
A general model for mass–growth–density relations across tree-dominated communities

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ABSTRACT

A general allometric scaling model predicts that plant body mass M_T will scale as the $-4/3$ power of plant density N . Here, we show how this model predicts numerous other scaling attributes of plant populations and communities, including annual growth rate G_T , standing leaf biomass M_L , basal stem diameter D , and above- and below-ground biomass, M_{SH} and M_R . These predictions are consistent with the ‘Law of Constant Yield’ (i.e. productivity is independent of plant density). Analysis of worldwide databases for woody plant-dominated communities spanning seven orders of magnitude in M_T and five orders of magnitude in N provides strong support of all of the model’s predictions. Our model thus offers a theoretical basis for understanding and predicting the effects of crowding on plant size, growth and biomass partitioning across diverse ecological communities.

Keywords: allometry, plant reproduction, scaling, self-thinning, trees.

INTRODUCTION

Previous treatments of the factors responsible for the scaling of total plant body size M_T with respect to plant density N have been largely based on *a posteriori* observations instead of a rigorous mechanistic (theoretical) framework (Yoda *et al.*, 1963; White, 1980, 1985; Lonsdale and Watkinson, 1983; Westoby, 1984; Zeide, 1985, 1987; Weller, 1987; Lonsdale, 1990). As a result, the empirical underpinnings for discovering how plant biomass–density relationships influence the functional and structural attributes of populations and communities remain problematic. Recently, however, a general model for plant allometry has been proposed based on the fractal-like construction of internal resource distribution networks (Enquist *et al.*, 1998; West *et al.*, 1999). This model predicts that M_T will scale as the $-4/3$ power of N (West *et al.*, 1999) and, because total community biomass $\hat{M}_T$ equals $M_T N$, it also predicts that $\hat{M}_T \propto M_T N \propto N^{-4/3} N \propto N^{-1/3}$.

Here, we extend this theoretical framework to predict other ecologically and evolutionarily important relationships among annual growth G_T , standing leaf biomass M_L , and

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above- and below-ground biomass (shoot M_{SH} and root M_{R} biomass, respectively) with respect to N . At the level of the individual plant, our model predicts that G_{T} and M_{L} will each scale inversely as the -1 power of N , whereas M_{SH} and M_{R} will each scale as the $-4/3$ power of N . At the level of an entire community, the model predicts that total community annual growth $\hat{G}_{\text{T}}$ and total leaf biomass $\hat{M}_{\text{L}}$ will be each independent of N , whereas total community shoot and root biomass ($\hat{M}_{\text{SH}}$ and $\hat{M}_{\text{R}}$) will each scale as the $-1/3$ power of N . We also show that these predictions are consistent with the data structure of a worldwide compendium for biomass and annual productivity spanning a broad spectrum of taxonomically and ecologically diverse tree-dominated communities (Cannell, 1982).

Our model is an *a priori* mechanistic approach to plant mass–growth–density relationships. It rests on only two fundamental scaling relationships that hold true at the level of the individual plant across a broad taxonomic array of vascular plants – that is, $G_{\text{T}} \propto M_{\text{L}} \propto M_{\text{T}}^{3/4}$ (Niklas, 1994; Niklas and Enquist, 2001, 2002a,b). Furthermore, we assume that the maximum number of individuals N_{max} that can be supported per unit area is related to rates of limiting resource supply R from the environment and the metabolic rate of an individual B . The predictions of our model are thus expected to be indifferent to community species composition, although residual variation will be influenced by local community environmental conditions and the supply rates of limiting resources.

