Ecology, 68(4), 1987, pp. 813–821
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SELF-THINNING EXPONENT CORRELATED WITH ALLOMETRIC MEASURES OF PLANT GEOMETRY[1]

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Abstract. The −3/2 power rule of self-thinning, which describes the course of growth and mortality in crowded, even-aged plant stands, predicts that average mass is related to plant density by a power equation with exponent −3/2. The rule is widely accepted as an empirical generalization and quantitative rule or law. Simple geometric models of space occupation by growing plants yield a power equation, but the exponent can differ from −3/2 when realistic assumptions about the allometric growth of plants are considered. Because such deviations conflict with the empirical evidence for the −3/2 value as a law-like constant, the geometric models have not produced an accepted explanation and the thinning rule remains poorly understood.

Recent studies have concluded that thinning exponents can deviate more widely from −3/2 than previously thought, motivating the present re-evaluation of the geometric explanation. I extend the simple models to predict the relationships of the thinning exponent to allometric exponents derived from commonly measured stand dimensions, such as height, average mass, average bole diameter at breast height (DBH), and average bole basal area. If the form and exponent of the thinning equation arise from the geometry of space filling, then thinning exponents should be systematically related to the exponents of allometric equations relating average height to average mass, average height to average DBH, and average height to average basal area. I also predict some values for the slopes and intercepts of regression lines relating thinning exponents to the allometric exponents.

The predictions are verified by statistically comparing the thinning exponents and allometric exponents of self-thinning populations. The expected negative correlations are present and statistically significant ($P \leq .05$), and the slopes and intercepts of linear regressions relating thinning exponents to allometric exponents are near the predicted values. These results support the hypothesis that the thinning equation arises from the geometry of space filling, but recognition that thinning exponents differ from −3/2 as predicted by simple geometric considerations weakens the case for a quantitative rule or law.

Key words: mass-density relationship; plant allometry; plant competition; plant geometry; plant population dynamics; self-thinning rule; −3/2 power law; Yoda's law.

INTRODUCTION

The −3/2 power rule of self-thinning for crowded but actively growing even-aged plant populations predicts that average mass ($\bar{m}$) and the number of plants per unit area (N) are related by a simple power equation $\bar{m} = KN^{\gamma}$, where $\gamma = -3/2$ and K is a population constant (Yoda et al. 1963). This relationship is accepted as a rule or law applying across the plant kingdom (Yoda et al. 1963, White and Harper 1970, Furnas 1981, Hutchings and Budd 1981, Westoby 1981, 1984, White 1981) and has been called the only law of plant ecology (Harper, as cited in Hutchings 1983). If fully substantiated, the self-thinning rule could be the first basic law in the science of ecology (McIntosh 1980). As a quantitative law, the thinning rule would have important scientific implications (Westoby 1981, 1984) and potential applications as a research and management tool for plant populations (Yoda et al. 1963, Drew and Flewelling 1977, 1979, Westoby 1981, 1984).

Proposed explanations of the self-thinning rule have primarily been attempts to derive the power equation and −3/2 exponent from the geometry of space occupation by growing plants. Two basic geometric models that both yield power equations have been proposed. The isometric model (Yoda et al. 1963) directly gives the −3/2 exponent by assuming that growing plants do not change shape (isometric growth). The allometric model (Westoby 1976, Mohler et al. 1978, Miyanishi et al. 1979, White 1981) recognizes that plants can change shape with increasing size (allometric growth), but predicts that thinning exponents will deviate from −3/2. The isometric model is unacceptable as a general explanation of the thinning rule because many species do not grow isometrically (Furnas 1981, White 1981), while the allometric model has been criticized because it predicts significant departures from the −3/2 exponent that seem at odds with the empirical constancy

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[1] Manuscript received 1 May 1986; revised 4 September 1986; accepted 16 October 1986.

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of the $-3/2$ value (White 1981). With the apparent inadequacies of both geometric models, the underlying rationale of the self-thinning rule remains unclear (Hutchings and Budd 1981, Westoby 1981, 1984, Hutchings 1983).

Weller (1985, 1987) re-examined the evidence for the self-thinning rule and found that many data sets do support a power relationship of the form $\bar{m} = KN^{\gamma}$, but the exponent γ can differ from the accepted value of $-3/2$ (also see Sprugel 1984, Zeide 1985). This result revives the allometric model as a possible explanation for the self-thinning equation. I here review the derivation of the isometric and allometric models and extend the allometric model to predict how the thinning exponent should vary with the exponents of allometric equations relating frequently measured plant population parameters, such as average mass, height, bole diameter at breast height (DBH), and bole basal area (BA). I test the predictions of the allometric model by statistically evaluating the relationships between thinning and allometric exponents as estimated from published data for many populations of different plant species.

