

THE INTERSPECIFIC SIZE-DENSITY RELATIONSHIP AMONG
CROWDED PLANT STANDS AND ITS IMPLICATIONS FOR THE
 $-3/2$ POWER RULE OF SELF-THINNING

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In a plot of the logarithm of average plant mass versus the logarithm of plant density, measurements of crowded stands of different plant species form a linear band of slope $-3/2$ that extends over 7 orders of magnitude of plant density and almost 10 orders of magnitude of average plant mass (Gorham 1979; White 1980, 1985; Westoby 1984). The existence of such a simple relationship across plant species ranging from mosses to trees has been judged remarkable (Gorham 1979) and cited as strong support for the self-thinning rule, which states that the temporal progress of growth and mortality within an individual crowded, even-aged stand will trace a line of slope $-3/2$ in the same double-logarithmic plot (White 1981; Hutchings 1983; Westoby 1984). The thinning rule is considered an important generalization (White and Harper 1970; Westoby 1981, 1984; White 1981), an ecological law (Yoda et al. 1963; Hutchings and Budd 1981a; Hutchings 1983), or even the only law in plant ecology (Harper, cited in Hutchings 1983).

However, interpretation of the inter- and intraspecific relationships in terms of a single thinning law de-emphasizes some important differences. The interspecific band is a static relationship among stands observed at single instants of time, whereas the intraspecific self-thinning trajectory describes the dynamic mutual adjustment between growth and mortality within an individual stand. Although the two phenomena may yield similar slopes and positions in a double-logarithmic plot, this does not necessarily mean that they are different facets of the single law. It is not obvious a priori that the two phenomena should even be related. I seek to explain and interpret the interspecific relationship separate from the intraspecific thinning rule and to explore the differences between the two relationships.

Advocates of the thinning rule have recently observed some important differences between inter- and intraspecific relationships. Westoby (1984) observed that the interspecific relationship gives a much better fit to the hypothetical $-3/2$ slope

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than do the self-thinning lines of individual populations and warned against interpreting the thinning rule in an unduly precise way (Westoby and Howell 1986). Although the interspecific band appears narrow, its width is important because a dynamic thinning trajectory of realistic length can vary substantially in slope from $-3/2$, yet still lie within the interspecific band of overall slope $-3/2$ (Westoby and Howell 1986). White (1985) noted that the thinning rule has severe limitations over small density ranges where precise predictions are required, but still holds as a coarse-grained rule over the entire plant kingdom.

Others have rejected the dynamic self-thinning rule. Sprugel (1984) suggested that, for trees, the $-3/2$ thinning slope is an exception rather than the rule. It has also been reported that thinning slopes change systematically with species, site, age, and tolerance and do not generally agree with the constant value predicted by the thinning rule (Weller 1985, 1987*a,b*; Zeide 1985, 1987). Zeide (1987) concluded that the intraspecific thinning law fails to describe the size-density dynamics of forest trees and is inconsistent with other well-documented knowledge of forest growth. The law became accepted despite these problems because of a variety of statistical and interpretive errors and the uncritical acceptance accorded an established paradigm (Weller 1985, 1987*a*; Zeide 1987).

The problems with the intraspecific thinning rule do not necessarily invalidate the interspecific relationship, which Zeide (1985, 1987) called an interesting regularity that should be considered separately and not confused with the self-thinning rule. Norberg (1988) suggested that the interspecific relationship reflects a principle of size-related design across species, whereas the dynamic thinning line reflects the growth mode of individual plants. Although intraspecific thinning slopes differ widely from the thinning-rule prediction (Weller 1985, 1987*a*), most individual stands still lie within the interspecific band defined by Gorham (1979). The inter- and intraspecific relationships are indeed different and may have fundamentally different explanations (Weller 1985, 1987*a*). Failure to recognize this dichotomy has helped to erroneously establish the thinning rule as a widely accepted law, and it has confused attempts to explain size-density relationships. The intraspecific thinning slope may be related to the way plants change shape dynamically as they grow (Weller 1987*b*; Norberg 1988); however, since the interspecific relationship is static, not dynamic, its explanation need not be based on dynamic principles that apply to individual stands.

Gorham (1979) proposed the first explanation for the interspecific relationship, suggesting that the same geometric model developed by Yoda et al. (1963) for dynamic self-thinning in crowded stands should apply. This model predicts the $-3/2$ slope by assuming that the plants considered are geometrically similar in shape (Yoda et al. 1963). To apply the model to the dynamics of a single stand, one must assume that growing plants maintain the same average shape (isometric growth; Weller 1987*b*). To apply the model across species, one must assume that average plant shape is roughly constant across the plant kingdom, that is, independent of mass. The assumption of constant shape with growth has been judged untenable, thus motivating many attempts to explain dynamic self-thinning with non-isometric models (Westoby 1976; Mohler et al. 1978; Miyanishi et al. 1979; White 1981; Pickard 1983; Perry 1984; Weller 1985, 1987*b*; Ellison 1986).

The equivalent assumption for the interspecific relationship remains largely unevaluated (but see Givnish 1986).

Givnish (1986) derived the slope and intercept of the self-thinning equation from biomechanical principles with the primary intent of explaining the interspecific size-density relationship on a priori grounds (Givnish, pers. comm.). He invoked the biomechanical principle of elastic similarity, which has been tested with data on tree trunks and limbs (McMahon 1973; McMahon and Kronauer 1976), and considered plants in which a single central stem supports a massive circular crown. Therefore, his derivation is somewhat less general than the interspecific relationship itself, which also applies to plants that do not fit this structural model for stem and crown (e.g., grasses) and do not have woody trunks and limbs. Also, it still requires that plant shape, as represented by the ratio of crown radius to height, remain roughly constant across the plant kingdom. Norberg (1988) considered two principles of variation in plant shape with size: geometric similarity and elastic similarity. He concluded that either principle could be consistent with observed interspecific trends if two parameters, the ratio of height to width and the packing density of material in the exclusive space, were appropriately constrained across the plant kingdom.

I develop here a simple model that relates the interspecific size-density band to static measures of plant form. I do not assume elastic similarity, isometric growth, or any other growth dynamic that may apply to only some groups of plants and thus be less general than the interspecific relationship that I seek to explain. Nor do I require that average plant form remain constant across the plant kingdom. I apply the model to the data from the first article on the interspecific relationship (Gorham 1979) and compare the results to a similar analysis of a larger data base (Weller 1985, 1987*a*). I test for systematic variation in the parameters of plant form across the plant kingdom. The model and analyses together clarify the biological significance of the slope, position, and width of the interspecific relationship; help to interpret these features in terms of constraints on plant form; and expose some important contrasts with the dynamic self-thinning lines of individual populations. I also identify a group of hypotheses about the self-thinning rule that actually have more relevance in the separate context of the interspecific relationship. I do not attempt to defend or explain the self-thinning "law," particularly the dynamic self-thinning rule for individual stands, whose foibles and explanations are considered elsewhere (Weller 1985, 1987*a,b*; Zeide 1985, 1987; Norberg 1988).

The logarithmic equation for the classic thinning law ($\log m = -\frac{3}{2} \log N + \log K$, where K is a constant) relating average mass (m in g) and density (N in plants per m^2) is a transformed version of a power relationship between the two variables ($m = K N^{-3/2}$). By definition, average mass is total biomass density (B in g per m^2) divided by the number density ($m = B/N$); thus, the mass-density relationship can be reexpressed as a relationship between stand biomass density and density ($\log B = -\frac{1}{2} \log N + \log K$ or $B = K N^{-1/2}$) (Yoda et al. 1963). The m - N and B - N relationships are mathematically equivalent, but there are statistical and interpretive reasons for preferring the B - N formulation in estimating, statistically testing, and interpreting size-density relationships (Westoby and Brown 1980; Westoby

1984; Weller 1985, 1987*a,b*; Zeide 1985, 1987). Therefore, the models and analyses presented here examine the interspecific relationship in B - N form.