THE MODEL AND DATA ANALYSES

Extension of allometric theory

Theory predicts (and observation indicates) that, at the level of the individual plant, whole-plant metabolism B is directly proportional to whole-plant growth rate G_{T} , which, in turn, scales as the $3/4$ power of M_{T} and isometrically with respect to the capacity to intercept sunlight H – that is, $G_{\text{T}} = \beta_0 M_{\text{T}}^{3/4}$ and $G_{\text{T}} = \beta_1 H^1$, where β_0 and β_1 are group-specific constants (West *et al.*, 1999; Niklas and Enquist, 2001). For vascular plants, H is proportional to M_{L} (Niklas and Enquist, 2001). Therefore, $B = G_{\text{T}} = \beta_0 M_{\text{T}}^{3/4} = \beta_1 H = \beta_3 M_{\text{L}}$ and $M_{\text{L}} = \beta_4 M_{\text{T}}^{3/4}$, where $\beta_4 = \beta_0/\beta_3$ (allometric constants, which may or may not vary across taxa). Based on hydraulic considerations for water transport through the plant body, we assume that M_{L} scales isometrically with respect to stem cross-sectional area, which is proportional to the square of basal stem diameter D^2 (Carlquist, 1975; Kramer, 1983; Enquist and Niklas, 2001, 2002). Therefore, $M_{\text{L}} = \beta_4 M_{\text{T}}^{3/4} = \beta_5 D^2$.

Provided that plants grow in size until they are limited by resources, the maximum number of individuals N_{max} that can be supported per unit area is related to the rate of limiting resource supply R per unit area and the metabolic rate per individual plant B , which is proportional to rates of resource use per individual Q . Specifically, $R \approx N_{\text{max}} Q \approx N_{\text{max}} (\beta M^{3/4})$. Therefore, at equilibrium, R is constant such that $N_{\text{max}} = (R/\beta_n) M^{-3/4}$. Because population density is ultimately constrained by R and the dependence of body size on B , it follows that $N_{\text{max}} = \beta_6 D^{-2}$, where β_6 is a group-specific constant that includes the term R/β_n . Under any circumstances, since the three-dimensional space a_i occupied by an individual is proportional to D^2 , and since N is the quotient of the total area occupied by all individuals A_{T} and the area occupied by an average individual in a community (i.e. $N \propto A_{\text{T}}/a_i$), we conclude that plant density will scale as the $-1/2$ power of average stem diameter. Indeed, Enquist and Niklas (2001) found this inverse-square relationship in the size

frequency distributions of individuals drawn from a broad spectrum of ecologically and taxonomically diverse communities. We will show here that this relationship also holds across communities differing in N .

Our derivations lead to four predictions at the level of the individual plant in its community: $M_T = (\beta_5\beta_6/\beta_4)^{4/3}N^{-4/3} = \beta_7^{4/3}N^{-4/3}$, $G_T = (\beta_0\beta_5\beta_6/\beta_4)N^{-1} = \beta_8N^{-1}$, $M_L = (\beta_5\beta_6)N^{-1} = \beta_9N^{-1}$, and $D = \beta_6^{1/2}N^{-1/2}$. These scaling relationships are influenced by potential taxon-specific variation in biomass allocation, a variety of allometric constants and by rates of limiting resource supply R for a given environment. Nevertheless, the exponents for these relationships are expected to be largely indifferent to these factors.

We note further that additional mass–density scaling relationships are evident for root, stem and shoot biomass with respect to N . Specifically, previous studies have shown that M_L scales as the 3/4 power of root and stem biomass (M_R and M_S , respectively) – that is, $M_L = \beta_{10}M_R^{3/4} = \beta_{11}M_S^{3/4}$ (Enquist and Niklas, 2002). Because M_L equals β_9N^{-1} and shoot biomass M_{SH} equals $M_T - M_R$, we see that $M_R = (\beta_9/\beta_{10})^{-4/3}N^{-4/3} = \beta_{12}N^{-4/3}$ and $M_{SH} = N^{-4/3} - \beta_{12}N^{-4/3} = (1 - \beta_{12})N^{-4/3} = \beta_{13}N^{-4/3}$. We stress again that the β -values for these relationships may vary among different taxa or body plan configurations. Nevertheless, we expect the scaling exponents to vary little in response to species- or site-specific differences.