Isometric model

Yoda et al. (1963) originally derived a geometric explanation of the self-thinning rule from two assumptions: plants of a given species maintain the same shape regardless of habitat, size, or age; and mortality occurs only when the total coverage of a plant stand exceeds the available area, then acts to maintain 100% cover. The first assumption allows the ground area covered by a plant (a) to be expressed mathematically as a power function of plant mass, $a \propto m^{2/3}$, while the second assumption implies that the average area covered is inversely proportional to density, that is, $\bar{a} \propto 1/N$. Combining these equations with a constant of proportionality, K, gives the thinning rule equation. White and Harper (1970) and Whittington (1984) present alternative derivations based on isometric models. In time-dynamic mathematical models of population growth and mortality, the assumption of isometric growth yields population trajectories in accordance with the $-3/2$ thinning rule (Aikman and Watkinson 1980, Slatkin and Anderson 1984, Weller 1985).

Allometric model

Unfortunately, the assumption of invariant plant shape is not generally valid, so the simple explanation of Yoda et al. is unsatisfactory as a general explanation of the thinning rule (Westoby 1976, Furnas 1981, White 1981). Miyanishi et al. (1979) proposed a more general explanation in their "generalized self-thinning law," which states that the thinning exponent depends on the proportionality between plant mass and ground area covered. This proposal can be stated mathematically by setting the area covered by a plant proportional to $m^{2\phi}$, where ϕ can vary from $\frac{1}{3}$ to reflect changes in shape with size (allometric growth). The thinning equation then becomes $\bar{m} = KN^{-1/(2\phi)}$, and the thinning exponent

$$\gamma = -1/(2\phi) \tag{1}$$

equals $-3/2$ only if shape is truly invariant (isometric growth, $\phi = \frac{1}{3}$). Westoby (1976), Mohler et al. (1978), and White (1981) present alternative allometric models. Dynamic simulation models confirm that allometric growth should yield thinning exponents different from $-3/2$ (Firbank and Watkinson 1985, Weller 1985, Jacob Weiner, *personal communication*).

Extensions of the allometric model

Ideally, the allometric model might be tested by comparing measured thinning exponents to values predicted from the area–mass allometric exponent by Eq. 1. However, it is difficult to measure the areas occupied by plants, so direct data for the area–mass allometric relationship are rarely available. I found no published studies in which both the thinning exponent and the area–mass allometric exponent of a given population could be estimated independently. One way to overcome this limitation is to estimate indirectly the area–mass allometric exponent from data that are readily available in the literature. For example, height is commonly measured, and the height–mass allometric exponent can be estimated. However, to use such estimates in testing the allometric model, one needs to know how the height–mass allometric exponent is related to the area–mass allometric exponent.

The required relationship between the height–mass and area–mass allometric exponents can be derived from basic biological principles. First, recognize that a plant can add mass in three basic ways: growing in height, expanding the area occupied, or packing more biomass within the volume already occupied. Now assume that height, area occupied, and density of biomass in occupied space (d), all vary with plant mass according to allometric power relationships $h \propto m^{\theta}$, $d \propto m^{\delta}$, and $R \propto m^{\phi}$, where R is the radius of the occupied area. Extensive work in forestry and ecology (e.g., Reinke 1933, Whittaker and Woodwell 1968, Curtis 1971, Hutchings 1975) has verified that the relationships among plant measurements are well described by power functions. If the volume of space occupied by a plant (v) is approximately cylindrical, then $v = \pi R^2 h$ and plant mass is $m = vd = \pi R^2 hd$. The equations combine to give $m \propto m^{2\phi} m^{\theta} m^{\delta}$, so that the allometric powers are constrained by $2\phi + \theta + \delta = 1$. Rearranging gives

$$\phi = 0.5 - 0.5\theta - 0.5\delta. \tag{2}$$

Eq. 2 is heuristically useful for its linearity, simple geometric derivation, and clear representation of the biological compromises inherent in plant growth—allocation of resources to height growth (higher θ) or to packing more biomass in the space already occupied (higher δ) leaves fewer resources for radial expansion (lower ϕ). Less radial expansion means less conflict with neighbors, so a given amount of biomass can be added with less attendant mortality. This would imply a steeper (more negative) thinning exponent. Thus, the intuitive implications of Eq. 2 agree with the quantitative predictions of Eq. 1.

