield tables are the predictions of curve-fitting procedures, so statistical inferences drawn from a single thinning line would not be valid. However, a large sample of FYD thinning lines can be examined to look at the frequency distributions and ranges of variation of thinning line parameters. In all of the following analyses, the EFD and FYD are considered separately because of the different levels of statistical testing possible in the two groups. Weller (1985) gives more detailed information on each thinning line.

Univariate statistics were computed to describe the frequency distributions of β and α . Some EFD data sets gave biomass measurements based on above-ground parts only, while 20 others also included roots. Nonparametric Kruskal-Wallis tests (Sokal and Rohlf 1981) were used to compare these two groups with respect to both β and α and to determine if the groups should be examined separately.

The thinning lines were then divided into broad plant groups. Six categories were used for the EFD: herbaceous monocots, herbaceous dicots, temperate angiosperm trees, temperate gymnosperm trees, Australian trees (genus *Eucalyptus*), and tropical angiosperm trees (Table A1). The FYD were divided into three categories: temperate gymnosperms, temperate angiosperms, and Eucalypts (Table A2). Kruskal-Wallis tests were applied to determine if β and α differed significantly among the groups. Spearman rank correlations were also calculated for the FYD to relate β and α to shade tolerance (Table A2). These correlations were tested to determine if thinning line parameters varied significantly with shade tolerance. Finally, tables of β and α were prepared for all species examined in more than one study. For the EFD, the 95% confidence intervals of the thinning line parameters were compared to test for significant differences among the estimates.

Results

Agreement with the self-thinning rule.—Sixty-three of the thinning lines had been reported in previous studies as demonstrations of the self-thinning rule. Nineteen of these did not show any significant correlation between $\log B$ and $\log N$ at the 95% confidence level. For the remaining 44 the correlation was significant, but the slopes of 20 were statistically different from the thinning rule prediction, with 7 greater than $-\frac{1}{2}$ and 13 less than $-\frac{1}{2}$. Only 24 of the slopes were both statistically significant and not significantly different from the predicted value. Thirty-one additional thinning lines from data not previously analyzed in a self-thinning context also showed significant $\log B$ - $\log N$ correlation. When combined with the 44 from the previously reported group, this gave a total of 75 statistically significant thinning lines. Of these 75, the slopes of 34 were not significantly different from $\beta =$

TABLE 1. Descriptive statistics for thinning line slope and intercept.

| Statistic | Field and experimental data* | | | | | | Forestry yield table data (bole biomass) | |
|-----------|------------------------------|----------|---------------|----------|---------------|----------|--|----------|
| | Shoot biomass | | Total biomass | | All data sets | | β | α |
| | β | α | β | α | β | α | | |
| <i>n</i> | 55 | 55 | 20 | 20 | 75 | 75 | 351 | 351 |
| Mean | -0.863 | 4.08 | -0.804 | 4.48 | -0.847 | 4.18 | -0.876 | 3.45 |
| Median | -0.649 | 3.84 | -0.468 | 4.13 | -0.622 | 3.97 | -0.618 | 3.68 |
| SD | 0.701 | 1.12 | 0.862 | 1.62 | 0.742 | 1.27 | 1.024 | 1.04 |
| CV(%) | 81 | 27 | 107 | 36 | 88 | 30 | 117 | 30 |
| SE | 0.095 | 0.15 | 0.193 | 0.36 | 0.086 | 0.15 | 0.055 | 0.06 |
| Skewness | -2.57 | 0.33 | -2.59 | 1.89 | -2.51 | 1.25 | -4.36 | -4.30 |
| Kurtosis | 7.14 | 2.03 | 7.21 | 6.86 | 6.59 | 5.64 | 21.04 | 23.45 |
| Minimum | -3.808 | 1.28 | -3.760 | 1.40 | -3.808 | 1.28 | -8.132 | -4.18 |
| Maximum | -0.146 | 7.54 | -0.204 | 9.93 | -0.146 | 9.93 | -0.119 | 4.42 |

* "Shoot biomass" thinning lines are based on stand biomass measurements of aboveground parts only, while "Total biomass" trajectories include aboveground and belowground parts. "All data sets" combines these two groups.

$-\frac{1}{2}$; of the remaining 41 slopes, 14 were greater than and 27 less than $\beta = -\frac{1}{2}$.

Frequency distributions.—Univariate statistics for the slopes and intercepts of these 75 thinning lines are presented for two groups: data sets with biomass measurements of aboveground parts only and data sets with biomass measurements that included roots (Table 1).

Kruskal-Wallis tests at the 95% confidence level detected no significant differences in β ($H_2 = 3.02, P = .08$) or α ($H_2 = 1.90, P = .16$) between the two groups, so the groups were pooled (Table 1, Fig. 5). Table 1 also includes statistics for the 351 thinning lines fitted to data sets in the FYD.

Differences among plant groups.—Kruskal-Wallis

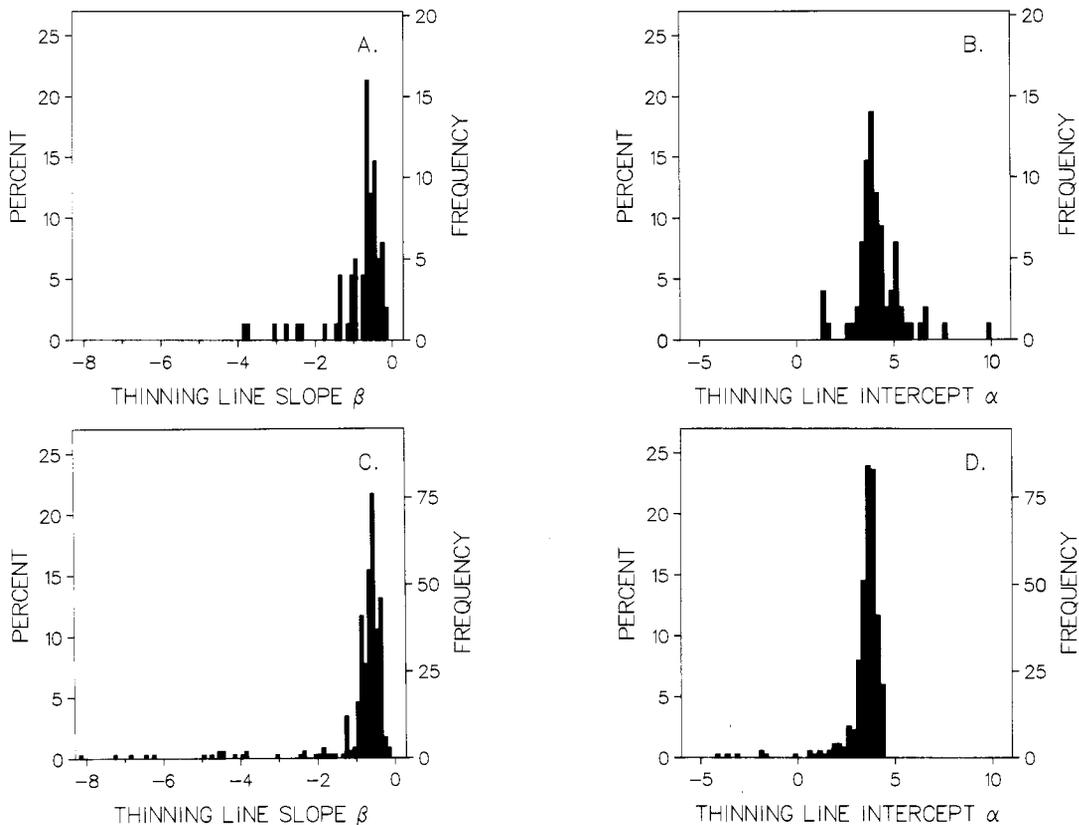


FIG. 5. Histograms for the slopes and intercepts of fitted thinning lines. (A) and (B) show the distributions of slope β and intercept α , respectively, for log B -log N thinning lines in the experimental and field data. (C) and (D) show the same distributions for thinning lines in the forestry yield tables.