GEOMETRIC MODEL

To derive the interspecific size-density band from basic geometric principles, begin by considering the maximum stand biomass possible at any plant density. Biomass is maximal when the available growing surface is fully used, the stand is as tall as possible, and the stand packs the maximum possible amount of biomass into each cubic meter of space occupied. Let H be the canopy height achieved under these conditions. The average volume of space occupied per plant is $v = Ha$, where a is the average ground area per plant, and the average mass is $m = vd = Had$, where d is average biomass per cubic meter of space occupied. All plants face energetic and structural constraints that must ultimately limit plant slenderness and biomass per unit of volume (see the Discussion). Let these two limits be represented by d_{\max} and the maximum value, τ_{\max} , of the dimensionless height-to-width ratio, where width is defined as the square root of the average ground area occupied ($\tau = H/(a)^{1/2}$).

For temporary pedagogical convenience, assume that the values of d_{\max} and τ_{\max} are approximately constant across the plant kingdom. Substituting these values into $m = Had$ gives $m_{\max} = a^{3/2} \tau_{\max} d_{\max}$, which is equivalent to $m_{\max} = N^{-3/2} \tau_{\max} d_{\max}$ because plant density and average area per plant are inversely related ($a = 1/N$) when the entire growing surface is covered (Yoda et al. 1963). Log transformation then yields $\log m_{\max} = -3/2 \log N + \log(\tau_{\max} d_{\max})$: a line in the plane of $\log m$ and $\log N$ that is the maximum average mass possible at any density. Since $B = m/N$ by definition, these equations can be equivalently expressed as $B = \tau_{\max} d_{\max} N^{-1/2}$ and $\log B = -1/2 \log N + \log(\tau_{\max} d_{\max})$. In reality, there will also be minimum values of the ranges of the ratio of height to width and biomass per unit of volume actually observed in crowded plant stands, and these minima (τ_{\min} and d_{\min}) define a parallel line, $\log B_{\min} = -1/2 \log N + \log(\tau_{\min} d_{\min})$, giving the lowest biomass possible at any density for a stand that covers the available growing surface. Stands below the lower boundary line are possible but uncrowded; stands above the upper boundary line are impossible because they require unrealistic values of τ or d . Of course, in fitting the interspecific relationship of $\log B$ and $\log N$ to real data, the fitted line passes through the middle of the data rather than representing the upper or lower boundary line (see the Methods).

The values of τ and d for any stand can be multiplied to yield a new constant $\kappa = \tau d$, which will be a composite measure of the shape and biomass per unit of volume of the stand. (This value is calculated for a single stand and is not the intercept of a self-thinning line or of the interspecific relationship.) Stands of tall, thin plants tend to have high values of τ and κ compared to short, squat plants. Similarly, stands that pack large amounts of biomass into the volume occupied have high values of d and κ compared to stands with less biomass per unit of occupied volume. After replacing the product τd with κ , the equation of the upper boundary line becomes

$$B = \tau_{\max} d_{\max} N^{-1/2} = \kappa_{\max} N^{-1/2}, \quad (1)$$

which can be logarithmically transformed to

$$\log B = -\frac{1}{2} \log N + \log(\tau_{\max} d_{\max}) = -\frac{1}{2} \log N + \log \kappa_{\max}, \quad (2)$$

and the lower-boundary equation becomes $\log B = -\frac{1}{2} \log N + \log \kappa_{\min}$. For any stand, κ can be calculated from biomass and density measurements by inverting equation (1) to yield $\kappa = B(N)^{1/2}$.

The derivation of equation (2) required only two assumptions: the maximum possible values of both d and τ are constant across the plant kingdom. No assumptions were required to introduce the quantities d , τ , and κ because these are simple measures defined for any plant stand. I did not consider whether growing plants maintain the same shape (Yoda et al. 1963; Gorham 1979) or change shape (Weller 1987*b*; Norberg 1988) or whether a growing stand maintains the same biomass per unit of volume (Lonsdale and Watkinson 1983; Weller 1987*b*). Because we are modeling a static relationship among stands observed at single instants of time, such consideration of growth dynamics would only unnecessarily complicate the model. Moreover, since different stands can and do show different dynamic trends of changing shape or biomass per unit of volume (Weller 1985, 1987*b*; Norberg 1988), a single dynamic would not be expected to govern all plant stands.

We need not assume a particular geometric form for the volumes occupied by plants because τ is the ratio of height to the square root of base area, regardless of the shape of that area. The volumes occupied might actually be cylindrical, columnar with hexagonal bases (as in a honeycomb), box-shaped, conical, etc. For each geometric solid, we could define a new variable τ' , which gives the ratio of the height to a relevant linear dimension of the base area. This variable would be the product of τ and a constant f , which depends on the particular geometric form of the plant (Norberg 1988). The slope and position of limiting lines (eq. 2) would be unaffected, but the transformation would be convenient for comparing τ values to other published ratios calculated by assuming a particular form (Givnish 1986; Norberg 1988). For $f = 1$, τ would be the height-to-side ratio for a square base, and $f = \pi^{1/2} = 1.773$ would yield the height-to-radius ratio for a circular base. For a hexagonal base, $f = 1.140$ gives the ratio of the height to the circumscribed radius, and $f = 1.316$ the ratio of the height to the inscribed radius.

Similarly, we have defined d as the average biomass per unit of volume in a column of height H and base area a , and another transformation can clarify the comparison of d to actual measurements of biomass per unit of volume if that column is not uniformly filled. For example, since a conical plant would pack all its biomass into just one-third of the available column, a measurement d' of biomass per unit of volume actually filled would be three times the d value defined by the equation $m = Had$. The transformation is again a matter of interpretive convenience: average mass ($m = Had = \frac{1}{3} Had'$) and equation (2) are unaffected. Of course, biomass is never distributed uniformly throughout the occupied volume. For example, trees concentrate mass in their heavy supporting boles and may have a large "empty" volume beneath the canopy. Nevertheless, the average biomass per unit of volume is easy to calculate and useful in comparisons across species.

The assumptions that the ranges of τ and d are constant across the plant kingdom have been heuristically useful but are not necessarily true. If τ and d vary systematically across the plant kingdom, then the constants τ_{\max} and d_{\max} in equation (2) should be replaced with expressions for that variation. Since extensive work in forestry and ecology shows that relationships between plant dimensions are well represented by power functions (Reineke 1933; Whittaker and Woodwell 1968; Curtis 1971; Hutchings 1975), let the systematic variation of τ_{\max} and d_{\max} across the kingdom be represented by two power relationships: $\tau_{\max} = \tau_0 B^\psi$ and $d_{\max} = d_0 N^\delta$, where τ_0 and d_0 are constants. I represent τ and d as functions of biomass and density, respectively, rather than as functions of the same variable, in order to avoid relating a derived variable to one of the measurements from which it was derived (see the Methods). Replacing the constants in equation (2) with these expressions yields $\kappa_{\max} = \tau_0 d_0 B^\psi N^\delta$ and

$$\log B = [(-1/2 + \delta)/(1 - \psi)] \log N + \log(\tau_0 d_0)/(1 - \psi). \quad (3)$$

The slope of the interspecific band is then

$$(-1/2 + \delta)/(1 - \psi). \quad (4)$$

The simpler, heuristic model (eq. 2) is now the special case of equation (3) when ψ and δ are both zero; that is, τ and d are constant. The slope of the interspecific relationship could still be $-1/2$ even if τ and d vary systematically across the plant kingdom, as long as those variations are compensatory ($\psi = 2\delta$) so that κ is constant (see also Norberg 1988). If τ and d are not constant and do not vary compensatorily ($\psi \neq 2\delta$), then equation (3) predicts that the slope of the interspecific relationship will not be $-1/2$. These alternatives provide a simple framework for understanding and interpreting the interspecific relationship.

