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

Karl J. Niklas,1* Jeremy J. Midgley2 and Brian J. Enquist3

1Department of Plant Biology, Cornell University, Ithaca, NY 14853, USA, 2Department of Botany, University of Cape Town, Rondebosch 7701, South Africa and 3Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721, USA

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 $M_T$ equals $M_TN$, it also predicts that $M_T \propto M_TN \propto N^{-4/3}N \propto N^{-1/3}$.

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...
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 $\dot{G}_T$ and total leaf biomass $\dot{M}_L$ will be each independent of $N$, whereas total community shoot and root biomass ($\dot{M}_{SH}$ and $\dot{M}_R$) 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, $G_T \propto M_L \propto M_T^{3/4}$ (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, $G_T = \beta_0 M_T^{3/4}$ and $G_T = \beta_1 H^\gamma$, where $\beta_0$ and $\beta_1$ 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, $B = G_T = \beta_0 M_T^{3/4} = \beta_1 H = \beta_1 M_L$ and $M_L = \beta_2 M_T^{3/4}$, where $\beta_1 = \beta_0 / \beta_1$ (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, $M_L = \beta_3 M_T^{3/4} = \beta_3 D^2$.

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, $R = N_{max} Q = N_{max} (\beta M_T^{3/4})$. Therefore, at equilibrium, $R$ is constant such that $N_{max} = (R/\beta_3) M_T^{-3/4}$. Because population density is ultimately constrained by $R$ and the dependence of body size on $B$, it follows that $N_{max} = \beta_4 D^{-1/2}$, where $\beta_4$ is a group-specific constant that includes the term $R/\beta_3$. Under any circumstances, since the three-dimensional space $a$ 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. $N \propto A_T/a$), 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: 

\[ M_T = (\beta_4 \beta_0 \beta_1) N^{-\frac{4}{3}} = \beta_4 N^{-\frac{4}{3}} \]

\[ G_T = (\beta_0 \beta_1 \beta_2) N^{-\frac{9}{5}} = \beta_0 N^{-\frac{9}{5}} \]

\[ M_L = (\beta_0 \beta_1 \beta_3) N^{-1} = \beta_0 N^{-1} \]

\[ D = \beta_6 N^{-\frac{11}{12}} \]  

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 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 \( M_{SI} \) 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, \( D = (4TBA/\pi N)^{\frac{1}{12}} \).
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 $M_{SO} = \beta_{14} M_{L}^{0.53} - \beta_{15} M_{L}$). 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; $\alpha$ and $\beta$, 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 $M_{SL}$ for each community (see Table 1).