TABLE 2. Comparisons of thinning line slope and intercept among plant groups.

| Group | n | Slope β | | Intercept α | |
|--|-----|---|--------|--------------------|--------|
| | | Mean | Median | Mean | Median |
| Experimental and field data (EFD) | | | | | |
| Herbaceous monocots | 8 | -0.44 | -0.39 | 4.45 | 4.24 |
| Herbaceous dicots | 25 | -0.74 | -0.65 | 5.17 | 5.09 |
| Temperate angiosperm trees | 15 | -0.65 | -0.53 | 3.78 | 3.72 |
| Temperate gymnosperm trees | 19 | -0.87 | -0.65 | 3.79 | 3.88 |
| <i>Eucalyptus</i> trees | 4 | -1.26 | -1.03 | 2.87 | 3.07 |
| Tropical angiosperm trees | 4 | -2.56 | -2.55 | 2.20 | 2.21 |
| Kruskal-Wallis tests for differences among six EFD groups | | $\beta H_5 = 17.9 P = .0031$ $\alpha H_5 = 41.1 P < .0001$ | | | |
| Forestry yield table data (FYD) | | | | | |
| Temperate angiosperm trees | 58 | -0.60 | -0.63 | 3.50 | 3.56 |
| Temperate gymnosperm trees | 281 | -0.80 | -0.61 | 3.54 | 3.72 |
| <i>Eucalyptus</i> trees | 12 | -3.90 | -4.39 | 1.09 | 1.79 |
| Kruskal-Wallis tests for differences among three FYD groups | | $\beta H_2 = 14.9 P = .0006$ $\alpha H_2 = 11.9 P < .0027$ | | | |
| Kruskal-Wallis tests for differences between gymnosperms and angiosperms | | $\beta H_1 = 3.77 P = .052$ $\alpha H_1 = 8.30 P < .004$ | | | |

tests revealed significant differences in both β and α among the six groups in the EFD and among the three groups in the FYD (Table 2). Because the *Eucalypt* group of the FYD is so extreme, two-way comparisons between the angiosperm and gymnosperm groups were also done. The differences in β between these two more similar groups are also statistically significant.

Correlations with shade tolerance.—Table 3 reports the correlation analysis separately for the angiosperms and gymnosperms because of the observed differences in β and α between these two groups. Shade tolerance data were not available for the *Eucalypt* group. For the 46 angiosperm thinning trajectories analyzed, β is significantly correlated with shade tolerance but α is not (Table 3). Both β and α are significantly correlated with tolerance in the gymnosperms; however, the sign of the correlation of β with shade tolerance is opposite to that observed for the angiosperms. For the angiosperms, more tolerant trees tend to have steeper, more negative thinning slopes, while the more tolerant gymnosperm trees have shallower thinning slopes. This difference further justifies separate analyses for the two groups.

Within-species constancy.—Both thinning slope and intercept show considerable variation within species in the EFD (Table 4). In some cases, parameter estimates for a given species are quite different, but the confidence intervals for the estimates are so large that the differences are not statistically significant. In other cases, the differences are statistically significant, as indicated by non-overlap of the 95% confidence intervals. Nine of the 42 possible pairwise within-species comparisons of β reveal significant differences, as do 11 of the 42 possible comparisons of α . Since the confidence level is 95%, 2 of 42 comparisons should be different by chance alone, but both analyses gave at least 4 times this number. For the FYD, although significance tests were not possible, the large observed ranges within a species (Table 5) again suggest that neither β nor α is a species constant.

DISCUSSION

The statistical tests of the 63 EFD thinning lines previously reported to demonstrate the self-thinning rule show that this body of evidence does not strongly

TABLE 3. Spearman correlation coefficients of shade tolerance with thinning line slope and intercept, from the forestry yield data.

| Thinning parameter | Means for shade tolerance groups* | | | | | Spearman correlation | |
|-----------------------|-----------------------------------|-------------|-------------|-------------|-------------|----------------------|--------|
| | 1 | 2 | 3 | 4 | 5 | r_s | P |
| Temperate angiosperms | | | | | | | |
| Slope β | -0.391 (10) | -0.547 (18) | -0.685 (18) | | | -0.52 (46) | .0002 |
| Intercept α | 3.632 (10) | 3.437 (18) | 3.517 (18) | | | -0.19 (46) | .22 |
| Temperate gymnosperms | | | | | | | |
| Slope β | -0.916 (32) | -0.748 (78) | -0.642 (47) | -1.149 (69) | -0.459 (41) | 0.35 (267) | <.0001 |
| Intercept α | 3.123 (32) | 3.438 (78) | 3.732 (47) | 3.280 (69) | 4.172 (41) | 0.57 (267) | <.0001 |

* Sample sizes are given in parentheses. Shade tolerances are ranked on a scale of 1 (least tolerant of shading) to 5 (most tolerant) as in Appendix Table A2.

TABLE 4. Thinning line slopes and intercepts of species for which several thinning lines were fit from experimental or field data.

| | Thinning slope | | | Thinning intercept | | | Reference‡ |
|-------------------------------|----------------|-------------------|--------|--------------------|---------------|--------|------------------|
| | β | [95% CI] | Diff.† | α | [95% CI] | Diff.† | |
| <i>Abies sachaliensis</i> | | | | | | | |
| A | -0.649 | [-0.776, -0.535]* | C | 4.16 | [4.15, 4.17] | C | 19A |
| B | -0.465 | [-0.965, -0.104] | C | 4.39 | [4.07, 4.83] | C | 24T |
| C | -2.786 | [-5.645, -1.722]* | AB | 1.71 | [-0.49, 2.49] | AB | 119A |
| <i>Beta vulgaris</i> | | | | | | | |
| A | -1.335 | [-3.355, -0.648]* | | 6.38 | [4.54, 11.80] | | 33T |
| B | -2.304 | [-5.478, -1.348]* | CDEF | 9.93 | [7.08, 19.38] | CDEF | 34T |
| C | -0.662 | [-0.839, -0.509]* | B | 4.79 | [4.17, 5.50] | B | 43A (18% L.I.) |
| D | -0.692 | [-0.973, -0.470] | B | 5.12 | [4.22, 6.25] | B | 43A (25% L.I.) |
| E | -0.668 | [-0.886, -0.486] | B | 5.09 | [4.39, 5.94] | B | 43A (37% L.I.) |
| F | -0.649 | [-0.838, -0.487] | B | 5.22 | [4.59, 5.95] | B | 43A (55% L.I.) |
| G | -0.648 | [-1.415, -0.197] | | 5.30 | [3.55, 8.27] | | 43A (100% L.I.) |
| <i>Erigeron canadensis</i> | | | | | | | |
| A | -0.621 | [-0.688, -0.558]* | B | 4.36 | [4.19, 4.55] | B | 15T |
| B | -1.038 | [-1.121, -0.962]* | A | 5.70 | [5.43, 6.00] | A | 21T |
| <i>Eucalyptus regnans</i> | | | | | | | |
| A | -2.478 | [-5.012, -1.559]* | | 1.39 | [-1.63, 2.48] | | 98A (S.I. 28.9) |
| B | -1.066 | [-2.132, -0.549]* | | 3.44 | [2.31, 3.99] | | 98A (S.I. 33.5) |
| <i>Lolium perenne</i> | | | | | | | |
| A | -0.324 | [-0.674, -0.034] | | 3.79 | [2.88, 4.89] | | 38A (100% L.I.) |
| B | -0.427 | [-0.543, -0.319] | | 4.80 | [4.37, 5.27] | | 91A (100% L.I.) |
| C | -0.245 | [-0.330, -0.163]* | | 4.20 | [3.87, 4.54] | | 91T (100% L.I.) |
| D | -0.544 | [-1.509, -0.011] | | 4.33 | [2.28, 8.06] | | 92A (23% L.I.) |
| E | -0.503 | [-1.273, -0.027] | | 4.28 | [2.48, 7.20] | | 92A (44% L.I.) |
| <i>Picea abies</i> | | | | | | | |
| A | -0.422 | [-0.462, -0.383]* | | 3.90 | [3.88, 3.92] | B | 137A |
| B | -0.433 | [-0.476, -0.392]* | | 3.97 | [3.95, 3.99] | A | 137T |
| <i>Pinus strobus</i> | | | | | | | |
| A | -0.724 | [-0.830, -0.628]* | B | 3.78 | [3.74, 3.83] | BC | 8A (Plot 2B) |
| B | -1.116 | [-1.278, -0.976]* | A | 3.34 | [3.22, 3.43] | A | 8A (Plot 2C) |
| C | -0.954 | [-1.189, -0.764]* | | 3.44 | [3.25, 3.60] | A | 93A |
| <i>Pinus taeda</i> | | | | | | | |
| A | -0.305 | [-0.499, -0.130]* | B | 4.21 | [4.11, 4.30] | B | 82A |
| B | -0.670 | [-0.837, -0.526]* | A | 3.42 | [3.23, 3.59] | A | 102A |
| <i>Trifolium subterraneum</i> | | | | | | | |
| A | -0.473 | [-0.660, -0.310] | | 4.60 | [3.97, 5.33] | | 10A (Full light) |
| B | -0.622 | [-0.928, -0.382] | | 5.17 | [4.33, 6.23] | | 35A |