At this juncture, we wish to point out that woody and non-woody plant bodies differ significantly. With increasing age and size, the woody plant body accumulates dead, albeit mechanically and hydraulically functional tissues annually. However, our model predicts that woody and non-woody plants will obey the same mass–growth–density relationships. Consider stem biomass, M_S , which must equal the sum of annual stem growth G_S and all previously accumulated stem biomass M_{SO} – that is, $M_S = \beta_{14}M_L^{4/3} = G_S + M_{SO}$. Since G_S is proportional to M_L such that $G_S = \beta_{15}M_L$ (Niklas and Enquist, 2001; Enquist and Niklas, 2002), we see that $M_{SO} = \beta_{14}M_L^{4/3} - \beta_{15}M_L$ and M_{SO} will scale as the 4/3 power of M_L when $\beta_{14} \gg \beta_{15}$. Note that for non-woody species, $M_{SO} = 0$ and $G_S = \beta_{16}M_L$ – that is, stem and leaf growth scale isometrically. However, for both non-woody and woody species, the *scaling* of living with respect to dead tissues is expected to be isometric.

Finally, our derivations can be modified to predict the mass–growth–density relationships for entire communities. Because the numerical value for G_T and each mass variable Y at the level of the individual equals the total community value for the variable $\hat{Y}$ divided by N (i.e. $Y = \hat{Y}/N$), the scaling relationship for an entire community becomes $\hat{Y} \propto N^{1+a}$ (see Table 2).

Data and analyses

We tested these predictions by using the Cannell (1982) compendium for standing community biomass and productivity. This compendium includes data from monospecific populations and communities composed of mixed species ranging between 42°S and 66°N latitude, elevations of 10 m and 3830 m above sea level, and plant densities of 20 and 150,000 individuals per hectare (Cannell, 1982). For each community, plant density, total community standing leaf, stem and root dry weight, and total annual leaf, stem and root dry weight production are reported. We computed M_T , G_T , M_L and M_R for a representative (average) plant in each community by dividing the total value of the relevant variable by N . The M_{SH} of an average individual was computed similarly based on total community standing leaf and stem biomass; the D of an average plant was computed based on total community basal stem area TBA and N – that is, $D = (4TBA/\pi N)^{1/2}$.

We tested the predictions for how M_{SO} scales with respect to new stem tissues M_{SL} and M_L by collecting and dissecting 1- to 10-year-old shoots of *Quercus alba* (age determined by terminal bud scars and wood growth rings). We used growth rings to distinguish between M_{SO} and M_{SL} ; M_{SL} was taken as the sum of all first year stem biomass and the biomass of the most recently produced wood, which was surgically removed along the entire length of each branch. Values of M_L were used to predict M_{SO} (using the formula $M_{SO} = \beta_{14} M_L^{4/3} - \beta_{15} M_L$). Predicted values M_{SO} and M_{SL} were then compared to those observed (see Fig. 2C).

All data were $\log_{10}$ -transformed. Model Type I (ordinary least squares) regression analysis was used to determine the scaling exponent and group-specific constant (the slope and y -intercept of the ordinary least squares regression line; α and β , respectively) for each pairwise comparison. Ordinary least squares regression was preferred for our analyses because the measurement error for N was negligible (Sokal and Rohlf, 1981). The sample sizes varied across different pairwise comparisons because some authors failed to report the information required to compute M_T , G_T , M_L , M_R or M_{SH} for each community (see Table 1).

Table 1. Predicted and observed scaling exponents for $\log_{10}$ -transformed data from the Cannell (1982) compendium