Eqs. 1 and 2 can now be combined to yield a linear equation relating the thinning exponent to the allometric exponents relating height and biomass per unit of occupied volume to mass. If the allometric model is true, then the area–mass allometric exponent can be calculated from a measured thinning exponent by the inverse transformation $\phi' = -1/(2\gamma)$, where the prime in ϕ' emphasizes that ϕ is calculated from the thinning exponent, not directly measured. Substituting into Eq. 2 yields

$$\phi' = -1/(2\gamma) = 0.5 - 0.5\theta - 0.5\delta. \qquad (3)$$

Eq. 3 could be used to compare measured thinning exponents to predictions calculated from measured values of the allometric exponents relating height and biomass per unit volume to mass. Unfortunately, biomass per unit volume is seldom directly measured, and I found no published studies of self-thinning populations where γ, θ, and δ could be independently estimated. This obstacle to testing the allometric model can be avoided by assuming that biomass per unit volume remains constant as a population develops ($\delta = 0$). This assumption simplifies Eq. 3 to give a relationship among exponents calculated from the commonly reported stand measurements biomass, density, and height:

$$\phi' = -1/(2\gamma) = 0.5 - 0.5\theta. \qquad (4)$$

Thus, the allometric model can be tested by determining if measured thinning exponents and height–mass allometric exponents from many populations obey a hypothesized relationship (Eq. 4) predicted by the allometric model. Linear statistics can be used to test if ϕ' and θ show a negative linear association, and if the slope and intercept of the linear relationship between them agree with the values predicted by Eq. 4.

However, the assumption that biomass per unit volume is constant with growth ($\delta = 0$) requires some further discussion. The few available data indicate that biomass per unit volume can change as the average mass of a population increases (Lonsdale and Watkinson 1983), so δ is not necessarily 0. Because the assumption of $\delta = 0$ is not generally valid, we need to know how nonzero values of δ will disrupt attempts to compare data to Eq. 4. A multiple regression analysis of the full linear model including δ (Eq. 3) would apportion the variance among transformed thinning exponents into two categories: variance explained by the regression on θ and δ, and unexplained variance or error. If the variable δ is removed from the statistical model (i.e., data is fit to Eq. 4 rather than Eq. 3), then the variance among thinning exponents that could be uniquely explained by δ will remain unexplained and will add to the error term in the regression model. Ignoring variations in δ then reduces the explanatory power of the regression model and reduces the chances of observing a statistically significant relationship between the transformed thinning exponent and the height–mass allometric exponent. However, if the relationship between the two exponents is strong enough, it could still be detected despite the loss in resolving power incurred by ignoring variations in δ. Therefore, it is useful to proceed with fitting data to Eq. 4 as a test of the allometric model. Failure to obtain a statistically significant regression would be inconclusive; it might reflect a failure of the allometric model or the confounding effects of ignoring δ. However, statistical agreement of the data with Eq. 4 would be encouraging because the analysis ignoring δ is a very conservative test of the allometric model. Such agreement would suggest that the relationship between the transformed thinning exponent and the height–mass allometric exponent is indeed robust.

The height–mass allometric exponent is not the only commonly measured parameter that might serve as a surrogate for the area–mass allometric exponent in testing the allometric model. For forest stands, average bole diameter at breast height (DBH) or average bole basal area (BA) can also be used to fit allometric relationships. However, these bole measurements are less sensitive to trade-offs between radial or height growth because bole size must increase to support any additional mass, regardless of the direction of growth. Therefore, the exponents of the $\overline{\mathrm{DBH}}$-$\bar{m}$ or $\overline{\mathrm{BA}}$-$\bar{m}$ allometric equations will not necessarily obey simple equations of mutual constraint with the area–mass allometric exponent ϕ nor correlate strongly with it. Interpretation of the allometric relationship between average height and average DBH ($\bar{h} \propto \overline{\mathrm{DBH}}^{\lambda}$) is similarly confounded; but because $\bar{h}$ is a measure of vertical growth, some aspects of the ϕ–λ relationship can be deduced. If individuals grow only radially, Eq. 4 gives $\phi = 0.5$ and $\theta = 0$, so λ will be zero since height is constant. If growth is both radial and upward, Eq. 4 gives $\phi < 0.5$, and λ must be positive because DBH increases to support added mass. The expected ϕ–λ relationship would pass through the point $(\lambda,\phi) = (0,0.5)$, and ϕ and λ would be negatively correlated. Since basal area is proportional to DBH^2, the same expectations apply to the relationship between ϕ and ψ, the exponent in $\bar{h} \propto \overline{\mathrm{BA}}^{\psi}$, and ψ should equal 2λ. The predicted relationships of ϕ to λ and ψ should again apply to the transformed thinning exponent ϕ' (through Eq. 1) if the allometric model is valid.

In summary, the extensions of the allometric model suggest several testable hypotheses. The transformed thinning exponent should be negatively correlated with three measures of the way plants change shape with growth: the average height–average mass allometric ex-

TABLE 1. Descriptive statistics for self-thinning and allometric exponents.