METHODS

The geometric models are easily tested because useful estimates of τ and d can be derived from just three measurements of each stand: density, biomass, and height. Since $a = 1/N$ for crowded stands, the average basal area a can be estimated from $1/N$, and the ratio of height to base width τ can be estimated from measurements of N and H by $\tau = H/(a)^{1/2} = H(N)^{1/2}$. Similarly, the ratio B/H provides a measure of average biomass per unit of volume d because B gives the biomass per square meter of surface area and the volume occupied by one square meter of stand is simply one times the canopy height (Lonsdale and Watkinson 1983). Even if height data are unavailable, κ can always be estimated from the two measurements B and N by $\kappa = B(N)^{1/2}$.

I evaluated the model with measurements of aboveground stand biomass B , density N , and height H in a data base compiled from published reports of 370 plant stands (Appendix). All the stands were considered crowded because density-dependent mortality was under way and each stand appeared to lie on the dynamic self-thinning line for that population (Weller 1985, 1987a,b). For comparative purposes, I made parallel analyses of the measurements of 65 stands of 29

species used by Gorham (1979), who originally reported the interspecific size-density relationship.

To look for systematic changes in τ , d , and κ across the plant kingdom, I examined three correlations: $\log \tau$ with $\log B$, $\log d$ with $\log N$, and $\log \kappa$ with $\log H$. I did not examine the correlation of $\log \tau$ with $\log N$ because τ is directly calculated from density according to the definition $\tau = H(N)^{1/2}$ and the correlation therefore could be spuriously inflated (Weller 1987a) and difficult to interpret. Similarly, since d is directly calculated from biomass by $d = B/H$, a correlation analysis relating $\log d$ to $\log B$ would be invalid, and since $\kappa = B(N)^{1/2}$, H is the only one of the original three measurements B , N , and H whose correlation with κ would be interpretable. Principal-components analysis (PCA; Jolicoeur and Heusner 1971; Jolicoeur 1973, 1975; Mohler et al. 1978; Weller 1987a) was used to fit linear models relating $\log d$ to $\log B$ and $\log \tau$ to $\log N$. I fit a double-logarithmic equation because the relationships between plant dimensions are well described by power functions (Reineke 1933; Whittaker and Woodwell 1968; Curtis 1971; Hutchings 1975). The log transformation also standardized variances (which were correlated with the mean value for all these variables) and normalized the dimensions for PCA analysis (Jolicoeur 1973). Finally, to further examine the constancy of τ , d , and κ across the plant kingdom, I divided the stands into broad plant groups (mosses, ferns, herbaceous monocots, herbaceous dicots, and trees) and looked for differences in τ , d , or κ among these groups. Trees were further subdivided into temperate angiosperms, temperate gymnosperms, eucalypts, and tropical angiosperms.

I examined the interspecific relationship by estimating the strength of linear association between $\log B$ and $\log N$ with the correlation coefficient, and fitting the principal-axis equation relating $\log B$ to $\log N$. This resulting interspecific slope and intercept represent a line passing through the middle of the interspecific band. If the width of the band is roughly constant across the plant kingdom, then the upper and lower boundary lines parallel that medial line. Two problems preclude a more direct estimation of the boundary lines. First, we lack a priori information to identify a subset of stands along a boundary line that, in fact, has maximal (or minimal) τ and d values. Second, curve-fitting methods do not fit boundary lines, but instead fit lines through the mean of the available data (Hutchings and Budd 1981b; Weller 1987a). Three interspecific slopes were fitted for each data base: stands that also had height measurements, stands that lacked height measurements, and the combination of these two subsets. Finally, I evaluated whether the observed slope of interspecific relationship and patterns of variation in τ and d were consistent with the heuristic model (eq. 2) or the more complex model (eq. 3).

RESULTS

Variables τ and d were not constant across the plant kingdom (figs. 1, 2; tables 1–3). For Gorham's data, the correlation of $\log d$ and $\log N$ was negative but weak and not statistically significant. This result does not invalidate the assumption that d is constant across the plant kingdom. However, the correlation between τ and B

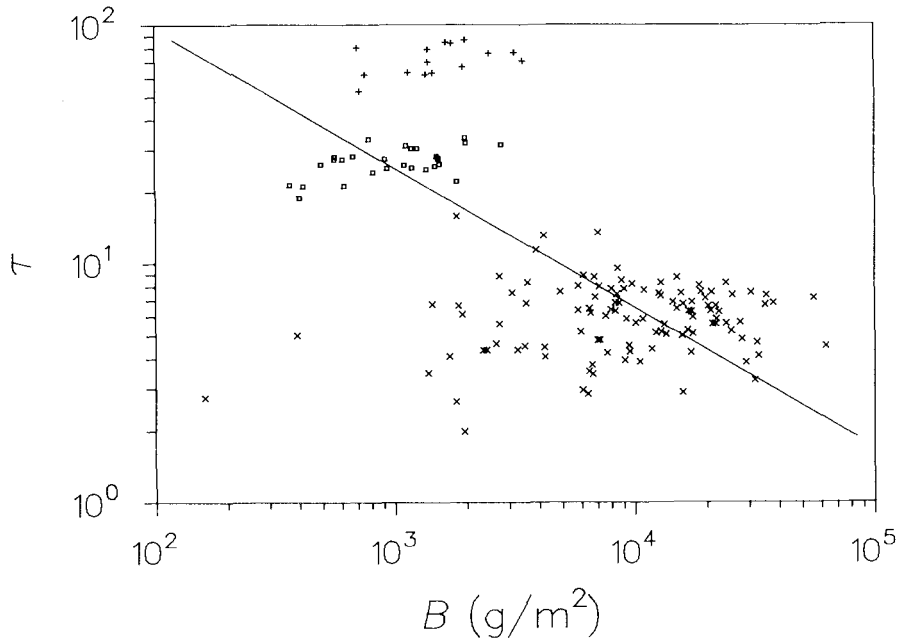


FIG. 1.—Trends in the ratio of height to width (τ) across the plant kingdom. *Crosses*, herbaceous monocots; *squares*, herbaceous dicots; *x*, trees. The solid line is the principal-axis relationship (table 2).

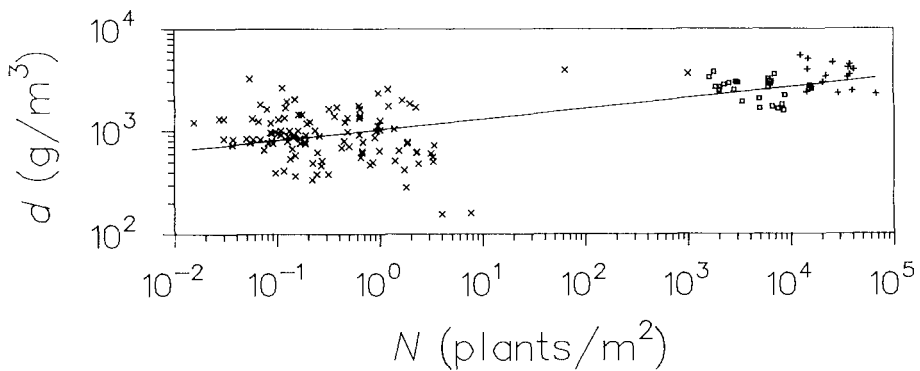


FIG. 2.—Trends in biomass per unit of volume (d) across the plant kingdom. The symbols and the solid line are the same as for figure 1.