† The letters in this column identify table entries (letters at left of table) for the species that are significantly different from the estimate of β or α in the given row, as indicated by non-overlap of 95% confidence intervals.

‡ Numbers in this column indicate ID codes (see Appendix Table A1). Letters indicate whether total stand biomass (T) or aboveground biomass only (A) was used to fit the thinning line. Information on particular field or experimental conditions is given above in parentheses (L.I. = light intensity, S.I. = site index). See source listed in reference or Weller (1985) for further details.

* Slopes different at the 95% confidence level ($P \leq .05$) from the thinning rule prediction $\beta = -1/2$.

support the rule. Many of the reported high correlations between $\log \bar{m}$ and $\log N$ proved spurious when the $\log B$ - $\log N$ data were reanalyzed, and 30% of the thinning lines did not show a significant relationship between stand biomass density and plant density. The remaining thinning lines did show the predicted significant linear relationship between $\log B$ and $\log N$, but the slopes of almost half of these were significantly different from $\beta = -1/2$, the value predicted by thinning rule. Deviations of the thinning slope from the predicted value are particularly important because β is the exponent of a power relationship, $B = KN^\beta$, so small

differences in β represent large differences in the predictions of the equation (Weller 1985, Zeide 1985). A total of 62% of the data sets are either useless for testing the rule or in quantitative disagreement with it, and only 38% potentially support the rule. These results confirm B. Zeide's prediction (as cited in Westoby 1984) that the apparent empirical strength of the self-thinning rule would dissolve if the data were reanalyzed in $\log B$ - $\log N$ form.

These significance tests are subject to an important caveat: the true confidence level of each test is less than the nominal 95% because the necessary step of editing

TABLE 5. Statistics for thinning line slope and intercept of species for which several thinning lines were fit from forestry yield data.

| Species | Sample size* | | Thinning slope β | | | | Thinning intercept α | | | |
|---|--------------|-------|------------------------|------|-------|-------|-----------------------------|------|-------|-------|
| | n_T | n_L | Mean | SD | Min. | Max. | Mean | SD | Min. | Max. |
| Species considered in more than one yield table | | | | | | | | | | |
| <i>Alnus rubra</i> | 3 | 8 | -0.41 | 0.19 | -0.65 | -0.12 | 3.46 | 0.42 | 2.69 | 4.08 |
| <i>Picea glauca</i> | 2 | 9 | -0.75 | 0.30 | -1.28 | -0.52 | 3.59 | 0.31 | 3.01 | 3.83 |
| <i>Pinus banksiana</i> | 3 | 10 | -0.79 | 0.39 | -1.73 | -0.24 | 3.06 | 0.27 | 2.51 | 3.51 |
| <i>Pinus echinata</i> | 4 | 20 | -0.72 | 0.23 | -0.97 | -0.40 | 3.53 | 0.35 | 3.14 | 4.05 |
| <i>Pinus elliotti</i> | 2 | 11 | -0.56 | 0.16 | -0.83 | -0.38 | 3.62 | 0.34 | 3.22 | 3.99 |
| <i>Pinus palustris</i> | 2 | 14 | -1.04 | 0.22 | -1.28 | -0.80 | 3.01 | 0.49 | 2.20 | 3.52 |
| <i>Pinus ponderosa</i> | 3 | 27 | -0.72 | 0.66 | -2.44 | -0.31 | 3.36 | 0.90 | 1.08 | 4.18 |
| <i>Pinus resinosa</i> | 2 | 8 | -1.07 | 0.48 | -1.97 | -0.63 | 3.46 | 0.47 | 2.73 | 4.21 |
| <i>Pinus strobus</i> | 3 | 12 | -0.74 | 0.18 | -1.07 | -0.53 | 3.68 | 0.15 | 3.43 | 3.88 |
| <i>Pinus taeda</i> | 3 | 17 | -0.69 | 0.20 | -0.90 | -0.25 | 3.48 | 0.34 | 3.05 | 4.10 |
| <i>Pseudotsuga menziesii</i> | 3 | 20 | -0.60 | 0.15 | -0.71 | -0.26 | 3.80 | 0.22 | 3.59 | 4.26 |
| <i>Sequoia sempervirens</i> | 2 | 10 | -2.68 | 1.45 | -4.75 | -1.22 | 1.20 | 2.24 | -1.93 | 3.44 |
| <i>Tsuga heterophylla</i> | 4 | 37 | -0.44 | 0.08 | -0.61 | -0.36 | 4.21 | 0.14 | 3.93 | 4.42 |
| Species considered in only one yield table | | | | | | | | | | |
| <i>Abies balsamea</i> | 1 | 4 | -0.59 | 0.00 | -0.60 | -0.59 | 3.80 | 0.02 | 3.77 | 3.81 |
| <i>Abies concolor</i> | 1 | 7 | -0.57 | 0.01 | -0.59 | -0.56 | 3.84 | 0.13 | 3.67 | 3.98 |
| <i>Castanea dentata</i> | 1 | 3 | -0.65 | 0.01 | -0.66 | -0.64 | 3.62 | 0.06 | 3.56 | 3.67 |
| <i>Chamaecyparis thyoides</i> | 1 | 6 | -0.53 | 0.01 | -0.54 | -0.51 | 3.80 | 0.14 | 3.53 | 3.89 |
| <i>Eucalyptus globus</i> | 1 | 4 | -5.80 | 1.86 | -8.13 | -3.80 | 1.06 | 0.98 | -0.21 | 2.06 |
| <i>Eucalyptus microtheca</i> | 1 | 3 | -6.84 | 0.39 | -7.22 | -6.44 | -3.67 | 0.51 | -4.18 | -3.17 |
| <i>Eucalyptus sieberi</i> | 1 | 3 | -0.62 | 0.07 | -0.69 | -0.55 | 4.12 | 0.03 | 4.09 | 4.14 |
| <i>Liriodendron tulipifera</i> | 1 | 3 | -1.15 | 0.12 | -1.24 | -1.02 | 2.69 | 0.18 | 2.53 | 2.88 |
| <i>Liquidambar styraciflua</i> | 1 | 6 | -0.39 | 0.03 | -0.42 | -0.33 | 3.87 | 0.11 | 3.74 | 4.03 |
| <i>Picea mariana</i> | 1 | 3 | -0.83 | 0.04 | -0.85 | -0.78 | 3.72 | 0.01 | 3.72 | 3.72 |
| <i>Picea rubens</i> | 1 | 5 | -0.54 | 0.00 | -0.55 | -0.54 | 3.86 | 0.10 | 3.72 | 3.97 |
| <i>Pinus monticola</i> | 1 | 4 | -0.79 | 0.02 | -0.80 | -0.77 | 3.88 | 0.11 | 3.75 | 4.01 |
| <i>Populus tremuloides</i> | 1 | 4 | -0.33 | 0.07 | -0.43 | -0.27 | 3.62 | 0.12 | 3.46 | 3.74 |
| <i>Thuja occidentalis</i> | 1 | 6 | -0.35 | 0.04 | -0.41 | -0.30 | 3.58 | 0.08 | 3.46 | 3.67 |

* n_T and n_L are, respectively, the number of yield tables and the total number of thinning lines examined for each species.

the data before fitting the thinning line increases the probability of a type I statistical error (rejection of a true null hypothesis) by some unknown amount (Weller 1985). Some additional percentage of the data sets actually showed no correlation between $\log B$ and $\log N$, while some slopes that tested as significantly different from $\beta = -1/2$ are actually different at some lower confidence level. I can only acknowledge this limitation and argue that the analysis is nevertheless more objective than using no statistical tests. Since my other analyses corroborate that thinning slopes vary widely from $\beta = -1/2$, confidence in the results of the significance tests seems justified.