				Percentiles				
Exponent	n	Mean	Std. dev.	Min. 0	5	Median 50	95	Max. 100
				Experimental and natural populations				
γ	75	−1.847	0.742	−4.808	−3.838	−1.622	−1.220	−1.146
ϕ'	75	0.298	0.075	0.104	0.130	0.308	0.410	0.436
θ	28	0.317	0.068	0.184	0.189	0.321	0.425	0.446
λ	6	1.070	0.134	0.860		1.078		1.215
ψ	24	0.401	0.118	0.229	0.229	0.399	0.609	0.615
				Forestry yield tables				
γ	351	−1.876	1.024	−9.132	−3.411	−1.618	−1.318	−1.119
ϕ'	351	0.298	0.067	0.054	0.147	0.309	0.379	0.447
θ	325	0.274	0.059	0.118	0.183	0.271	0.371	0.517
λ	323	0.770	0.230	0.327	0.473	0.733	1.225	1.762
ψ	309	0.387	0.130	0.131	0.232	0.362	0.617	1.058

ponent, the average height–average DBH allometric exponent, and the average height–average BA allometric exponent. The linear relationship of the transformed thinning exponent to the average height–average mass allometric exponent is further specified to have a slope of −0.5 and an intercept of 0.5. The slopes of lines relating the transformed thinning exponent to the average height–average DBH and average height–average BA allometric exponents are not specified, but the intercepts of both lines should be near 0.5. The slope of the line relating the transformed thinning exponent to the average height–average BA allometry should be approximately twice the slope of the line relating the transformed thinning exponent to the average height–average DBH allometry. These predictions have a clear biological interpretation: plants can be more massive at a given density and can grow with less attendant mortality (i.e., have a steeper, more negative thinning exponent) if they allocate more resources to height growth than to radial growth. The derivations presented here provide quantitative mathematical relationships to test this intuition.

METHODS

I tested the predictions of the allometric model with self-thinning and allometric exponents estimated from published studies of experimental and natural populations and from forestry yield tables (see Appendix). Thinning exponents were estimated as the principal axis (Jolicoeur and Heusner 1971, Jolicoeur 1973, 1975, Mohler et al. 1978) of logarithmically transformed measurements of B (stand biomass in grams per square metre) and N (in plants per square metre), which yields the exponent β in $B = KN^{\beta}$ (Weller 1985, 1987) Since $\bar{m} = B/N$ by definition, γ is calculated from β by $\gamma = \beta - 1$. Log $\bar{m}$ was not directly related to log N because of the statistical and interpretive problems associated with that analysis (Westoby and Brown 1980, Westoby 1984, Weller 1985, 1987). Where dimensional measurements were available for the stands used to estimate thinning exponents, the log-log principal axis method was used to fit allometric relationships relating average height (in metres) to average mass (in grams), average height to average DBH (in metres), and average height to average BA (in square metres per tree). In fitting thinning and allometric exponents, only data from stands that fell along a linear thinning trajectory in a log B–log N plot were included. See Weller (1985, 1987) for further details on the sources and analyses of these data.

Data sets from experimental or natural populations that did not show a significant ($P \leq .05$) negative linear association between log B and log N were removed from consideration as possible self-thinning relationships and omitted from all further analyses. Similarly, allometric exponents from relationships that were not statistically significant ($P \leq .05$) were discarded.

Unfortunately, these statistical tests could not be used to screen the information from forestry yield tables. Yield tables are predictions (model output) from regression or regression-like models, not data, and cannot be subjected to the same statistical tests that would be applied to data. The biological variability and measurement errors in the original forestry data are absent in a yield table, so statistical inferences drawn from a single thinning or allometric relationship fitted to such information would be meaningless (Weller 1985, 1987). Despite this limitation, it is still useful to review yield table information because the tables are distilled from vast amounts of data that are not readily available in original form and because evidence from yield tables has been important in establishing the self-thinning rule (White 1980, 1981). Furthermore, a large sample of thinning or allometric exponents from many different yield tables can be examined to look at the ranges of variability in these exponents or to test statistically for relationships between thinning and allometric exponents. Such comparisons are legitimate because they rely on model output from many different yield table models parameterized for different sets of real data.

TABLE 2. Regressions of transformed thinning exponent ϕ' against three allometric exponents.

Allometric exponent	n	r	r^2	P	Slope	95% confidence limits	Intercept	95% confidence limits
				Experimental and natural populations				
θ	28	−0.55	0.30	.0026*	−0.71	−1.14, −0.26	0.50	0.36, 0.64
λ	6	0.15	0.02	.78	0.06	−0.45, 0.56	0.18	−0.36, 0.72
ψ	24	−0.44	0.19	.032*	−0.35	−0.67, −0.03	0.41	0.28, 0.55
				Forestry yield tables				
θ	325	−0.46	0.21	<.0001*	−0.54	−0.65, −0.43	0.45	0.41, 0.48
λ	323	−0.67	0.45	<.0001*	−0.20	−0.23, −0.18	0.45	0.43, 0.47
ψ	309	−0.71	0.50	<.0001*	−0.36	−0.40, −0.32	0.44	0.42, 0.45

* Correlation significant at the 95% confidence level ($P \leq .05$).