log y vs log x	Predicted	Observed					
		α (S.E.)	95% CI	$\log_{10}\beta$ (S.E.)	r^2	n	F
Across all communities							
log M_T vs log N	-4/3	-1.27 (0.03)	-1.33 to -1.16	5.96 (0.11)	0.801	342	1368
log G_T vs log N	-1.0	-0.98 (0.03)	-1.03 to -0.92	3.99 (0.09)	0.861	205	1257
log M_L vs log N	-1.0	-1.00 (0.03)	-1.05 to -0.95	3.78 (0.09)	0.669	670	1348
log D vs log N	-1/2	-0.53 (0.01)	-0.56 to -0.51	0.86 (0.04)	0.673	792	1624
log M_{SH} vs log N	-4/3	-1.31 (0.03)	-1.36 to -1.25	5.99 (0.10)	0.753	668	2029
log M_R vs log N	-4/3	-1.17 (0.03)	-1.23 to -1.10	4.97 (0.11)	0.773	347	1172
Across angiosperm-dominated communities							
log M_T vs log N	-4/3	-1.30 (0.05)	-1.36 to -1.23	5.74 (0.16)	0.759	174	542.2
log G_T vs log N	-1.0	-1.00 (0.05)	-1.11 to -0.90	3.76 (0.15)	0.833	74	359.9
log M_L vs log N	-1.0	-1.00 (0.03)	-1.05 to -0.95	3.37 (0.10)	0.751	331	993.1
log D vs log N	-1/2	-0.51 (0.02)	-0.55 to -0.48	0.75 (0.06)	0.685	342	740.1
log M_{SH} vs log N	-4/3	-1.25 (0.04)	-1.33 to -1.17	5.81 (0.14)	0.733	325	888.3
log M_R vs log N	-4/3	-1.08 (0.05)	-1.18 to -0.98	4.72 (0.16)	0.729	178	465.9
Across conifer-dominated communities							
log M_T vs log N	-4/3	-1.34 (0.04)	-1.42 to -1.25	5.96 (0.11)	0.846	168	909.3
log G_T vs log N	-1.0	-1.04 (0.03)	-1.11 to -0.98	3.99 (0.09)	0.880	131	949.8
log M_L vs log N	-1.0	-1.12 (0.04)	-1.19 to -1.05	4.41 (0.12)	0.746	339	992.1
log D vs log N	-1/2	-1.28 (0.05)	-1.37 to -1.19	5.33 (0.16)	0.827	169	800.8
log M_{SH} vs log N	-4/3	-1.31 (0.03)	-1.36 to -1.25	5.99 (0.10)	0.753	668	2029
log M_R vs log N	-4/3	-1.39 (0.04)	-1.46 to -1.31	6.26 (0.13)	0.782	343	1220

Note: In all cases, $P < 0.001$ or less.

RESULTS AND DISCUSSION

Our statistical analysis of the Cannell (1982) compendium provides strong support for our model (Table 1). As predicted, M_T scales as the -1.27 power of N (Fig. 1A); the 95%