was marginally significant ($P = 0.09$), suggesting that τ may change systematically across the plant kingdom. The negative correlation means that the volumes occupied by larger plants tend to be squatter in shape when compared to the more slender shapes filled by smaller plants. Among my data, both correlations were highly significant. The negative correlation of τ with B would have the same interpretation given above, but the slope of the relationship in my data is more

TABLE 1
SIMPLE STATISTICS FOR MEASUREMENTS (B , N , AND H) AND DERIVED VARIABLES (m , τ , d , AND κ)

STATISTIC	QUANTITY						
	H	τ	d	B	N	m	κ
	GORHAM (1979) DATA						
n	19	19	19	65	65	65	65
Mean	2.06	14.69	1010	7854	476	45660	12490
SD	3.03	7.40	1149	21330	1940	163700	8676
Percentiles*							
0	0.05	5.42	303	167	0.08	0.02	1002
1	0.05	5.42	303	167	0.08	0.02	1002
5	0.05	5.42	303	201	0.12	0.50	2844
10	0.27	5.87	386	294	0.19	0.67	4191
25	0.75	6.83	488	608	5.27	3.42	6052
50	1.30	13.00	572	1112	99.0	13.3	11500
75	2.18	21.31	1139	3847	206.0	925.0	15500
90	4.32	24.85	2162	21690	459.4	129400	23260
95	13.9	26.94	5299	43120	887.3	417900	31160
99	13.9	26.94	5299	121100	13800	1072000	47280
100	13.9	26.94	5299	121100	13800	1072000	47280
	WELLER (1985, 1987a) DATA						
n	154	154	154	370	370	370	370
Mean	9.35	16.13	1574	8442	5064	69150	35340
SD	8.48	20.25	1119	14640	9835	195900	56240
Percentiles*							
0	0.22	1.98	156	40	0.02	0.002	125
1	0.22	2.34	158	62	0.03	0.003	487
5	0.30	3.38	390	137	0.08	0.01	2659
10	0.32	4.07	501	200	0.12	0.03	3928
25	0.63	5.10	756	572	0.35	0.09	6386
50	7.15	6.85	1206	1805	563.2	1.87	14580
75	16.48	21.50	2316	9353	6136	26670	43650
90	21.95	43.10	3291	24090	15350	207400	75770
95	26.00	71.68	3924	37830	26970	400100	135600
99	29.45	85.42	5227	70430	46070	1082000	315900
100	30.00	86.47	5449	119700	71450	2053000	385500

* 0, minimum; 50, median; 100, maximum.

than double the slope for Gorham's data. The positive correlation of d with N indicates that plants growing at higher densities tend to pack more biomass into each unit of volume occupied. At the gross level across the plant kingdom, higher density trivially entails smaller plants (Gorham 1979; White 1981); we can therefore also interpret this correlation to say that larger plants pack less biomass per unit of volume than do smaller plants. Because τ and d are not constant across the plant kingdom, equation (3) must be used rather than the simpler heuristic model of equation (2) to interpret the interspecific relationship.

Interspecific relationships fitted to the same stands used to estimate the τ - B and d - N relationships provide the most direct test of the models. Neither fitted interspecific relationship had a slope of exactly $-\frac{1}{2}$. The slope of -0.43 for Gorham's data was not statistically different from $-\frac{1}{2}$, but the slope of -0.23 for my data was different from $-\frac{1}{2}$ (table 2; fig. 3). In both cases, the departure from

TABLE 2
BIVARIATE RELATIONSHIPS ACROSS THE PLANT KINGDOM

<i>Y</i>	<i>X</i>	<i>n</i>	\bar{X}	\bar{Y}	r^2	<i>P</i>	Slope (95% CI)	Intercept (95% CI)
GORHAM (1979) DATA								
log <i>H</i> vs. log <i>N</i>		19	2.092	0.060	0.814	<.0001	-0.413 (-0.519, -0.315)	0.925 (0.719, 1.145)
log <i>d</i> vs. log <i>N</i>		19	2.092	2.870	0.006	.76	-0.021 (-0.172, 0.128)	2.915 (2.602, 3.230)
log <i>H</i> vs. log <i>B</i>		19	2.930	0.060	0.685	<.0001	0.947 (0.657, 1.355)	-2.715 (-3.912, -1.865)
log τ vs. log <i>B</i>		19	2.930	1.106	0.158	.092	-0.224 (-0.526, 0.043)	1.763 (0.979, 2.647)
log <i>H</i> vs. log <i>m</i>		19	0.838	0.060	0.805	<.0001	0.282 (0.212, 0.355)	-0.177 (-0.237, -0.118)
log κ vs. log <i>H</i>		19	0.060	3.976	0.101	.19	-0.190 (-0.528, 0.111)	3.988 (3.970, 4.008)
log <i>B</i> vs. log <i>N</i> *		19	2.092	2.930	0.820	<.0001	-0.434 (-0.543, -0.333)	3.839 (3.627, 4.067)
log <i>B</i> vs. log <i>N</i> *		46	1.325	3.347	0.762	<.0001	-0.504 (-0.593, -0.421)	4.015 (3.905, 4.133)
log <i>B</i> vs. log <i>N</i> *		65	1.550	3.225	0.789	<.0001	-0.491 (-0.557, -0.429)	3.987 (3.890, 4.089)
WELLER (1985, 1987a) DATA								
log <i>H</i> vs. log <i>N</i>		154	0.730	0.619	0.942	<.0001	-0.326 (-0.339, -0.313)	0.858 (0.848, 0.867)
log <i>d</i> vs. log <i>N</i>		154	0.730	3.090	0.459	<.0001	0.104 (0.086, 0.122)	3.014 (3.001, 3.027)
log <i>H</i> vs. log <i>B</i>		154	3.709	0.619	0.805	<.0001	1.278 (1.181, 1.384)	-4.120 (-4.514, -3.763)
log τ vs. log <i>B</i>		154	3.709	0.985	0.350	<.0001	-0.585 (-0.721, -0.463)	3.153 (2.700, 3.660)
log <i>H</i> vs. log <i>m</i>		154	2.979	0.619	0.968	<.0001	0.268 (0.260, 0.275)	-0.178 (-0.201, -0.154)
log κ vs. log <i>H</i>		154	0.619	4.075	0.600	<.0001	-0.931 (-1.061, -0.816)	4.651 (4.580, 4.732)
log <i>B</i> vs. log <i>N</i> *		154	0.730	3.709	0.686	<.0001	-0.227 (-0.252, -0.202)	3.875 (3.857, 3.893)
log <i>B</i> vs. log <i>N</i> *		216	2.432	3.084	0.780	<.0001	-0.392 (-0.421, -0.365)	4.039 (3.971, 4.108)
log <i>B</i> vs. log <i>N</i> *		370	1.724	3.344	0.752	<.0001	-0.326 (-0.345, -0.307)	3.906 (3.873, 3.939)

* Relationships between log *B* and log *N* were fitted three ways: for all stands with height measurements (smallest *n*), for stands without height measurements (intermediate *n*), and for the combination of both groups (largest *n*).

the $-\frac{1}{2}$ slope predicted by the heuristic model can be explained when the more complex model is invoked to account for systematic trends in τ and *d*. For Gorham's data, equation (3) combines the fitted τ -*B* and *d*-*N* equations to predict an interspecific relationship of $\log B = -0.43 \log N + 3.82$. The slope and intercept of this predicted equation are quite close to the actual estimates of -0.43 and 3.83 , respectively, as fitted to the 19 stands with height data. For my data, the predicted equation ($\log B = -0.25 \log N + 3.86$) is again quite close to the fitted