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

<table>
<thead>
<tr>
<th></th>
<th>Observed</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$\log y$ vs $\log x$</td>
<td>Predicted</td>
<td>$\alpha$ (s.e.)</td>
<td>95% CI</td>
<td>$\log_{10} \beta$ (s.e.)</td>
<td>$r^2$</td>
</tr>
<tr>
<td><strong>Across all communities</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\log M_T$ vs $\log N$</td>
<td>$-4/3$</td>
<td>$-1.27$ (0.03)</td>
<td>$-1.33$ to $-1.16$</td>
<td>$5.96$ (0.11)</td>
<td>$0.801$</td>
<td>342</td>
</tr>
<tr>
<td>$\log G_T$ vs $\log N$</td>
<td>$-1.0$</td>
<td>$-0.98$ (0.03)</td>
<td>$-1.03$ to $-0.92$</td>
<td>$3.99$ (0.09)</td>
<td>$0.861$</td>
<td>205</td>
</tr>
<tr>
<td>$\log M_L$ vs $\log N$</td>
<td>$-1.0$</td>
<td>$-1.00$ (0.03)</td>
<td>$-1.05$ to $-0.95$</td>
<td>$3.78$ (0.09)</td>
<td>$0.669$</td>
<td>670</td>
</tr>
<tr>
<td>$\log D$ vs $\log N$</td>
<td>$-1/2$</td>
<td>$-0.53$ (0.01)</td>
<td>$-0.56$ to $-0.51$</td>
<td>$0.86$ (0.04)</td>
<td>$0.673$</td>
<td>792</td>
</tr>
<tr>
<td>$\log M_{SL}$ vs $\log N$</td>
<td>$-4/3$</td>
<td>$-1.31$ (0.03)</td>
<td>$-1.36$ to $-1.25$</td>
<td>$5.99$ (0.10)</td>
<td>$0.753$</td>
<td>668</td>
</tr>
<tr>
<td>$\log M_R$ vs $\log N$</td>
<td>$-4/3$</td>
<td>$-1.17$ (0.03)</td>
<td>$-1.23$ to $-1.10$</td>
<td>$4.97$ (0.11)</td>
<td>$0.773$</td>
<td>347</td>
</tr>
<tr>
<td><strong>Across angiosperm-dominated communities</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\log M_T$ vs $\log N$</td>
<td>$-4/3$</td>
<td>$-1.30$ (0.05)</td>
<td>$-1.36$ to $-1.23$</td>
<td>$5.74$ (0.16)</td>
<td>$0.759$</td>
<td>174</td>
</tr>
<tr>
<td>$\log G_T$ vs $\log N$</td>
<td>$-1.0$</td>
<td>$-1.00$ (0.05)</td>
<td>$-1.11$ to $-0.90$</td>
<td>$3.76$ (0.15)</td>
<td>$0.833$</td>
<td>74</td>
</tr>
<tr>
<td>$\log M_L$ vs $\log N$</td>
<td>$-1.0$</td>
<td>$-1.00$ (0.03)</td>
<td>$-1.05$ to $-0.95$</td>
<td>$3.37$ (0.10)</td>
<td>$0.751$</td>
<td>331</td>
</tr>
<tr>
<td>$\log D$ vs $\log N$</td>
<td>$-1/2$</td>
<td>$-0.51$ (0.02)</td>
<td>$-0.55$ to $-0.48$</td>
<td>$0.75$ (0.06)</td>
<td>$0.685$</td>
<td>342</td>
</tr>
<tr>
<td>$\log M_{SL}$ vs $\log N$</td>
<td>$-4/3$</td>
<td>$-1.25$ (0.04)</td>
<td>$-1.33$ to $-1.17$</td>
<td>$5.81$ (0.14)</td>
<td>$0.733$</td>
<td>325</td>
</tr>
<tr>
<td>$\log M_R$ vs $\log N$</td>
<td>$-4/3$</td>
<td>$-1.08$ (0.05)</td>
<td>$-1.18$ to $-0.98$</td>
<td>$4.72$ (0.16)</td>
<td>$0.729$</td>
<td>178</td>
</tr>
<tr>
<td><strong>Across conifer-dominated communities</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\log M_T$ vs $\log N$</td>
<td>$-4/3$</td>
<td>$-1.34$ (0.04)</td>
<td>$-1.42$ to $-1.25$</td>
<td>$5.96$ (0.11)</td>
<td>$0.846$</td>
<td>168</td>
</tr>
<tr>
<td>$\log G_T$ vs $\log N$</td>
<td>$-1.0$</td>
<td>$-1.04$ (0.03)</td>
<td>$-1.11$ to $-0.98$</td>
<td>$3.99$ (0.09)</td>
<td>$0.880$</td>
<td>131</td>
</tr>
<tr>
<td>$\log M_L$ vs $\log N$</td>
<td>$-1.0$</td>
<td>$-1.12$ (0.04)</td>
<td>$-1.19$ to $-1.05$</td>
<td>$4.41$ (0.12)</td>
<td>$0.746$</td>
<td>339</td>
</tr>
<tr>
<td>$\log D$ vs $\log N$</td>
<td>$-1/2$</td>
<td>$-1.28$ (0.05)</td>
<td>$-1.37$ to $-1.19$</td>
<td>$5.33$ (0.16)</td>
<td>$0.827$</td>
<td>169</td>
</tr>
<tr>
<td>$\log M_{SL}$ vs $\log N$</td>
<td>$-4/3$</td>
<td>$-1.31$ (0.03)</td>
<td>$-1.36$ to $-1.25$</td>
<td>$5.99$ (0.10)</td>
<td>$0.753$</td>
<td>668</td>
</tr>
<tr>
<td>$\log M_R$ vs $\log N$</td>
<td>$-4/3$</td>
<td>$-1.39$ (0.04)</td>
<td>$-1.46$ to $-1.31$</td>
<td>$6.26$ (0.13)</td>
<td>$0.782$</td>
<td>343</td>
</tr>
</tbody>
</table>

*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. 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 $\alpha$ for $M_{SH}$ versus $N$ is statistically indistinguishable from that observed (see Table 1). (B) The $\alpha$ 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 $M$, 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 $M$, 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. $\beta$-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 $\hat{G}_T \propto \hat{M}_T \propto N^0$. Indeed, White (1985) reported that $M_T$ 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 $M_T$) is independent of $N$— that is,
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

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