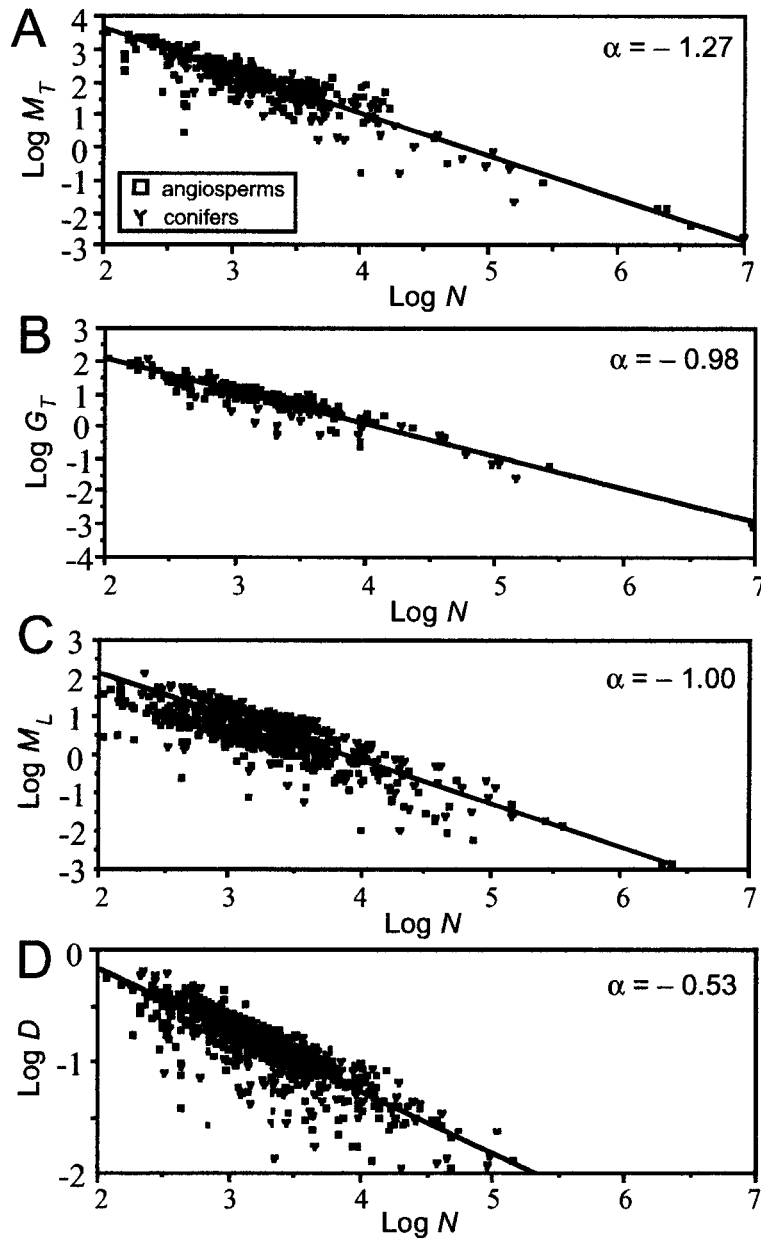


Fig. 1. The scaling of M_T , G_T , M_L and D with respect to N across angiosperm- and conifer-dominated communities. The observed scaling exponent α for each relationship is statistically indistinguishable from that predicted (see Table 1).