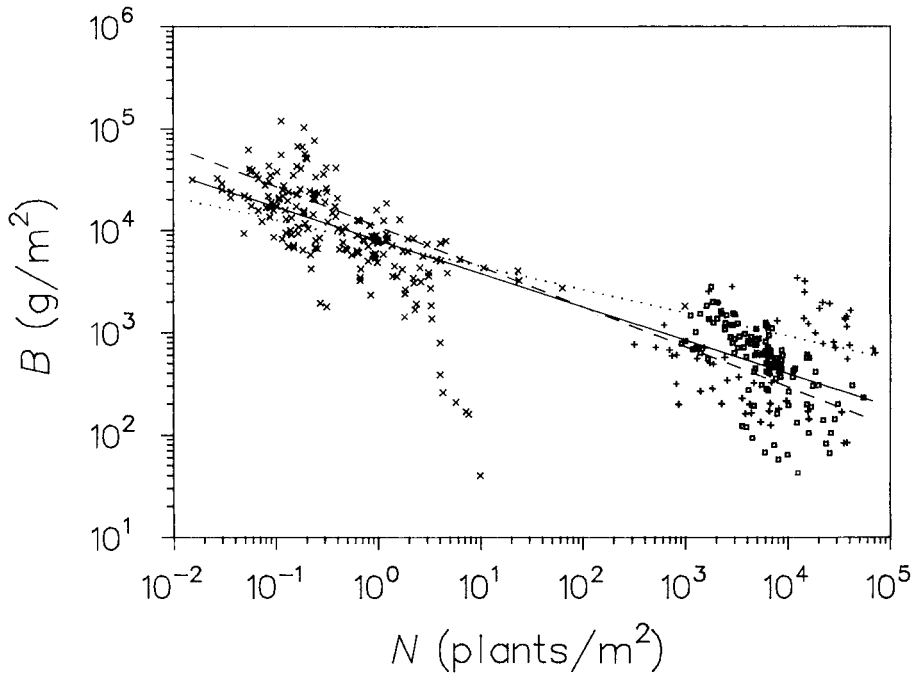


FIG. 3.—The interspecific relationship. The symbols are the same as for figure 1. Interspecific relationships (table 2): *dotted line*, stands with height measurements; *dashed line*, stands without height measurements; *solid line*, all stands.

equation for 154 stands ($\log B = -0.23 \log N + 3.88$). More-rigorous statistical analysis of the agreement between the predicted and fitted equations is not possible, because τ and d are both derived from H and are not independent measurements.

The systematic trends in τ and d can be partly understood in terms of differences among plant groups. For example, trees are bigger and occur at lower density than herbaceous plants. This truism is important because the across-species trends are dominated by the juxtaposition of trees and herbs. When the 19 stands of the Gorham data for which τ and d could be estimated are divided into plant groups, the group sizes are too small to exhibit convincing differences among groups (table 3). However, differences are evident among the same groups in my larger data base. Herbaceous monocots, herbaceous dicots, and trees are resolved into three distinct clusters of stands in figures 1 through 3. The tendency of smaller plants to occupy volumes that are more slender than those of larger plants is largely due to the more slender shape of herbs. Similarly, much of the change in biomass per unit of volume across the plant kingdom results from the tendency of herbs to pack more biomass into each unit of volume than do trees. Herbaceous monocots tend to be the most slender (highest τ values) and to pack the most biomass per unit of volume (highest d values). Since $\kappa = \tau d$, the two trends are compounded and the monocots also have the highest values of κ (fig. 4).

TABLE 3

MEDIAN, FIFTH, AND NINETY-FIFTH PERCENTILE VALUES OF THE RATIO OF HEIGHT TO WIDTH (τ), BIOMASS PER UNIT OF VOLUME (d), AND CONSTANT (κ) FOR DIFFERENT PLANT GROUPS (PERCENTILES IN PARENTHESES)

GROUP	STANDS WITH HEIGHT MEASUREMENTS				STANDS WITHOUT HEIGHT MEASUREMENTS		ALL STANDS	
	<i>n</i>	τ	<i>d</i>	κ	<i>n</i>	κ	<i>n</i>	κ
GORHAM (1979) DATA								
Herbs	16	16.11 (5.87–26.94)	556 (303–5299)	10595 (3646–31126)	30	11548 (2329–27624)	46	11416 (3495–28883)
Mosses	1	5.87	5299	31126	0		1	31126
Ferns	0				1	7464	1	7464
Monocots	14	17.87 (6.22–26.94)	540 (303–1138)	9749 (3646–17702)	29	11593 (2208–27947)	43	11328 (3460–23993)
Dicots	1	12.20	1235	15067	0		1	15067
Trees	3	5.91 (5.42–7.20)	1804 (792–2162)	9778 (5701–12783)	16	12835 (2224–47281)	19	12346 (2224–47281)
Temperate angiosperms	0				8	5316 (2224–24305)	8	5316 (2224–24305)
Temperate gymnosperms	3	5.91 (5.42–7.20)	1804 (792–2162)	9778 (5701–12783)	8	17164 (4984–47281)	11	13325 (4984–47281)
All plants	19	13.00 (5.42–26.94)	572 (303–5299)	9861 (3646–31126)	46	11697 (2356–37380)	65	11504 (2844–31162)
WELLER (1985, 1987 <i>a</i>) DATA								
Herbs	42	30.28 (21.04–84.41)	2842 (1645–4984)	87458 (34282–375589)	144	33535 (6947–113175)	186	42909 (8046–254422)
Monocots	15	70.26 (52.51–86.47)	3530 (2274–5449)	261931 (121220–385455)	46	19148 (9203–152517)	61	27012 (9573–331714)
Dicots	27	27.24 (19.70–33.46)	2656 (1604–3677)	73103 (32916–109503)	98	41065 (6391–63630)	125	45032 (6971–89450)
Trees	112	6.13 (2.91–9.09)	881 (377–2412)	4939 (1963–15961)	72	9977 (523–31861)	184	6810 (1677–23254)
Temperate angiosperms	55	6.10 (2.86–11.68)	651 (261–1951)	4385 (1691–13344)	36	8665 (3958–20443)	91	5073 (2124–16717)
Temperate gymnosperms	39	6.26 (3.53–8.46)	1002 (673–3620)	6969 (2765–21748)	36	12881 (406–41023)	75	8696 (529–38437)
Eucalypts	3	7.29 (6.79–7.50)	1236 (1196–1327)	9011 (8967–9016)	0		3	9011 (8967–9016)
Tropical angiosperms	15	4.65 (2.64–7.34)	1297 (383–3257)	6903 (1010–18723)	0		15	6903 (1010–18723)
All plants	154	6.85 (3.38–71.68)	1206 (390–3924)	6865 (2428–266513)	216	21357 (5092–89930)	370	14575 (2659–135627)

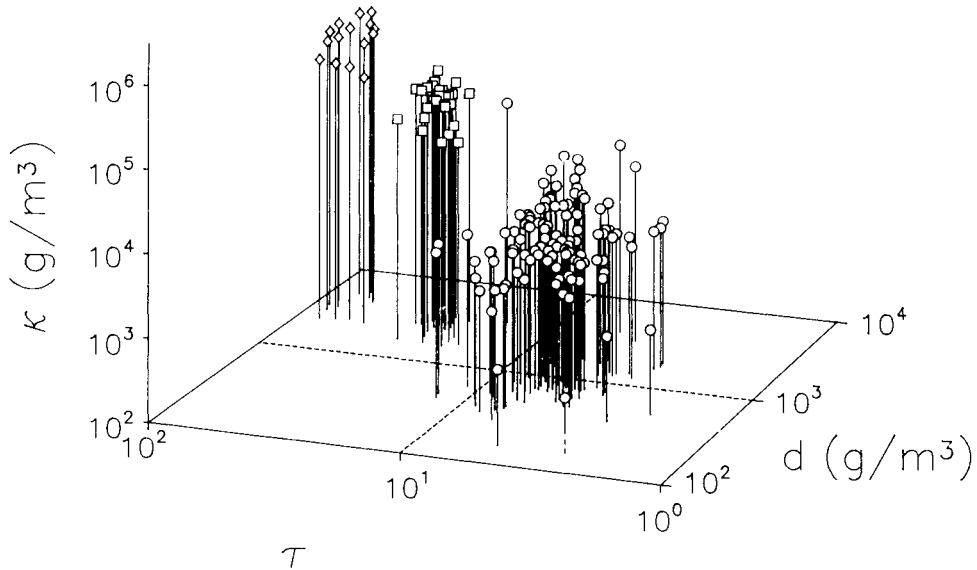


FIG. 4.—Joint variation in τ , d , and κ across the plant kingdom. *Diamonds*, herbaceous monocots; *squares*, herbaceous dicots; *circles*, trees. Note that the τ axis is arranged in descending order from left to right.