The frequency distributions of thinning slope and intercept (Table 1, Fig. 5) show greater variation in these parameters than suggested by the often cited ranges $-0.8 \leq \beta \leq -0.3$ and $3.5 \leq \alpha \leq 4.4$, proposed by White (1980). Both distributions have single modes near their accepted mean values of $\beta = -1/2$ and $\alpha = 4$, but the median of β was $< -1/2$, supporting Zeide's (1985) observation that thinning slopes are most often steeper than $-1/2$. Much more extreme values are also present. Sixty-seven percent of the 426 β values in the combined EFD and FYD were within White's range, as were 63% of the α values, so these ranges do include a large percentage of the observations, but not all. The

greater variation observed here has a simple explanation: White's ranges were based on 36 data sets chosen precisely because their thinning slopes were close to $\beta = -1/2$, but I attempted to avoid any a priori criteria. White (1981) has suggested that thinning slopes steeper than $\gamma = -2$ ($\beta = -1$) are prima facie evidence of significant departure from the classic thinning rule. Seventeen (23%) of the EFD and 45 (13%) of the FYD slopes meet this criterion, and so argue against the classic interpretation of the thinning rule.

Additional evidence of variation in thinning line parameters was found in the existence of statistically significant differences among plant groups, and in the observation of significant correlations with shade tolerance. These results argue further against a single, quantitative thinning rule for all plants. Slope and intercept values are not even constant among thinning lines for a particular species, so these parameters are not species constants (as suggested by Mohler et al. 1978, Hozumi 1980, White 1981, Hutchings 1983). Differences in thinning intercept among stands of a species have also been reported by Hara (1984) and Westoby (1984). Furnas (1981) has shown experimentally that the position of a thinning line can respond to changes in nutrient availability.

These analyses also address an important question

raised by Miyanishi et al. (1979), Perry (1984), and Westoby (1984): do fitted thinning slopes differ from the thinning rule prediction because of experimental error or actual biological differences? The observed significant relationships between thinning slope and each of two biological variables—plant group and shade tolerance—indicate that differences in thinning slopes are at least partly due to systematic biological differences and are not simply random measurement errors about a value described by a “law.” Zeide (1985) also concluded that the thinning slope is not a constant, but rather changes systematically with species and site. As suggested by Sprugel (1984), the thinning slope of $\gamma = -\frac{3}{2}$ ($\beta = -\frac{1}{2}$) is the exception rather than the rule.

The observed differences in $\log K$ are difficult to interpret because the set of thinning intercepts is not independent of the set of slopes (see also Zeide 1985). Values of $\log K$ are not directly comparable unless they come from lines of equal slopes (White and Gould 1965), so differences in $\log K$ may reflect differences in slope rather than interpretable differences in biomass levels. Also, most data sets do not include measurements at densities near 1 plant/m², so the calculated intercept at $\log N = 0$ is an extrapolation beyond the domain of the data (Westoby and Howell 1981). Biological interpretation of such extrapolated constants is not valid (White and Gould 1965). My analysis documents the variations in $\log K$ within a species and among plant groups, but biological interpretation of the observed differences is unwarranted until some analysis is devised to remove the confounding effects of differences in slope.

Deviations of thinning slopes from $\beta = -\frac{1}{2}$ may initially seem at odds with the interspecific size–density relationship. If the average mass and plant density measurements of many species follow a $-\frac{3}{2}$ power relationship for plant densities from 10² to 10⁵ plants/m² (Gorham 1979, White 1980), how can the thinning lines of individual species deviate significantly from this grand trend? Fig. 6A presents Gorham’s (1979) data for 65 mature stands of 29 species, replotted in $\log B$ – $\log N$ form to avoid the distortions of the \bar{m} – $\log N$ analysis. The line fit by Gorham to represent the interspecific relationship, $\log B = -0.5 \log N + 4.0$, is shown, as well as parallel lines with intercepts of 2.98 and 4.68 that enclose data from all 65 stands (rather than lines enclosing data from only 75% of the stands, as in the original analysis). Although Gorham’s analysis would seem to allow little variation from the interspecific relationship, the more appropriate $\log B$ – $\log N$ plot shows that individual thinning lines can vary in both slope and intercept and still fall within the limiting bands. For both a plot of the 75 significant EFD thinning lines (Fig. 6B) and a plot of the 351 thinning lines of the FYD (Fig. 6C) thinning lines deviate from the interspecific relationship, yet lines describing more than 99% of the 3300 individual stands used to fit thinning lines in the FYD and 87% of the

1337 EFD stands still fall within the band defined by Gorham’s data. Although it is difficult to distinguish the individual thinning lines of Fig. 6C, it is clear that almost all the lines lie within the band, despite the extensive variation in slope and intercept documented in Table 1 and Fig. 5. Even though not all of the slopes for the individual populations are close to $\beta = -\frac{1}{2}$, a clear negative correlation between stand biomass density and plant density is present across the entire collection of thinning lines, and Gorham’s line still provides a good linear representation of this interspecific trend. The few thinning lines that extend below the band may represent populations that were not really self-thinning and were erroneously included. Such errors are inevitable given the inherent subjectivities in selecting data for self-thinning analysis. I did not remove these outliers because they can only be eliminated by arbitrary, a posteriori decisions.

The existence of the interspecific relationship is, then, consistent with either of two hypotheses about the self-thinning lines of individual populations: the accepted view that all thinning slopes are near $\beta = -\frac{1}{2}$, as dictated by the self-thinning rule, and the alternative view that thinning slopes need not be near $\beta = -\frac{1}{2}$. Since the interspecific relationship is consistent with both acceptance and rejection of the self-thinning rule for individual populations, it cannot be cited as strong evidence for that rule. The apparent persistence of the interspecific relationship despite the failure of the intraspecific thinning rule suggests that the within-population and intraspecific relationships are not simply facets of the same rule, but fundamentally different relationships that may arise from different constraints and should be tested and explained separately (see also Zeide 1985).