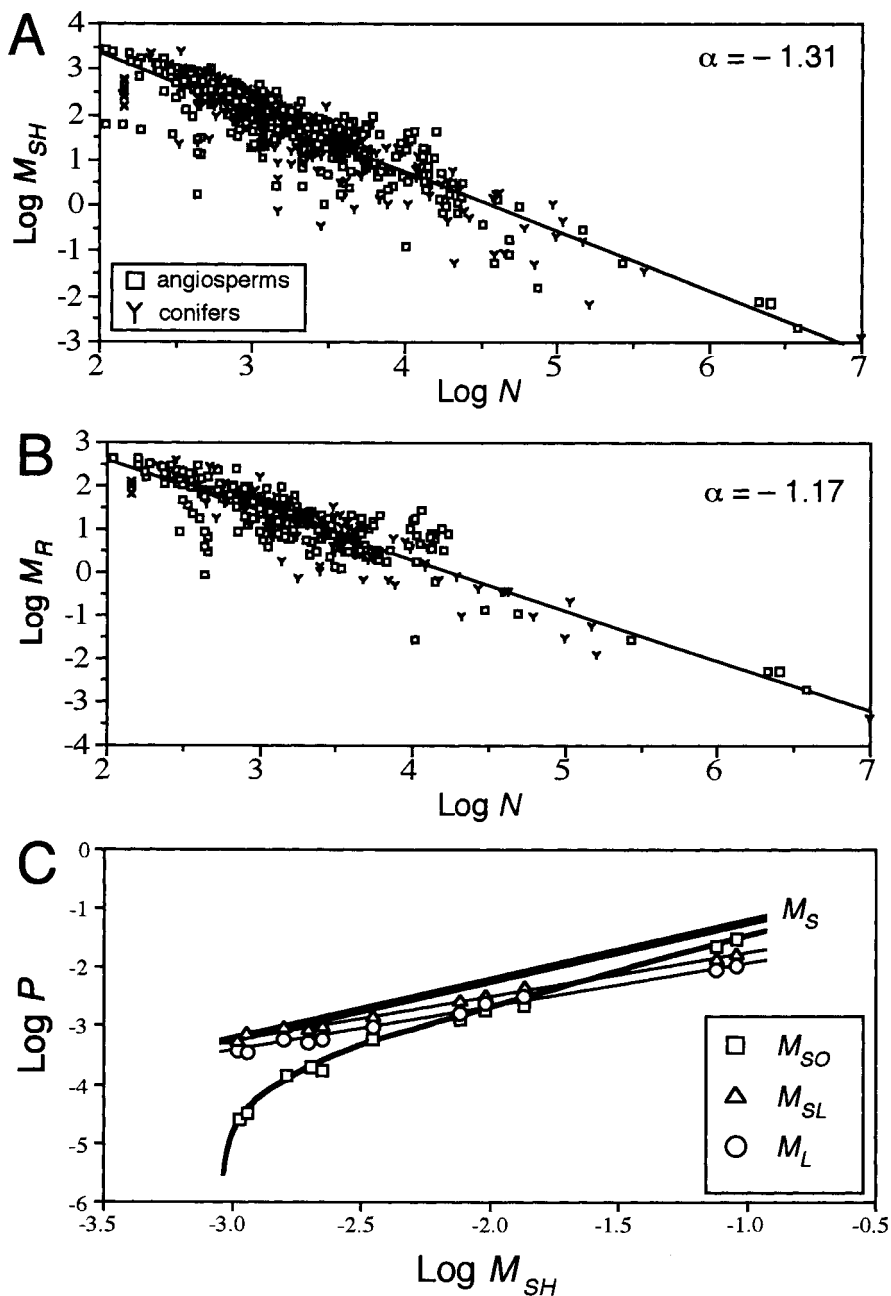


Fig. 2. The scaling of M_{SH} and M_R with respect to N across angiosperm- and conifer-dominated communities (A, B) and the scaling of old M_{SO} and living stem tissues M_{SL} in M_{SH} across *Quercus alba* shoots (C). (A) The observed scaling exponent α for M_{SH} versus N is statistically indistinguishable from that observed (see Table 1). (B) The α for M_R versus N deviates from that predicted as a result of a systematic size-dependent underestimate of angiosperm M_R (see text and Table 1). (C) Theoretical values (curves) and observed values (symbols) for M_{SO} , M_{SL} , M_S and M_L plotted against M_{SH} .

confidence intervals of -1.27 include $-4/3$ and exclude $-3/2$ (Table 1). As predicted, G_T and M_L each scale isometrically with respect to N (i.e. $\alpha = -0.98$ and -1.00 , respectively), whereas D scales as the -0.53 power of N (Fig. 1B–D). The predicted scaling relationship for M_{SH} versus N is also supported. Specifically, M_{SH} scales as the -1.31 power of N (Fig. 2A); the 95% confidence intervals for -1.31 include $-4/3$ and exclude $-3/2$ (i.e. -1.36 to -1.25) (Table 1). However, M_R scales as the -1.17 power of N (Fig. 2B), and the 95% confidence intervals for -1.17 preclude the predicted $-4/3$ value (Table 1). We attributed this discrepancy to a systematic, size-dependent underestimation of fine and small root biomass – that is, progressively larger plants have disproportionately more fine and small root biomass, which is systematically more difficult to excavate with increasing plant size (see Makkonen and Helmissar, 2001). This bias is expected to elevate the numerical value of the scaling exponent for M_R versus N . This conjecture is supported by the exponent for conifer M_R versus N . Conifer M_R , which tends to be more shallowly buried and thus more easily excavated than angiosperm M_R (K.J. Niklas, personal observation), scales as the -1.28 power of N . The 95% confidence intervals for -1.28 include the predicted value of $-4/3$ (Table 1).

The data gathered from dissected *Quercus* shoots differing in size (and age) also comply well with the model (Fig. 2C). The biomass of accumulated dead stem tissues M_{SO} quickly converges on total M_S , and the scaling of living stem and leaf tissues is defined by parallel and isometric curves. Thus, M_L scales as the $4/3$ power of M_S due to the yearly accumulation of dead stem tissues, whereas the annual production of living leaf and stem biomass is isometric.

Our model is also supported based on total community mass–growth–density relationships (Fig. 3). For example, individual M_T and G_T are predicted to scale as the $-4/3$ and the -1 power of N , respectively, but total community biomass $\hat{M}_T$ is predicted to scale as the $-1/3$ power of N , whereas total community growth $\hat{G}_T$ is predicted to be independent of N . Indeed, regression of $\hat{M}_T$ against N and $\hat{G}_T$ against N obtains scaling exponents of $-0.266 (\pm 0.03)$ and $0.007 (\pm 0.03)$, which are statistically compatible with the predictions of the model (Table 2). Similarly, total community leaf biomass $\hat{M}_L$ is also predicted to be independent of N . Fitted regression models to observed data for $\hat{M}_L$ versus N gives a scaling exponent indistinguishable from zero. Similar comparisons show that the predicted and observed scaling exponents for total community mass–density relationships are statistically indistinguishable, although it is evident that the correlation coefficients are low (Table 2). Such residual scatter may reflect variation in the supply rates of limiting resources R across differing environments and differences in leaf, stem and root biomass partitioning patterns (i.e. β -values).