Therefore, the variability among exponents from different yield tables is preserved, even though the variability among stands *within* a given yield table is lost in preparing the yield table. All the yield tables used here claimed to predict the course of growth and mortality in crowded even-aged forests, and all predicted that increasing yields would be accompanied by mortality (i.e., self-thinning). However, my results for yield table information are presented separately from results for experimental and natural populations because of the different levels of statistical testing possible.

RESULTS

The fitted thinning exponents were not all close to the idealized value $\gamma = -3/2$ (Table 1). The reasons why important deviations from $\gamma = -3/2$ have long been overlooked are reported and interpreted elsewhere (Weller 1985, 1987). The central question here is: Does the transformed thinning exponent ϕ' show the predicted systematic relationships with the allometric exponents θ, λ, and ψ? Among the forestry yield tables, all three predicted negative correlations were present and significant ($P \leq .05$), as were two of three correlations among the experimental and natural populations (Table 2, Fig. 1). The failure of the average height–average DBH allometric exponent λ to correlate significantly with ϕ' in the experimental and natural data is inconclusive because of the small sample size ($n = 6$). The regression equation relating the transformed thinning exponent ϕ' to the average height–average mass allometric exponent θ in experimental and natural data does not differ significantly from the predicted form of Eq. 4 in either slope or intercept. For the same relationship among the forestry yield tables, the difference between the regression intercept of 0.45 and the expected 0.5 was statistically significant, but numerically small.

Among the experimental and natural populations, the intercept of the ϕ'–ψ relationship (0.41) was not significantly different from the predicted 0.5. Among the forestry yield tables the intercepts of the ϕ'–ψ relationship (0.44) and the ϕ'–λ relationship (0.45) were significantly different from 0.5, but the differences from the predicted value were again numerically small. The slope of the ϕ'–ψ among the forestry yield tables (−0.36) was approximately twice the slope of the ϕ'–λ relationship (−0.20), as predicted.

DISCUSSION

The results verify the predictions of the allometric model, and thus support the geometric factors embodied in that model as explanations of the thinning relationship. However, the best regression relating the thinning exponent to an allometric exponent explained only 50% of the variation among thinning exponents. In addition to the routine problems of measurement errors and biological variability, four sources of error particular to the analyses of Table 2 added to the uncertainties: errors from inappropriate choices of data points for estimating the thinning exponent (Mohler et al. 1978, Westoby 1984, Weller 1985, 1987), major differences in the criteria for counting plants and measuring biomass or stand height among the studies from which the data were taken, and errors from incorrectly assuming that the density of biomass per unit of occupied volume (d) is constant. As explained previously, this assumption is not generally true, but provides a way to test the allometric model despite the lack of data to define the relationship of d to plant size for any of the populations considered here. This assumption reduces the explanatory power of the regressions, so that the significant relationships seen here had to be robust to remain detectable.

There are several reasons why I found evidence supporting the allometric model while previous studies (Westoby 1976, Mohler et al. 1978, White 1981) have not. My analysis showed that thinning exponents vary from $\gamma = -3/2$, so I looked for relationships between thinning exponents and allometric powers, rather than for mechanisms by which γ would always be $-3/2$ in spite of geometric differences among plants. I had more data to test the hypothesis because I analyzed the models to predict the relationship of the thinning exponent with allometric exponents fit to frequently measured plant dimensions. Others (Mohler et al. 1978, White 1981) had fewer data because they tried to relate the thinning exponent γ directly to crown area, which is difficult to measure and infrequently reported. There