If the evidence for a quantitative thinning rule is so insubstantial, how has the thinning rule gained such widespread acceptance? The general approach in establishing the self-thinning rule has been to compile many examples of thinning lines with slopes near $-\frac{3}{2}$. However, it is usually easy to find evidence for a hypothesis, regardless of whether or not it is generally true. Therefore, the mere existence of such evidence does not verify the hypothesis. Rigorous verification comes from the failure of an attempt to find evidence that contradicts or falsifies the hypothesis (Popper 1963). The emphasis on compiling corroborative evidence for the thinning rule has diverted attention from rigorously testing that evidence and searching for data that do not conform. Violations of the rule have been discussed only for shoot populations of clonal perennials (Hutchings 1979, Mook and van der Toorn 1982, Pitelka 1984) and for thinning under very low illumination (Lonsdale and Watkinson 1982, Westoby and Howell 1982), but there are other violations besides these special cases, such as thinning slopes of $\gamma = -3.2$ for seedling populations of the woodland herb *Allium ursinum* (Ernst 1979) and $\gamma = -2.59$ and -4.5 for the

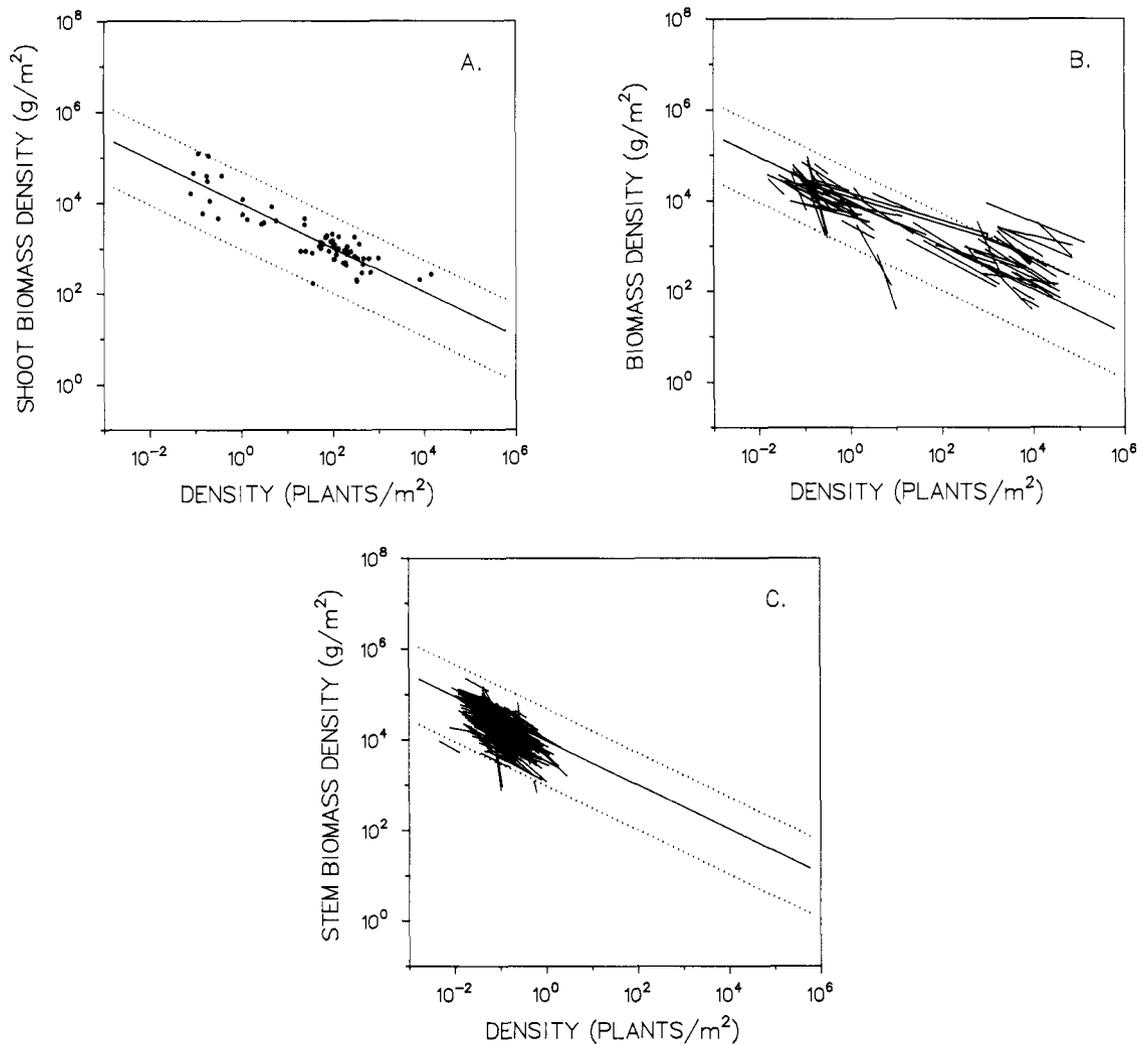


FIG. 6. Reanalysis of the interspecific size-density relationship. In (A), Gorham's (1979) data for 65 mature stands of 29 species are replotted in the $\log B$ - $\log N$ plane. The solid line is Gorham's interspecific relationship, $\log B = 0.49 \log N + 3.99$, and the parallel dotted lines with intercepts of 2.98 and 4.68 enclose all of the observations. Data provided by E. Gorham. (B) and (C), respectively, plot the 75 thinning lines of the experimental and field data and the 351 thinning lines of the forestry yield table data, as fit here. Solid and dotted lines are as in (A).

tropical trees *Shorea robusta* and *Tectona grandis* (O'Neill and DeAngelis 1981). For temperate trees, extreme reported slopes include $\gamma = -1.1$ for *Pinus radiata* (West and Borough 1983) and $\gamma = -1.2$ for *Abies balsamea* (Sprugel 1984). Zeide (1985) gives additional examples. Information contradicting the self-thinning rule has been missed even in the very sources from which supporting evidence has been drawn. For example, data for one stand of *Pinus strobus* (Spurr et al. 1957) have been repeatedly cited in self-thinning studies (Hozumi 1977, 1980, Hara 1984), and a self-thinning slope of $\gamma = -1.7$ has been fit (White 1980). However, the report of Spurr et al. also presented data for a second stand for which the slope of the thinning line is $\gamma = -2.11$ (Weller 1985). The uncited data on this second stand contradict the self-thinning rule in

two ways: the thinning slope is quite different from the predicted value, and both the slope and intercept change from stand to stand.

In summary, many data sets do show a region of linear association between $\log B$ and $\log N$ as predicted by the self-thinning rule, but the slope of the relationship varies among populations so that all populations do not obey a single quantitative rule. What are the consequences of deviations in thinning slopes from the idealized value $\beta = -1/2$? Would a more general qualitative rule predicting a linear relationship of variable slope be useful? Miyanishi et al. (1979) attempted to generalize the self-thinning rule to accommodate such variation, but their proposal was criticized by White (1981), while Westoby (1984) states that such a generalization would so dissipate the strength of the rule

that it would no longer be worth calling it a rule. However, the data demand such a generalization. The thinning rule as a quantitative law should be discarded, and the many claims made for the generality, theoretical importance, and applicability of the rule should be carefully reevaluated. Happily, Zeide (1985) has noted a positive aspect of the demise of the thinning rule: the thinning slope may be more useful as a variable than as a spurious constant. The differences among slopes may provide a valuable measure of the ecological differences among species and stands, and a powerful stimulus for further research on intraspecific competition.

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APPENDIX

TABLE A1. Experimental and field data.