Our model and statistical results are consistent with other reported mass–density relationships, although no other treatment has covered as broad a spectrum of mass–growth–density relationships as ours, nor has any previous treatment provided as robust a theoretical framework for predicting these relationships. For example, based on an analysis of many data sets, Weller (1987) reported that the average scaling exponent for $\hat{M}_T$ versus N is $-1/3$, whereas Lonsdale (1990) reported an average value of -0.379 . Similarly, many workers have shown that $\hat{G}_T$ is proportional to N^0 (i.e. unity). Thus, we have the ‘Law of Constant Yield’: *total community productivity is independent of plant density* (Harper, 1977), which is consistent with $\hat{G}_T \propto \hat{M}_L \propto N^0$. Indeed, White (1985) reported that M_L scales as the -1 power of N , from which it follows that total yield or net primary production G_T (which is dependent on total light harvesting capacity as gauged by M_L) is independent of N – that is,

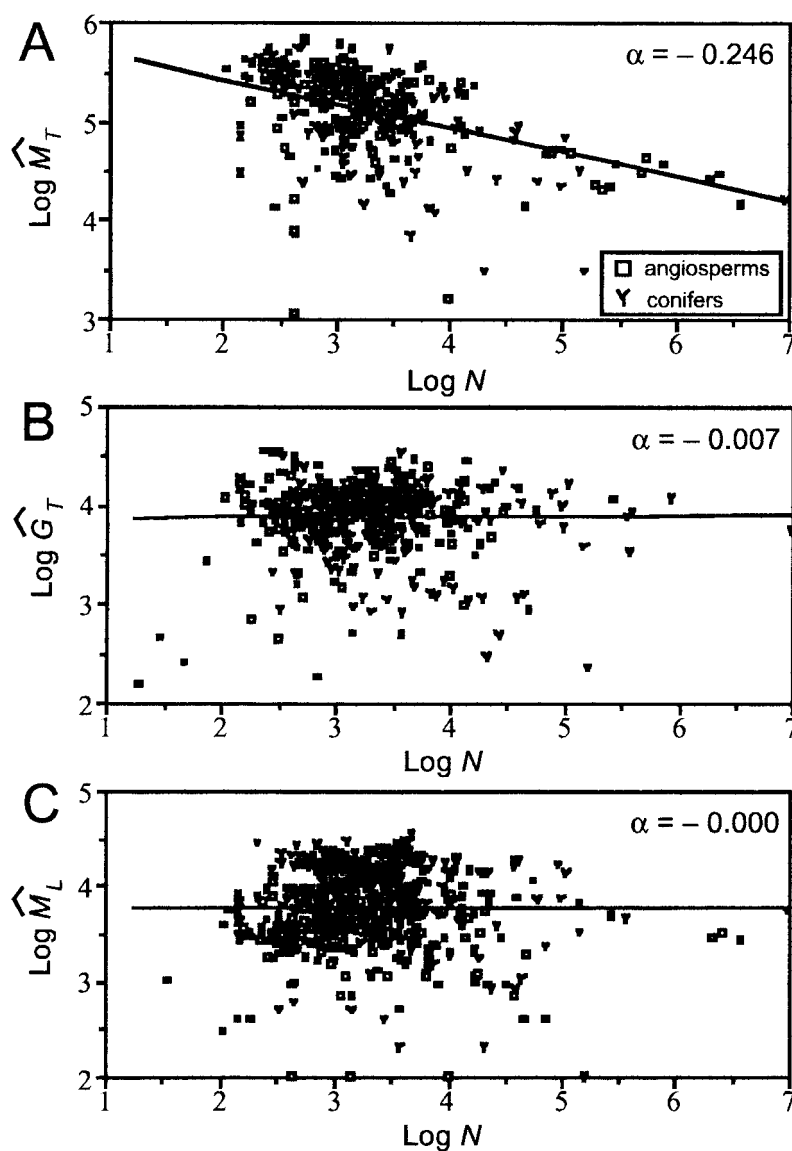


Fig. 3. The scaling of $\hat{M}_T$, $\hat{G}_T$ and $\hat{M}_L$ with respect to N across angiosperm- and conifer-dominated communities. The observed scaling exponent α for each relationship is statistically indistinguishable from that predicted (see Table 2).