Conversely, trees had the lowest values of τ and d and the lowest values of $\kappa = \tau d$. Herbaceous dicots were intermediate for all three measures. The implications for the interspecific slope are clear. Herbaceous monocots—which inhabit the smallest, highest-density stands at the right side of the interspecific plot (fig. 3)—have higher values of τ and d , and hence κ . Conversely, the stands of trees at the left side of figure 3 have lower values of τ , d , and κ . The variable κ decreases systematically with plant size and increases with density. Combining this positive trend with density with the $-\frac{1}{2}$ slope predicted by the model if κ were constant should produce a final trend with a slope less negative than $-\frac{1}{2}$, as observed.

DISCUSSION

Gorham's data base and mine verified the usefulness of the geometric model (eq. 3) for understanding the interspecific size-density relationship. Although the estimated slope of the interspecific relationship differed between the data bases, the interspecific slopes were still explained in terms of systematic changes in biomass per unit of volume and the ratio of height to width across the plant kingdom. Gorham's data give an interspecific slope closer to $-\frac{1}{2}$ than do mine because Gorham's data more closely meet the assumptions about the constancy of τ and d that would necessarily yield a $-\frac{1}{2}$ slope.

Some of the differences between the two data bases result from different sampling intensities among plant groups (table 3). My larger data base also includes more stands at the extremes of possible ratios of height to width or

biomass per unit of volume, such as greenhouse populations of grasses, which tend to pack unusually high amounts of biomass per unit of volume (Lonsdale and Watkinson 1982, 1983). These particular stands contributed to the shallower interspecific slope for my data because the sampled grasses have higher values of κ (fig. 4) and tend to pull the right side of the interspecific relationship upward, producing a shallower slope.

The differences between the two data bases in the estimates of $B-N$, $\tau-B$, and $d-N$ trends (table 2) and median group values of τ , d , and κ (table 3) reveal an important pitfall: the exact estimates of grand trends across the plant kingdom or the results of comparisons between plant groups are fairly sensitive to the sample of stands used. It is important to consider this sensitivity and avoid unwarranted overinterpretation of exact estimates from a particular data base, even if the data base contains hundreds of stands. For example, the -0.49 slope of the interspecific relationship estimated from Gorham's data for 65 plant stands gave a nearly ideal agreement with the hypothetical $-\frac{1}{2}$ value, but the subset of 19 stands that also reported height measurements gave a less ideal slope of -0.43 . The nearly exact agreement of -0.49 with $-\frac{1}{2}$ may have been an accident of sampling rather than a reproducible description of the interspecific trend. For my data, the interspecific slope was significantly shallower than $-\frac{1}{2}$ (table 2). Since my data base is larger and more diverse than Gorham's, its shallower interspecific slope of -0.33 may be a more representative value than Gorham's -0.49 estimate. Equation (3) predicts a thinning slope shallower than $-\frac{1}{2}$ if κ decreases with increasing size across the plant kingdom. Such a decrease is verified in table 2, and White (1985) has also observed a decrease in $\log K$ with increasing plant height. If further analysis confirms that the slope of the interspecific relationship is indeed shallower than $-\frac{1}{2}$, then the $-\frac{1}{2}$ slope may not hold even as a coarse-grained rule, as proposed by White (1985). It is an interesting comment on the history of the thinning "law" that, despite the importance attached to Gorham's (1979) results, this study is the first to refit the relationship to a larger, more diverse data base.

Implications for Intraspecific Self-Thinning Rule

The interspecific relationship has been interpreted primarily as a facet of the self-thinning rule. The existence and slope of the interspecific band have been cited as evidence that (1) the model for intraspecific thinning of Yoda et al. (1963) also applies to interspecific mass-density relationships (Gorham 1979); (2) the same self-thinning law applies across the plant kingdom (Hutchings and Budd 1981a; Hutchings 1983); (3) the slope and position of the thinning line are insensitive to plant geometry (Furnas 1981); and (4) the empirical generality of the self-thinning rule is beyond question (White 1981).

The present model and results are useful in understanding the dichotomy between the intraspecific thinning trajectory and the interspecific size-density band and the resulting problems with the above interpretations. My data base is composed of data sets defining intraspecific thinning trajectories for single populations that show a significant negative correlation between $\log B$ and $\log N$ (Weller 1987a). The thinning slopes differ widely from the idealized $-\frac{1}{2}$ value and do not

support a self-thinning "law" (Weller 1985, 1987*a,b*). Nevertheless, the aggregated data still define an interspecific band (fig. 3) because thinning lines of very different slopes can fit within a single band if the self-thinning lines span realistic ranges of density change (Westoby 1984; Westoby and Howell 1986; Weller 1987*a*). Therefore, it has never been justifiable to treat the slope of the interspecific relationship as a piece of *prima facie* evidence for a thinning law.

Departures of dynamic self-thinning slopes from the slope of the interspecific band are consistent with the geometric model. The slope of a thinning line should match the slope of the interspecific relationship only if the product τd changes with increasing size in the growing stand in exactly the same way that the product τd varies statically with size across the plant kingdom (eq. 3). In fact, since dynamic allometry varies considerably among stands (White 1981; Weller 1985, 1987*b*), thinning slopes should be expected to deviate from the average interspecific slope across the plant kingdom. The interspecific relationship does not show that self-thinning lines are insensitive to plant geometry (as claimed by Furnas 1981). Instead, the width of the band accommodates considerable variation in thinning slopes (Weller 1987*a*), which reflect real geometric differences among self-thinning stands (Weller 1987*b*).

The Constants K and κ

Many hypotheses about the meaning of the constant K in the dynamic self-thinning equation ($\log B = -\frac{1}{2} \log N + \log K$) can be more meaningfully applied to the constant κ of the interspecific relationship. Values of K from different thinning lines are not comparable unless the slopes of those lines are identical (White and Gould 1965; Westoby 1984; Weller 1985, 1987*a*; Zeide 1985). The physical units of K also change; K is measured in grams per cubic meter only if the thinning slope is exactly $-\frac{1}{2}$. We can eliminate this problem and more directly relate position in the size-density plane to plant dimensions by interpreting κ values for single crowded stands rather than K values from dynamic thinning lines. Unlike K , κ is not confounded by variation in the thinning slope, subjective errors in fitting a thinning line (Mohler et al. 1978; Hutchings and Budd 1981*b*; Weller 1985, 1987*a*), extrapolation beyond the domain of the data (Westoby 1984; Weller 1985, 1987*a*), or dynamic changes in plant shape (Weller 1987*b*; Norberg 1988). Values of κ can even be calculated for stands that are not self-thinning, as long as the stand is crowded such that $N = 1/a$.

Position in the plane of $\log B$ and $\log N$, as measured by κ , is related to the concentration of mass in space (White 1981, 1985) and another factor (Lonsdale and Watkinson 1983), namely, the height-to-width ratio of the exclusive space (Norberg 1988). The relationship between κ and the biomass per unit of volume is not monotonic (see White 1985): a stand with a biomass per unit of volume d lower than that of another may actually have a higher value of κ if the difference in the height-to-width ratio more than offsets the difference in d (fig. 4). Information on the amount of tolerable overlap between the zones of influence of neighbors may also be contained in κ (and K ; Weller 1985; Norberg 1988).