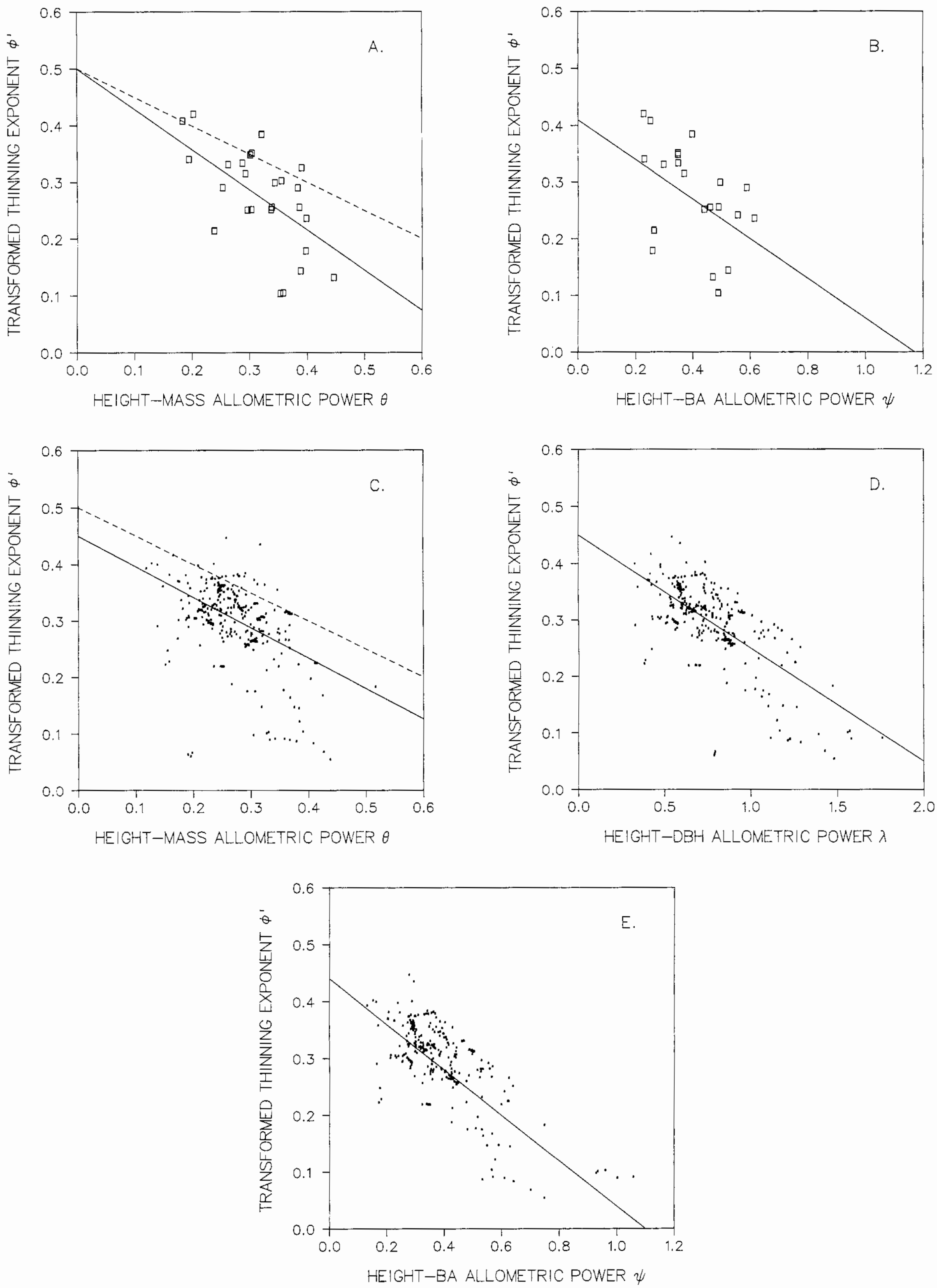

FIG. 1. The relationship of the transformed self-thinning exponent to three allometric exponents. (A), (B): Data from experimental and natural populations. (C), (D), (E): Information from forestry yield tables. Solid lines are regressions (Table 2) and dashed lines show the expected ϕ'–θ relationship (Eq. 4).

are such large variations around the regressions of the thinning exponent against an allometric exponent (Fig. 1) that small samples would be useless in detecting the trends.

My method of estimating allometric exponents also increased the chances of detecting relationships between plant allometry and the thinning exponent. I fit allometric exponents to aggregate stand measurements, such as average mass or average height, as reported for the same stands from which biomass and density data were used to fit the thinning exponents. The resulting allometric exponents directly measure the dynamics of shape change with stand growth. Typical allometric exponents relate two variables measured for a sample of individuals (Hutchings 1975, Mohler et al. 1978) so the allometric equation more directly describes the static size structure within that sample. The whole-stand approach gives allometric exponents more commensurate with thinning exponents, because thinning is also a dynamic, whole-stand process, not a static relationship among individuals. My method also permits allometric exponents to be estimated from the same stands of plants used to estimate the thinning exponent γ, rather than from small subsamples of individuals (Mohler et al. 1978) or from different sources (White 1981). It is crucial to estimate the thinning and allometric exponents from the same stands because allometric relationships (Hutchings 1975) and thinning exponents (Weller 1985, 1987) can vary among populations with site, time, and environmental factors.

Controlled experiments with plants of contrasting patterns of allometric growth will be required to verify completely the causal link implied by the correlations in Table 2. The significant proportion of unexplained variance in the regression models admits the possibility that other factors may also affect the thinning exponent, such as the physiological parameters considered in recent models (Pickard 1983, Perry 1984). Also, meaningful experiments will need to consider many populations, since the relationships of Fig. 1 could not be detected from just a few data points.