$M_L N \propto \hat{M}_L N \propto N^0$. This relationship is also consistent with the ‘energetic equivalence rule’ (see Damuth, 1981, 1987), which states that all plant species can achieve the same rates of local resource use, regardless of their size. The energetic equivalence rule may be one of the most widespread ecological regularities, as it has also been reported within and across animal communities. Together, these results indicate that rates of limiting resource supply

Table 2. Predicted scaling exponents at the levels of the individual plant (see Table 1) and entire community and those observed for total community mass–growth–density relationships

Predicted		Observed				
Individual	Community	α (S.E.)	95% CI	r^2	n	F
$M_T \propto N^{-4/3}$	$\hat{M}_T \propto N^{-1/3}$	−0.266 (0.03)	−0.33 to −0.16	0.135	342	53.28***
$G_T \propto N^{-1.0}$	$\hat{G}_T \propto N^0$	0.007 (0.03)	−1.03 to 0.92	0.000	495	0.002
$M_L \propto N^{-1.0}$	$\hat{M}_L \propto N^0$	0.000 (0.03)	−0.05 to 0.05	0.000	675	0.000
$D \propto N^{-1/2}$	$\hat{D} \propto N^{1/2}$	0.467 (0.01)	0.42 to 0.51	0.610	792	1237
$M_{SH} \propto N^{-4/3}$	$\hat{M}_{SH} \propto N^{-1/3}$	−0.310 (0.03)	−0.36 to −0.25	0.143	668	111.8***
$M_R \propto N^{-4/3}$	$\hat{M}_R \propto N^{-1/3}$	−0.165 (0.03)	−0.23 to −0.10	0.034	347	23.44**

*** $P < 0.001$; * $P < 0.01$.

and a seemingly ubiquitous allometric rate of metabolism and biomass production (Enquist *et al.*, 1998) constrain numerous attributes of plant density–growth–mass relationships within and across plant populations and communities.

Our model sheds light on the effects of the annual accumulation of dead secondary tissues on self-thinning. Non-woody and woody plants are shown to obey the same ‘self-thinning rules’ despite the differences in their body constructions, because the amounts of living stem, root and leaf tissues in each type of plant body scale in an equivalent manner with respect to N regardless of species-specific differences. As tree communities ‘thin’, the amount of living tissues in survivors equals the sum of the living tissues of the total number of individuals that are displaced. However, as a tree increases in total biomass, its fractal branching pattern yields progressively more leafy twigs such that the ‘surviving’ living biomass (and thus annual biomass production) in any community remains comparatively constant regardless of M_T or N .

The accumulation of total community biomass in tree-dominated communities is clearly important, but the distinction between the ‘living’ and the ‘dead’ components is critical to the issue of community productivity. Franco and Kelly (1998) emphasized this point and provided a model for the scaling of ‘necro- vs vivo-biomass’ based on leaf area and other morphological features. However, their model rests on problematic assumptions – for example, stem height and diameter relationships obey the elastic self-similarity model – which are clearly violated by many species that nevertheless ‘thin’ as the $-4/3$ power of N (Norberg, 1988; Niklas, 1994). In contrast, our model correctly predicts the scaling of leaf, stem and root biomass. Furthermore, it shows how rates of resource, leaf biomass and net primary productivity per unit area are independent of plant density and plant size, regardless of the differences in the scaling of organ biomass scaling at the level of the individual (Enquist *et al.*, 1998).

In summary, we have shown that a general allometric model is able to account for a suite of scaling relationships within and across plant populations and communities. All the available evidence known to us supports our general mass–growth–density model. Our results indicate that despite enormous variation in phylogenetic and morphological diversity, plant communities are characterized by a canonical self-thinning phenomenon.

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