Grasses tend to have higher thinning intercepts (K) than dicot herbs, whereas conifers have higher intercepts than broad-leaved trees, possibly because plants with erect leaves or needles pack more biomass per unit of canopy volume than do

broad-leaved species (Lonsdale and Watkinson 1983; Westoby 1984) or because of differences in canopy shape (Harper 1977). Since κ provides a more direct index of position in the plane of $\log B$ and $\log N$ than does K , it is useful to reexamine these comparisons for κ . Monocot herbs do have higher κ values than dicot herbs for two reasons: monocots pack more biomass per unit of volume (higher d) and are more slender (higher τ) (table 3; figs. 1, 4). The difference in the height-to-width ratio accounts for more of the difference in κ than does the difference in packing density (fig. 4; see also Givnish 1986; Norberg 1988). For trees, conifer stands have higher κ values than temperate broad-leaved stands, reflecting higher values for both τ and d for conifers (table 3). In this comparison, more of the difference in κ was due to the difference in biomass per unit of volume than to the difference in the height-to-width ratio. In general, trees had lower values of biomass per unit of volume than herbaceous plants, possibly because of the relatively large amount of unfilled volume often present beneath a forest canopy.

These comparisons of plant groups also illustrate the confounding effect of slope on the interpretation of the intraspecific thinning parameter K . Intraspecific thinning lines fit to stands in table 1 gave lower average values of $\log K$ for monocots than for dicots (Weller 1985, 1987a). In contrast, κ values were higher for monocots, as expected from the higher values of both τ and d (table 3). The comparison of K values does not accurately reflect the pattern of difference in biomass per unit of volume and height-to-width ratio because the two groups had very different median thinning slopes (Weller 1985, 1987a). In comparisons of conifers and broad-leaved trees, the differences in K (Weller 1985, 1987a) follow the same pattern as κ , despite significant differences in thinning slope between the groups. Values of K are less confounded by differences in thinning slope in the conifer-broad-leaved comparison because the tree data fall near $\log N = 0$ in the plane of $\log B$ and $\log N$; thus, estimation of the thinning-line intercept at $\log N = 0$ requires little extrapolation beyond the domain of the data. $\log K$ provides a good estimate of the mean position of the data in the plane of $\log B$ and $\log N$. In contrast, since crowded stands of monocots and dicots occur at densities several orders of magnitude above one plant per square meter, the intercept at $\log N = 0$ is well outside the domain of the data and differences in thinning slope interact with the gross extrapolation to yield confounded K values.

The Ultimate Thinning Line

The ultimate thinning line, which describes the maximum average mass possible at any plant density, constrains all populations, even those that do not describe a classic self-thinning trajectory (Hutchings and Barkham 1976; Hutchings 1979; Mook and van der Toorn 1982; Cousens and Hutchings 1983; Pitelka 1984). For the equation of this line, Hutchings (1979) proposed $\log m = -\frac{3}{2} \log N + 4.3$ and White (1985) suggested that few plant populations exceed the size-density combinations defined by $\log m = -\frac{3}{2} \log N + 5.0$. All of Gorham's stands and 93% of mine fall below $\kappa = 5.0$, confirming that most stands fall below the line $\log m = -\frac{3}{2} \log N + 5.0$ (White 1985). However, since some stands do exceed $\kappa = 5.0$, White's value is not a true upper limit.

The ultimate thinning is simply the upper boundary of the interspecific size-

density band. White (1981) stated that the constraint it imposes demonstrates the importance of the self-thinning rule, even for species whose stand dynamics do not necessarily trace a line of slope $-\frac{3}{2}$ in the plane of $\log m$ and $\log N$. However, we have seen above that the interspecific band and interspecific self-thinning are different phenomena and that the interspecific relationship does not support the self-thinning rule. In fact, the term "ultimate thinning line" is a misnomer, since the existence and meaning of this constraint are most clearly investigated in a static, interspecific context, not as a dynamic mortality or "thinning" process. The constraint should hold regardless of how growth and mortality proceed in a given stand. A stand could approach this line by decreasing in average weight or actually increasing the density of individuals per unit of area (Pitelka 1984), rather than by undergoing a mortality process as implied by the term "thinning."

Biological Significance of the Interspecific Relationship

Five features of the interspecific size-density band require explanation and may be of biological importance: the existence of a narrow band, and the linearity, slope, width, and position of that band. Crowded stands form a narrow band in the plane of $\log B$ and $\log N$ because the ranges of possible values of the height-to-width ratio (τ) and the biomass per unit of volume (d) are restricted to biologically realistic values and vary much less across the plant kingdom than do density or biomass (table 2; fig. 2; Norberg 1988). Thus, the narrowness of the band is symptomatic of constraints on τ and d . The band is linear because the volumes and base areas of geometric objects are related by power functions, which are linear after logarithmic transformation. Linearity then reflects the fact that plants are geometric objects and is not a symptom of any unique biological properties of plants.

The slope of the interspecific relationship depends on three factors (eq. 4). If the ranges of the height-to-width ratio and the biomass per unit of volume are approximately constant across the plant kingdom, then the slope of $\log B$ versus $\log N$ will be $-\frac{1}{2}$ ($-\frac{3}{2}$ in the plane of $\log m$ and $\log N$) because the volume of any geometric solid is proportional to its base area to the $\frac{3}{2}$ power. However, if these parameters vary systematically across the plant kingdom, then, according to equation (4), the interspecific slope will deviate from $-\frac{1}{2}$. The $-\frac{1}{2}$ term of equation (4) represents a geometric process: the packing of three-dimensional objects onto a two-dimensional surface. As such, it is the least interesting component of the slope. The deviation from $-\frac{1}{2}$ is more interesting because it represents systematic variations in plant shape or biomass per unit of volume across the plant kingdom. Even if the deviation were zero and the slope exactly $-\frac{1}{2}$, the feature of primary biological interest would not be the value $-\frac{1}{2}$ but the fact that τ and d were either both roughly constant across the plant kingdom or varied in an exactly compensatory manner ($\delta = 2\psi$).

Previous models for the interspecific relationship have not accommodated systematic trends in plant form across the plant kingdom. Gorham's (1979) isometric model assumes that the mass of a plant is always a function of the cube of an underlying linear dimension and can only predict an interspecific slope of $-\frac{1}{2}$. Givnish (1986) derived the $-\frac{1}{2}$ slope for idealized plants with a massive

circular crown supported by a single, central stem. He used the biomechanical principle of elastic similarity (McMahon 1973; McMahon and Kronauer 1976) to predict how stem mass should increase with height to maintain a margin of safety against buckling under the weight of the canopy. His derivation indicates that stem mass should be proportional to height cubed, thus supplying biomechanical justification for Gorham's assumption of geometric similarity and identifying height as the relevant linear dimension. Givnish also cited some evidence that plant shape, as measured by the ratio of crown radius to height, is roughly constant across the plant kingdom. The $-1/2$ slope predicted by the models of Gorham and Givnish is consistent with Gorham's (1979) data, but not with my larger data base (tables 1, 2) because neither model accommodates systematic trends in height-to-width ratio and biomass per unit of volume across the plant kingdom (figs. 1, 2).