Weller (1985, 1987) presented several lines of evidence to show that the exponent of the self-thinning equation was not always near the idealized value of $-3/2$. The deviations of thinning exponents from $-3/2$ are now shown to be systematically related to differences in plant allometric exponents. These systematic relationships confirm that the observed deviations from $-3/2$ are real, not errors or artifacts. More happily, the present results put those deviations in a more positive light. Although the recognition of important departures of the thinning exponent from $-3/2$ dissipates the strength of the self-thinning rule (White 1981, Westoby 1984) and forces a re-evaluation of its scientific importance (Weller 1985, 1987, Zeide 1985), the relationship of the thinning exponent to allometric exponents helps to explain the self-thinning relationship and to suggest directions for further research. Even though thinning exponents vary according to plant geometry, the self-thinning equation may continue to be a concise and useful representation of competition within even-aged populations.

ACKNOWLEDGMENTS

I thank R. H. Gardner, H. H. Shugart, Jr., M. J. Hutchings, S. Gleeson, J. Weiner, D. M. G. Weller, and two anonymous reviewers for helpful comments on the manuscript, which was written while I was employed by the Smithsonian Institution's Environmental Sciences Program. This research was sponsored by the National Science Foundation's Ecosystems Studies Program under Interagency Agreement BSR-8313185 with the U.S. Department of Energy under contract Number DE-AC05-84OR21400 with Martin Marietta Energy Systems, Inc. Publication Number 2609, Environmental Sciences Division, Oak Ridge National Laboratory.

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APPENDIX

Sources of information. For each source, the species studied and the numbers of fitted exponents used here are given.

		Number of exponents used†			
Source*	Species	γ	θ	λ	ψ
Experimental and natural populations					
Herbaceous monocots					
86	*Festuca pratensis*	1	1		
38	*Lolium perenne*	1			
91	*Lolium perenne*	3			
92	*Lolium perenne*	2			
7	*Triticum*	1			
Herbaceous dicots					
87	*Agrostemma githago*	1	1		
17	*Amaranthus retroflexus*	1			
18	*Ambrosia artimisiifolia*	1			
33	*Beta vulgaris*	1			
34	*Beta vulgaris*	1			
43	*Beta vulgaris*	5			
53	*Brassica napus* and *Raphanus sativus*	1			
89	*Capsella bursa-pastoris*	2			
20	*Chenopodium album*	1			
88	*Chicorium endivium*	1	1		
15	*Erigeron canadensis*	1			
21	*Erigeron canadensis*	1			
29	*Fagopyrum esculentum*	1			
44	*Helianthus annuus*	1			
56	*Medicago sativa*	1			
57	*Medicago sativa* and *Trifolium pratense*	1			
16	*Plantago asiatica*	1			
28	*Trifolium pratense*	1			
10	*Trifolium subterraneum*	1			
35	*Trifolium subterraneum*	1			
Temperate angiosperm trees					
106	*Acer spicatum*	1	1		
131	*Alnus rubra*	2	2		2
26	*Betula*	1			
121	*Betula*	1	1		1
123	*Castanea sativa*	1	1		1
48	*Corylus avellana*	1	1		
112	*Cyclobalanopsis*	1			
104	*Fagus sylvatica*	1	1		1
14	*Liquidambar styraciflua*	1			
133	*Populus deltoides*	1	1		1
5	*Populus tremuloides*	1			
22	*Prunus pensylvanica*	1			
126	*Quercus pubescens*	1	1		1
41	*Quecus robur*	1			
Temperate gymnosperm trees					
23	*Abies balsamea*	1			
19	*Abies sachalinensis*	1			
24	*Abies sachalinensis*	1			
119	*Abies sachalinensis*	1	1		1
114	*Abies veitchii*	2	2		2
122	*Cryptomeria japonica*	1	1		1
54	*Larix occidentalis* and *Pinus monticola*	1			
137	*Picea abies*	2	2		2
45	*Picea mariana*	1			
135	*Pinus banksiana* and mixed hardwoods	1			
84	*Pinus densiflora*	1			
8	*Pinus strobus*	2	2	2	2

Appendix. Continued.