| ID code* | Species† | Numbers of thinning lines‡ | | | | Reference |
|---------------------|--|----------------------------|-------|-------|-------|---|
| | | n_L | n_S | n_A | n_C | |
| Herbaceous monocots | | | | | | |
| 86 | <i>Festuca pratensis</i> | 1 | 1 | 0 | 1 | Lonsdale and Watkinson 1983: Figs. 1 and 2C |
| 38 | <i>Lolium perenne</i> (Illumination) | 3 | 1 | 1 | 2 | Kays and Harper 1974: Fig. 4 |
| 91 | <i>Lolium perenne</i> (Illumination) | 4 | 3 | 1 | 2 | Lonsdale and Watkinson 1982: Fig. 1 |
| 92 | <i>Lolium perenne</i> (Illumination) | 4 | 2 | 2 | 3 | Lonsdale and Watkinson 1982: Fig. 5 |
| 90 | <i>Poa annua</i> (Grazing level) | 2 | 0 | 0 | 2 | Dirzo and Harper 1980: Fig. 3 |
| 7 | <i>Triticum</i> | 1 | 1 | 0 | 1 | Puckridge and Donald 1967: Fig. 1, Table 2; White and Harper 1970: Fig. 5 |
| Herbaceous dicots | | | | | | |
| 87 | <i>Agrostemma githago</i> | 1 | 1 | 0 | 1 | Lonsdale and Watkinson 1983: Figs. 1 and 2C |
| 17 | <i>Amaranthus retroflexus</i> | 1 | 1 | 1 | 1 | Yoda et al. 1963: Fig. 16 |
| 18 | <i>Ambrosia artimisiifolia</i> | 1 | 1 | 1 | 1 | Yoda et al. 1963: Fig. 15 |
| 33 | <i>Beta vulgaris</i> | 1 | 1 | 0 | 1 | Furnas 1981: Fig. 4.2 |
| 34 | <i>Beta vulgaris</i> | 1 | 1 | 0 | 0 | Furnas 1981: Fig. 4.5 |
| 43 | <i>Beta vulgaris</i> (Illumination) | 5 | 5 | 4 | 5 | Westoby and Howell 1981: Fig. 1 |
| 58 | <i>Beta vulgaris</i> and <i>Brassica juncea</i> | 1 | 0 | 0 | 0 | Furnas 1981: Figs. 4.8 and 4.9 |
| 50 | <i>Brassica juncea</i> (Illumination) | 2 | 0 | 0 | 0 | Furnas 1981: Fig. 4.10 |
| 53 | <i>Brassica napus</i> and <i>Raphanus sativus</i> | 1 | 1 | 1 | 1 | White and Harper 1970: Fig. 2 |
| 89 | <i>Capsella bursa-pastoris</i> (Grazing level) | 2 | 2 | 2 | 2 | Dirzo and Harper 1890: Fig. 3 |
| 20 | <i>Chenopodium album</i> | 1 | 1 | 0 | 1 | Yoda et al. 1963: Fig. 17 |
| 88 | <i>Chicorium endivium</i> | 1 | 1 | 0 | 1 | Lonsdale and Watkinson 1983: Figs. 1 and 2C |
| 15 | <i>Erigeron canadensis</i> | 1 | 1 | 0 | 1 | Yoda et al. 1963: Fig. 14 |
| 21 | <i>Erigeron canadensis</i> | 1 | 1 | 0 | 1 | Yoda et al. 1963: Tables 2 and 3 |
| 29 | <i>Fagopyrum esculentum</i> | 1 | 1 | 0 | 1 | Yoda et al. 1963: Fig. 21 |
| 32 | <i>Fagopyrum esculentum</i> (Fertility) | 2 | 0 | 0 | 2 | Furnas 1981: Fig. 4.1 |
| 49 | <i>Fagopyrum esculentum</i> | 1 | 0 | 0 | 0 | Furnas 1981: Fig. 4.6 |
| 44 | <i>Helianthus annuus</i> (Experiment, Illumination) | 7 | 1 | 0 | 4 | Hiroi and Monsi 1966: Figs. 1, 5, and 6, Table 2 |

TABLE A1. Continued.

| ID code* | Species† | Numbers of thinning lines‡ | | | | Reference |
|-----------------------------------|--|----------------------------|-------|-------|-------|--|
| | | n_L | n_S | n_A | n_C | |
| 31 | <i>Medicago sativa</i> | 1 | 0 | 0 | 1 | Black 1960: Fig. 1, Tables 1-3 |
| 56 | <i>Medicago sativa</i> | 1 | 1 | 1 | 1 | Malmberg and Smith 1982: Fig. 4 |
| 57 | <i>Medicago sativa</i> and <i>Trifolium pratense</i> | 1 | 0 | 0 | 1 | Malmberg and Smith 1982: Fig. 3 |
| 16 | <i>Plantago asiatica</i> | 1 | 1 | 1 | 1 | Yoda et al. 1963: Fig. 13 |
| 51 | <i>Sinapsis alba</i> and <i>Lepidium sativum</i> | 1 | 0 | 0 | 1 | Bazzaz and Harper 1976: Fig. 1 |
| 40 | <i>Tagetes patula</i> | 1 | 0 | 0 | 1 | Ford 1975: Fig. 12 |
| 27 | <i>Trifolium pratense</i> | 1 | 0 | 0 | 1 | Westoby and Brown 1980: Fig. 2 |
| 28 | <i>Trifolium pratense</i> (Illumination) | 3 | 1 | 1 | 3 | Hutchings and Budd 1981b: Fig. 4 |
| 30 | <i>Trifolium pratense</i> | 1 | 0 | 0 | 1 | Black 1960: Fig. 1, Tables 1-3 |
| 55 | <i>Trifolium pratense</i> | 1 | 0 | 0 | 1 | Malmberg and Smith 1982: Fig. 4 |
| 10 | <i>Trifolium subterraneum</i> | 1 | 1 | 1 | 1 | Westoby and Howell 1982: Table 1 |
| 35 | <i>Trifolium subterraneum</i> | 1 | 1 | 1 | 1 | Westoby 1976: Fig. 1 |
| Shrubs | | | | | | |
| 36 | <i>Ceanothus megacarpus</i> | 1 | 0 | 0 | | Schlesinger and Gill 1978: Fig. 3, Table 1 |
| Temperate angiosperm trees | | | | | | |
| 106 | <i>Acer spicatum</i> | 1 | 1 | 1 | | Cannell 1982:33 |
| 138 | <i>Alnus incana</i> and <i>Salix</i> | 2 | 0 | 0 | | Cannell 1982:251 |
| 131 | <i>Alnus rubra</i> | 2 | 2 | 1 | | Cannell 1982:252 |
| 26 | <i>Betula</i> | 1 | 1 | 0 | 1 | Yoda et al. 1963: Fig. 23 |
| 39 | <i>Betula</i> (Site) | 2 | 0 | 0 | | Hozumi and Shinozaki 1970: Tables 2B and 2C |
| 121 | <i>Betula</i> | 2 | 1 | 1 | | Cannell 1982:238 |
| 115 | <i>Camellia japonica</i> | 1 | 0 | 0 | | Cannell 1982:99 |
| 123 | <i>Castanea sativa</i> | 1 | 1 | 0 | | Cannell 1982:239 |
| 48 | <i>Corylus avellana</i> | 1 | 1 | 1 | 1 | Jeffers 1956: Tables 16-18 |
| 112 | <i>Cyclobalanopsis myrsinaefolia</i> | 1 | 1 | 0 | | Cannell 1982:108 |
| 103 | <i>Fagus sylvatica</i> | 2 | 0 | 0 | | Cannell 1982:31 |
| 104 | <i>Fagus sylvatica</i> | 1 | 1 | 1 | | Cannell 1982:58 |
| 105 | <i>Fagus sylvatica</i> | 2 | 0 | 0 | | Cannell 1982:72 |
| 14 | <i>Liquidambar styraciflua</i> | 1 | 1 | 1 | 1 | Tepper and Bamford 1960: Table 1 |
| 109 | Mixed hardwoods, Canada | 1 | 0 | 0 | | Cannell 1982:34 |
| 133 | <i>Populus deltoides</i> | 1 | 1 | 0 | | Cannell 1982:266 |
| 5 | <i>Populus tremuloides</i> | 1 | 1 | 0 | 1 | Pollard 1971: Table 1; Pollard 1972: Table 2 |
| 1 | <i>Prunus pensylvanica</i> | 2 | 0 | 0 | 1 | Marks 1974: Tables 2 and 3 |
| 22 | <i>Prunus pensylvanica</i> | 1 | 1 | 1 | 1 | Mohler et al. 1978: Fig. 1a |
| 126 | <i>Quercus pubescens</i> | 1 | 1 | 1 | | Cannell 1982:68 |
| 41 | <i>Quercus robur</i> | 1 | 1 | 1 | 1 | Barkham 1978: Table 5 |
| Temperate gymnosperm trees | | | | | | |
| 124 | <i>Abies</i> | 1 | 0 | 0 | | Cannell 1982:133 |
| 23 | <i>Abies balsamea</i> | 1 | 1 | 0 | 1 | Mohler et al. 1978: Fig. 1b |
| 117 | <i>Abies firma</i> and <i>Tsuga sieboldii</i> | 1 | 0 | 0 | | Cannell 1982:124 |
| 19 | <i>Abies sachalinensis</i> | 1 | 1 | 0 | 1 | Yoda et al. 1963: Fig. 22 |
| 24 | <i>Abies sachalinensis</i> | 1 | 1 | 1 | | Hozumi and Shinozaki 1970: Table 2A |
| 119 | <i>Abies sachalinensis</i> | 1 | 1 | 1 | | Cannell 1982:126 |
| 114 | <i>Abies veitchii</i> | 2 | 2 | 0 | | Cannell 1982:129 |
| 81 | <i>Abies veitchii</i> and <i>Abies mariesii</i> | 1 | 0 | 0 | | Oshima et al. 1958: Table 2, Fig. 4 |
| 52 | <i>Cryptomeria japonica</i> | 1 | 0 | 0 | 1 | Tadaki and Shidei 1959: Tables 1-3 |
| 120 | <i>Cryptomeria japonica</i> | 2 | 0 | 0 | | Cannell 1982:151 |
| 122 | <i>Cryptomeria japonica</i> | 1 | 1 | 1 | | Cannell 1982:146 |
| 132 | <i>Cryptomeria japonica</i> | 1 | 0 | 0 | | Cannell 1982:146 |
| 54 | <i>Larix occidentalis</i> and <i>Pinus monticola</i> | 1 | 1 | 0 | 1 | Foiles 1956: Tables 1 and 2 |
| 136 | <i>Picea abies</i> | 2 | 0 | 0 | | Cannell 1982:73 |
| 137 | <i>Picea abies</i> | 2 | 2 | 0 | | Cannell 1982:361 |
| 45 | <i>Picea mariana</i> | 1 | 1 | 1 | 1 | Hatcher 1963: Table 11 |
| 130 | <i>Pinus nigra</i> | 1 | 0 | 0 | | Cannell 1982:243 |
| 110 | <i>Pinus banksiana</i> | 2 | 0 | 0 | | Cannell 1982:44 |
| 135 | <i>Pinus banksiana</i> and mixed hardwoods | 1 | 1 | 0 | | Cannell 1982:300 |