Givnish's (1986) biomechanical model provides a more mechanistic explanation of the $-1/2$ slope than the Gorham model or equation (3) but suffers from several potential limitations. The theory predicts stem mass, not total plant biomass, for plants with a massive canopy supported by a single central stem. Therefore, its predictions are less relevant to plants that do not fit that structural model, such as grasses and some herbs. Since interspecific trends are dominated by the juxtaposition of trees and herbs (see the Results), an inclusive explanation must accommodate growth forms relevant for herbs. Even many forest stands do not show the predicted relationship $m \propto H^3$. Estimates of the exponent in this equation for growing stands deviate widely from 3 (Weller 1985, 1987b), and interspecific powers of 3.7 and 3.5 for my data and Gorham's, respectively, are greater than 3 (table 2). These observations do not invalidate the biomechanical principles invoked by Givnish, but they suggest that factors other than mechanical stability (e.g., root competition; Norberg 1988) also have important effects on the mass-height relationships of crowded stands. My results also suggest that it would be appropriate to modify the biomechanical model to accommodate observed interspecific trends in plant shape and biomass per unit of volume.

Norberg (1988) drew somewhat different conclusions about the implications of elastic similarity for size-density relationships. In his analysis, elastic similarity does not imply a dynamic thinning gradient of slope $-1/2$, but rather a variable gradient that would increase from -1 to -0.33 over the life of a stand. For interspecific comparisons, Norberg concluded that the elastic-similarity model should apply, provided that all the species compared obey the elastic-similarity rule and are similar in height-to-width ratio and biomass per unit of volume. Equations (2) and (3) show that the latter condition alone would be sufficient to yield an interspecific relationship of slope $-1/2$, regardless of whether or not all the species obey elastic similarity.

The width and position of the interspecific band reflect biological rather than purely geometric properties of plants. The existence of upper and lower limits of the band imply fundamental constraints on plant growth and reflect the range of solutions that have evolved to meet those constraints. Energetic limits are important, and some of the width of the interspecific size-density band is due to variation in light income and its interaction with the canopy and leaf shape

(Westoby and Howell 1981; Lonsdale and Watkinson 1982, 1983; Westoby 1984). Variation in nutrient availability is also important (Furnas 1981; White 1981; Weller 1985, 1987*a*). Structural requirements must also limit how tall and thin plants can become and still remain upright in the face of gravity, wind, and rain (Givnish 1986; Norberg 1988).

Givnish (1986) considered how mechanical constraints, the physical properties of plant materials, and constraints on photosynthesis determine the position of stands in the size-density plane. In the present context, his results relate to the interpretation of my parameter κ . Givnish concluded that requirements for structural support play a key role in determining κ (Givnish 1986) because self-support requires the allocation of energy to the construction and maintenance of unproductive support tissue and the associated costs increase sharply with height. His model predicts that κ should decrease with plant height (as in table 2) and increase with light and nutrient availability. Givnish suggested that the radius-to-height ratio of the canopy (analogous to my τ) may be set by selection in order to maximize the rate of individual height growth and presumed competitive ability in crowded stands, under the biomechanical constraints imposed by the need to remain erect.

Norberg (1988) concluded that variation in the local elevation in the size-density plane depends on differences in the height-to-width ratio, the packing density in the volume occupied, and the degree of overlap between neighbors, which in turn depends on site quality. Norberg listed four universal constraints affecting the range of κ : the necessity of growing in height to compete for light; demands for structural strength against gravity; the necessity to claim ground area from which to draw light, water, and nutrients; and shade tolerance, which limits foliage packing and tolerable overlap among neighbors. The need for height growth would tend to increase the height-to-width ratio (my τ), whereas demands for structural strength require packing more biomass into the occupied space; both requirements force κ upward and define a lower limit of observed κ values. In contrast, the need to obtain resources decreases the height-to-width ratio, and resources and the metabolic cost of maintaining biomass limit packing density, thus tending to reduce κ and defining its upper limit (Norberg 1988).

CONCLUSION

The interspecific size-density relationship remains biologically interesting in its own right, but not because its slope supports a self-thinning "law." The existence of a single, simple interspecific relationship in spite of the vast differences in architecture among plants has been judged remarkable (Gorham 1979). However, the interspecific relationship does not exist in spite of architectural diversity but, rather, incorporates that diversity as an intrinsic part of the relationship. The width of the band represents the complete ranges of values possible in crowded plant stands for two architectural parameters, shape and biomass per unit of volume, and accommodates a 44-fold variation in τ , 35-fold variation in d , and over 1000-fold variation in the product $\kappa = \tau d$ (table 1). These ranges and their systematic variations across the plant kingdom are the features of the interspecific band that have important biological implications and demand biological explana-

tions. Our understanding of how basic structural and resource constraints act to produce these ranges remains incomplete and presents a fertile field for further research, although recent theories have explored some particular constraints (Givnish 1986; Norberg 1988). Attention should focus on identifying the energetic and structural limits on plants and on understanding how those limits have operated over the course of evolution to yield the present range of plant forms represented by the interspecific size-density band.

SUMMARY

I present a geometric model that explains the interspecific size-density relationship among crowded plant stands in terms of two descriptors of the volume occupied by an average individual in each stand: the density of biomass per unit of occupied volume and the ratio of height to base width. The model predicts that stand measurements form a linear band when the logarithm of aboveground stand biomass is plotted against the logarithm of plant density. The band appears narrow because biomass per unit of volume and the ratio of height to width are biologically constrained and vary much less than stand biomass or density. In the absence of systematic trends in either parameter, simple geometry would fix the slope of the band at $-1/2$. Thus, the extent of deviation from $-1/2$ is of primary biological interest, since that deviation reflects biological trends in plant shape or packing density across the plant kingdom.

Aboveground biomass, density, and height data from 370 plant stands revealed systematic trends in both parameters across the plant kingdom. Small plants growing at high densities tend to be relatively more slender and to pack more biomass per unit of volume than do larger plants in less dense stands. These trends relate to differences among plant groups. Herbaceous monocots are more slender and pack more biomass per unit of volume than herbaceous dicots, which are in turn higher in both measures than trees. As predicted by the model, such trends yield an interspecific relationship with a slope shallower than the ideal $-1/2$ value.

The interspecific band encloses dynamic self-thinning lines that differ widely in slope; therefore, the static and dynamic relationships can be considered independently and are not simply facets of a single thinning "law." Many proposed interpretations of the constant in the dynamic self-thinning equation can be more clearly applied to a new constant calculated for single stands from the product of biomass per unit of volume and the ratio of height to width.

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APPENDIX

The 370 stands of my data base are a subset of a data base described elsewhere (Weller 1985, 1987*a*). Stands for which aboveground biomass was not reported separately from total biomass were excluded, as were stands for which stem biomass was reported without leaves and branches. Identification (ID) codes (table 1; Weller 1987*a*) are used to identify the plant species and literature references for particular data sets within the data base. For each data set included in this analysis, three numbers are given below: the ID code; the total number of stands with measurements of biomass, density, and height; and the number of stands with measurements of biomass and density. The list is in order by plant group and ID code (as in Weller 1987*a*, table A1). The stands for each ID code have also been used to fit one or more self-thinning lines for individual populations (Weller 1985, 1987*a*) and to investigate the relationship between the self-thinning slope and the geometry of dynamic plant growth (Weller 1987*b*).

Herbaceous monocots: 86-15/15, 38-0/8, 91-0/23, 92-0/10, 7-0/5; herbaceous dicots: 87-12/12, 43-0/36, 89-0/8, 88-15/15, 56-0/11, 57-0/13, 28-0/7, 10-0/10, 35-0/13; temperate angiosperm trees: 106-8/8, 131-6/6, 26-0/27, 121-8/8, 123-4/4, 48-7/7, 112-3/3, 104-6/6, 133-8/8, 5-0/4, 126-5/5, 41-0/5; temperate gymnosperm trees: 19-0/26, 119-4/4, 114-9/9, 122-5/5, 137-12/12, 135-0/5, 102-9/9, 80-0/5; *Eucalyptus* trees: 116-3/3; tropical angiosperm trees: 111-10/10, 113-5/5.

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