		Number of exponents used†			
Source*	Species	γ	θ	λ	ψ
93	*Pinus strobus*	1	1	1	1
82	*Pinus taeda*	1			
102	*Pinus taeda*	1	1		1
80	*Taxodium distichum*	1			
Eucalyptus trees					
99	*Eucalyptus deglupta*	1	1	1	1
116	*Eucalyptus obliqua*	2			
98	*Eucalyptus regnans*	2	1	2	2
Tropical angiosperm trees					
111	*Shorea robusta*	2	2		2
113	*Tectona grandis*	2	2		2
Forestry yield tables					
Temperate angiosperm trees					
202	*Alnus rubra*	3	3	3	
242	*Alnus rubra*	3	3	3	3
243	*Alnus rubra*	2	2		
207	*Carya*	1	1	1	
204	*Castanea dentata*	3	3	3	3
205	*Castanea dentata* and *Quercus*	3	3	3	3
250	*Fraxinus*	2			
265	*Fraxinus americana*	1	1	1	1
277	*Liquidambar styraciflua*	6	6	6	6
249	*Liriodendron tulipifera*	3	3	3	3
245	Northern mixed hardwoods	3			
267	Northern mixed hardwoods	1	1	1	1
268	Northern mixed hardwoods	1	1	1	
225	*Populus*	1	1	1	
246	*Populus* (aspen)	5	5	5	5
210	*Populus deltoides*	1	1	1	
209	*Populus tremuloides*	4	1	1	1
206	*Quercus*	3	3	3	3
216	*Quercus*	3			
269	*Quercus* (red oaks)	1	1	1	1
236	*Quercus* (upland oaks)	5	5	5	5
244	Southern mixed hardwoods	3	3	3	3
Temperate gymnosperm trees					
238	*Abies balsamea*	4	4	4	4
203	*Abies concolor*	7	7	7	7
224	Cedar (USSR)	1	1	1	
211	*Chamaecyparis thyoides*	6	6	6	6
215	*Picea*	6			
241	*Picea* and *Abies*	5	5	5	5
237	*Picea glauca*	5	5	5	5
239	*Picea glauca*	4	4	4	4
263	*Picea mariana*	3	3	3	3
213	*Picea rubrens*	5	5	5	5
255	*Picea sitchensis*	1	1	1	
212	*Picea sitchensis* and *Tsuga heterophylla*	8	8	8	8
262	*Picea sitchensis* and *Tsuga heterophylla*	9	9	9	9
214	*Pinus*	6			
223	*Pinus*	1	1	1	
256	*Pinus banksiana*	3	3	3	3
257	*Pinus banksiana*	5	5	5	5
264	*Pinus banksiana*	2	2	2	2
232	*Pinus echinata*	7	7	7	7
253	*Pinus echinata*	3	3	3	3
254	*Pinus echinata*	3	3	3	3
273	*Pinus echinata*	7	7	7	7
230	*Pinus elliottii*	6	6	6	6
274	*Pinus elliottii*	5	5	5	5
208	*Pinus monticola*	4	4	4	4
231	*Pinus palustris*	6	6	6	6
235	*Pinus palustris*	8	8	8	8
271	*Pinus palustris*	8	8	8	8
201	*Pinus ponderosa*	13	13	13	13
227	*Pinus ponderosa*	9	9	9	9
272	*Pinus ponderosa*	5	5	5	5
222	*Pinus resinosa*	5	5	5	5
258	*Pinus resinosa*	3	3	3	3
233	*Pinus serotina*	6	6	6	6
217	*Pinus strobus*	3	3	3	3
218	*Pinus strobus*	3	3	3	3
220	*Pinus strobus*	6	6	6	6
229	*Pinus taeda*	7	7	7	7
234	*Pinus taeda*	3	3	3	3
270	*Pinus taeda*	7	7	7	7
221	*Pseudotsuga menziesii*	14	14	14	14
251	*Pseudotsuga menziesii*	1	1	1	
266	*Pseudotsuga menziesii*	5	5	5	5
252	*Sequoia sempervirens*	7	7	7	7
276	*Sequoia sempervirens*	3	3	3	3
228	*Thuja occidentalis*	6	6	6	6
259	*Tsuga heterophylla*	12	12	12	12
260	*Tsuga heterophylla*	13	13	13	13
261	*Tsuga heterophylla*	11	11	11	11
278	*Tsuga heterophylla*	1	1	1	1
Eucalyptus trees					
279	*Eucalyptus delegatensis*	1	1	1	1
247	*Eucalyptus globus*	4	4	4	4
248	*Eucalyptus microtheca*	3	3	3	
280	*Eucalyptus regnans*	1	1	1	1
281	*Eucalyptus sieberi*	3			

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* The source column provides a unique study identification number that can be cross-referenced to published tables (Weller 1985, 1987) to obtain further biological and bibliographic information. Weller (1985, 1987) details the methods of selecting data and fitting self-thinning exponents.

† Column γ is the number of self-thinning exponents, while column θ is the number of average height–average mass allometric exponents. For trees, average DBH–average height (column λ) and average basal area–average height (column ψ) allometric exponents were calculated where measurements were available. For experimental and natural populations, only thinning or allometric exponents that were statistically significant ($P \leq .05$) were used, but similar statistical screening of the forestry yield tables was not possible (see Methods).