TABLE A1. Continued.

| ID code* | Species† | Numbers of thinning lines‡ | | | | Reference |
|---------------------------|---|----------------------------|-------|-------|-------|---|
| | | n_L | n_S | n_A | n_C | |
| 84 | <i>Pinus densiflora</i> | 1 | 1 | 1 | 1 | Yoda et al. 1963: Fig. 24 |
| 128 | <i>Pinus pumila</i> | 1 | 1 | 0 | | Cannell 1982:176 |
| 125 | <i>Pinus sylvestris</i> | 1 | 0 | 0 | | Cannell 1982:243 |
| 8 | <i>Pinus strobus</i> (Plot) | 2 | 2 | 0 | 1 | Spurr et al. 1957: Tables 1 and 2 |
| 93 | <i>Pinus strobus</i> | 1 | 1 | 0 | | Beck 1978: Table 2; Wahlenberg 1955: Fig. 2 |
| 82 | <i>Pinus taeda</i> | 1 | 1 | 0 | 1 | Peet and Christensen 1980: Fig. 3; Christensen and Peet 1982: Fig. 15.2 |
| 102 | <i>Pinus taeda</i> | 1 | 1 | 0 | | Cannell 1982:320 |
| 80 | <i>Taxodium distichum</i> | 1 | 1 | 1 | | Schlesinger 1978: Fig. 3C |
| <i>Eucalyptus</i> trees | | | | | | |
| 99 | <i>Eucalyptus deglupta</i> | 1 | 1 | 1 | | Hillis and Brown 1978: Table 10.34 |
| 101 | <i>Eucalyptus grandis</i> | 1 | 0 | 0 | | Cannell 1982:11 |
| 95 | <i>Eucalyptus obliqua</i> | 1 | 0 | 0 | | Hillis and Brown 1978: Table 10.17 |
| 116 | <i>Eucalyptus obliqua</i> | 1 | 1 | 0 | | Cannell 1982:14 |
| 96 | <i>Eucalyptus pilularis</i> | 1 | 0 | 0 | | Hillis and Brown 1978: Table 10.21 |
| 97 | <i>Eucalyptus regnans</i> | 1 | 0 | 0 | | Hillis and Brown 1978: Table 10.24 |
| 98 | <i>Eucalyptus regnans</i> (Site index) | 3 | 2 | 0 | | Hillis and Brown 1978: Table 10.26 |
| 118 | <i>Eucalyptus tereticornis</i> | 2 | 0 | 0 | | Cannell 1982:78 |
| Tropical angiosperm trees | | | | | | |
| 111 | <i>Shorea robusta</i> | 2 | 2 | 0 | | Cannell 1982:79 |
| 113 | <i>Tectona grandis</i> | 2 | 2 | 0 | | Cannell 1982:83 |

* An arbitrary number for cross-referencing among data tables.

† Site differences or experimental treatments that divided a given study into several possible thinning trajectories are given in parentheses after the species name. "Plot" and "Site" indicate that populations from different locations were measured, while "Illumination," "Grazing level," and "Fertility" indicate that populations received different levels of the specified stress or resource. "Experiment" indicates that the reference reports several experiments, while "Site index" indicates that trees were measured on sites of differing quality.

‡ n_L is the total number of $\log B$ - $\log N$ relationships fit from a given study. n_S is the number that demonstrated a statistically significant ($P < .05$) correlation between $\log B$ and $\log N$. n_A is the number of thinning lines that potentially agree with the self-thinning rule, that is, the number of thinning slopes that were statistically significant but not statistically different ($P < .05$) from the predicted slope $\beta = -1/2$. n_C is the number of thinning lines claimed in the reference (or by some other author) to agree with the self-thinning rule. Weller (1985) gives additional information for each of the 137 data sets, including the number of points available, number of points used, ranges and means of $\log B$ and $\log N$, correlation coefficient, slope, intercept, and confidence intervals for slope and intercept. Weller (1985) also gives references and other information for each thinning line previously claimed to support the thinning rule.

TABLE A2. Forestry yield table data.

| ID code* | Species | n_L † | Shade tol.‡ | Reference |
|-----------------------|--|---------|-------------|---|
| Temperate angiosperms | | | | |
| 202 | <i>Alnus rubra</i> | 3 | 2 | Smith 1968: Table 3 |
| 242 | <i>Alnus rubra</i> | 3 | 2 | Smith 1968: Table 5 |
| 243 | <i>Alnus rubra</i> | 2§ | 2 | Smith 1968: Table 6 |
| 207 | <i>Carya</i> | 1 | 2 | Boisen and Newlin 1910: Table 14 |
| 204 | <i>Castanea dentata</i> | 3 | 3 | Frothingham 1912: Tables 17-19 |
| 205 | <i>Castanea dentata</i> and <i>Quercus</i> | 3 | 3 | Frothingham 1912: Tables 20-22 |
| 250 | <i>Fraxinus</i> | 2 | 3 | Sterrett 1915: Table 15 |
| 265 | <i>Fraxinus americana</i> | 1 | 3 | Patton 1922:37 |
| 277 | <i>Liquidambar styraciflua</i> | 6 | 2 | Winters and Osborne 1935: Tables 4-8 |
| 249 | <i>Liriodendron tulipifera</i> | 3 | 2 | McCarthy 1933: Table 17 |
| 245 | Northern mixed hardwoods | 3 | | Gevorkiantz and Duerr 1937: Table 3 |
| 267 | Northern mixed hardwoods | 1 | | Forbes 1961: Table 14 |
| 268 | Northern mixed hardwoods | 1 | | Vermont Ag. Expt. Sta. 1914: Table 8 |
| 225 | <i>Populus</i> | 1 | | Tseplyaev 1961: Table 134 |
| 246 | <i>Populus</i> (aspen) | 5 | 1 | Kittredge and Gevorkiantz 1929: Table 1 |
| 210 | <i>Populus deltoides</i> | 1 | 1 | Williamson 1913: Table 3 |
| 209 | <i>Populus tremuloides</i> | 4 | 1 | Baker 1925: Tables 14-17 |
| 206 | <i>Quercus</i> | 3 | 3 | Frothingham 1912: Tables 23-25 |

TABLE A2. Continued.

| ID code* | Species | n_L † | Shade tol.‡ | Reference |
|-----------------------|---|---------|-------------|--|
| 216 | <i>Quercus</i> | 3 | | Khil'mi 1957: Tables 23, 50 |
| 269 | <i>Quercus</i> (red oaks) | 1 | 3 | Patton 1922: 37 |
| 236 | <i>Quercus</i> (upland oaks) | 5 | 3 | Shnurr 1937: Table 2 |
| 244 | Southern mixed hardwoods | 3 | | Frothingham 1931: Table 8 |
| Temperate gymnosperms | | | | |
| 238 | <i>Abies balsamea</i> | 4 | 5 | Meyer 1929: Tables 35–49 |
| 203 | <i>Abies concolor</i> | 7 | 4 | Schumacher 1926: Table 1 |
| 224 | Cedar (USSR) | 1 | | Tseplyaev 1961: Table 81 |
| 211 | <i>Chamaecyparis thyoides</i> | 6 | 4 | Korstian 1931: Tables 22, 25 |
| 215 | <i>Picea</i> | 6 | | Khil'mi 1957: Tables 18, 45 |
| 241 | <i>Picea</i> and <i>Abies</i> | 5 | 4 | Bakuzis and Hansen 1965: Tables 89, 91, 93, 95, 97 |
| 237 | <i>Picea glauca</i> | 5§ | 4 | Stiell 1976: Tables 10–13 |
| 239 | <i>Picea glauca</i> | 4 | 4 | Meyer 1929: Tables 29–33 |
| 263 | <i>Picea mariana</i> | 3 | 4 | Fox and Kruse 1939: Table 2 |
| 213 | <i>Picea rubrens</i> | 5 | 4 | Meyer 1929: Tables 2–6 |
| 255 | <i>Picea sitchensis</i> | 1 | 4 | Cary 1922: Tables 6–9 |
| 212 | <i>Picea sitchensis</i> and <i>Tsuga heterophylla</i> | 8 | 4 | Meyer 1937: Tables 1–5 |
| 262 | <i>Picea sitchensis</i> and <i>Tsuga heterophylla</i> | 9 | 4 | Taylor 1934: Table 4–8 |
| 214 | <i>Pinus</i> | 6 | | Khil'mi 1957: Tables 13, 14 |
| 223 | <i>Pinus</i> | 1 | | Tseplyaev 1961: Table 47 |
| 256 | <i>Pinus banksiana</i> | 3 | 1 | Eyre 1944: Table 8 |
| 257 | <i>Pinus banksiana</i> | 5 | 1 | Bella 1968: Tables 2–6 |
| 264 | <i>Pinus banksiana</i> | 2 | 1 | Boudoux 1978: Tables 3, 4 |
| 232 | <i>Pinus echinata</i> | 7 | 2 | Schumacher and Coile 1960: Table 4 |
| 253 | <i>Pinus echinata</i> | 3 | 2 | Mattoon 1915: Table 14 |
| 254 | <i>Pinus echinata</i> | 3 | 2 | Mattoon 1915: Table 16 |
| 273 | <i>Pinus echinata</i> | 7 | 2 | USDA 1929: Tables 98–102 |
| 230 | <i>Pinus elliotii</i> | 6 | 3 | Schumacher and Coile 1960: Table 2 |
| 274 | <i>Pinus elliotii</i> | 5 | 3 | USDA 1929: Tables 130–134 |
| 208 | <i>Pinus monticola</i> | 4 | 3 | Haig 1932: Table 1 |
| 231 | <i>Pinus palustris</i> | 6 | 1 | Schumacher and Coile 1960: Table 3 |
| 235 | <i>Pinus palustris</i> | 8 | 1 | Wahlenberg 1946: Tables 4b, 6c, 7a, 7b |
| 271 | <i>Pinus palustris</i> | 8 | 1 | USDA 1929: Tables 68–70 |
| 201 | <i>Pinus ponderosa</i> | 13 | 2 | Meyer 1938: Tables 3–6 |
| 227 | <i>Pinus ponderosa</i> | 9 | 2 | Behre 1928: Tables 2–6 |
| 272 | <i>Pinus ponderosa</i> | 5 | 2 | Show 1925: Table 2 |
| 222 | <i>Pinus resinosa</i> | 5§ | 2 | Stiell and Berry 1973: Tables 4–8 |
| 258 | <i>Pinus resinosa</i> | 3 | 2 | Eyre and Zehngraff 1948: Table 10 |
| 233 | <i>Pinus serotina</i> | 6 | 2 | Schumacher and Coile 1960: Table 5 |
| 217 | <i>Pinus strobus</i> | 3 | 3 | Marty 1965: Table 1 |
| 218 | <i>Pinus strobus</i> | 3 | 3 | Marty 1965: Table 2 |
| 220 | <i>Pinus strobus</i> | 6 | 3 | Marty 1965: Table 4 |
| 229 | <i>Pinus taeda</i> | 7 | 2 | Schumacher and Coile 1960: Table 1 |
| 234 | <i>Pinus taeda</i> | 3 | 2 | Ashe 1915: Tables 19, 35, 42 |
| 270 | <i>Pinus taeda</i> | 7 | 2 | USDA 1929: Tables 33–38 |
| 221 | <i>Pseudotsuga menziesii</i> | 14 | 3 | McArdle 1930: Table 12 |
| 251 | <i>Pseudotsuga menziesii</i> | 1 | 3 | McArdle et al. 1949: Table 25 |
| 266 | <i>Pseudotsuga menziesii</i> | 5 | 3 | Schumacher 1930: Tables 2–5, 7 |
| 252 | <i>Sequoia sempervirens</i> | 7 | 4 | Linguist and Palley 1963: Tables 1, 2, 4–6 |
| 276 | <i>Sequoia sempervirens</i> | 3 | 4 | Bruce 1923: Tables 1–3 |
| 228 | <i>Thuja occidentalis</i> | 6 | 4 | Gevorkiantz and Duerr 1939: Tables 18–24 |
| 259 | <i>Tsuga heterophylla</i> | 12 | 5 | Barnes 1962: Tables 3, 5, 7, 9, 12 |
| 260 | <i>Tsuga heterophylla</i> | 13 | 5 | Barnes 1962: Tables 4, 6, 8, 10, 13 |
| 261 | <i>Tsuga heterophylla</i> | 11 | 5 | Barnes 1962: Tables 4, 6, 8, 10, 14 |
| 278 | <i>Tsuga heterophylla</i> | 1 | 5 | Barnes 1962: Table 27 |
| <i>Eucalyptus</i> | | | | |
| 279 | <i>Eucalyptus delegatensis</i> | 1 | | Hillis and Brown 1978: Table 10.1 |
| 247 | <i>Eucalyptus globus</i> | 4 | | Jacobs 1979: Table A3.5 |
| 248 | <i>Eucalyptus microtheca</i> | 3 | | Jacobs 1979: Table A3.13 |
| 280 | <i>Eucalyptus regnans</i> | 1 | | Hillis and Brown 1978: Table 10.22 |
| 281 | <i>Eucalyptus sieberi</i> | 3 | | Hillis and Brown 1978: Table 10.27 |

* An arbitrary number for cross-referencing among data tables.

† The number of thinning lines fit from each yield table.

‡ Shade tolerance is taken from Baker (1949) or the reference indicated. Tolerances are ranked from 1 (least tolerant of shading) to 5 (most tolerant).

§ All yield tables with more than one thinning line are subdivided by site index, except for number 243, which gives data for closed and open canopy forests, and numbers 222 and 237, which give data for different initial spacings.