Global Allocation Rules for Patterns of Biomass Partitioning in Seed Plants

Brian J. Enquist$^{1,2*}$ and Karl J. Niklas$^3$

A general allometric model has been derived to predict intraspecific and interspecific scaling relationships among seed plant leaf, stem, and root biomass. Analysis of a large compendium of standing organ biomass sampled across a broad sampling of taxa inhabiting diverse ecological habitats supports the relations predicted by the model and defines the boundary conditions for above- and below-ground biomass partitioning. These canonical biomass relations are insensitive to phyletic affiliation (conifers versus angiosperms) and variation in averaged local environmental conditions. The model thus identifies and defines the limits that have guided the diversification of seed plant biomass allocation strategies.

Despite its importance to ecology, global climate research, and evolutionary and ecological theory, the general principles underlying how plant metabolic production is allocated to above- and below-ground biomass remain unclear (1–6). Indeed, there are few large data sets with which to evaluate patterns of standing biomass within and across the broad spectrum of vascular plant species (2, 7). The resulting uncertainty severely limits the accuracy of models for many ecologically and evolutionarily important phenomena across taxonomically diverse communities (8–11). Thus, although quantitative assessments of biomass allocation patterns are central to biology, theoretical or empirical assessments of these patterns remain contentious (2, 8, 10, 11).

Nonetheless, the scaling relations among standing leaf, stem, and root (below-ground) biomass ($M_L$, $M_S$, and $M_R$, respectively) can be derived analytically by first noting that the amount of resource used per individual plant, $R$, approximates metabolic demand and gross photosynthesis ($B$) (12–14). Because $B$ is predicted to scale proportionally to total $M_L$, $R \propto B \propto M_L$, theory predicts that the surface areas over which resources are exchanged with the environment (e.g., leaf surface area, which correlates with $M_L$) are proportional to the $3/4$ power of the total plant biomass ($M_L$) (12–14). Thus, $B \propto M_L^{3/4}$ and $M_L \propto D_L^2$, where $D_L$ is stem diameter. Empirical studies confirm that plant metabolic rate scales as the $3/4$ power of $M_L$ (which equals the sum of $M_L$, $M_S$, and $M_R$) and that metabolic rates scale isometrically with respect to $M_L$ (7, 12, 13, 15). Here, we extend this theory (16) on the basis of three assumptions: (i) Stem and root bulk tissue densities are approximately constant during ontogeny (13), (ii) the effective hydraulic cross-sectional areas of stems and roots are equivalent (owing to the conservation of water mass flowing through a plant) (17, 18), and (iii) stem length scales roughly isometrically with respect to root length ($L_R$). If valid, these three basic assumptions corroborate the predictions that standing $M_L$ will scale as the $3/4$ power of $M_S$ and as the $3/4$ power of $M_R$ and that standing $M_S$ and $M_R$ will scale isometrically with respect to each other ($M_S \propto M_L^{3/4} \propto M_R^{3/4}$ and $M_R \propto M_L^{3/4}$). It also follows that above-ground biomass ($M_L$) will scale in a nearly isometric manner with respect to $M_R$ (i.e., $M_L + M_S + M_R$) across and within clades and different habitats.

These predictions were tested against data gathered from a variety of sources for standing $M_L$, $M_S$, and $M_R$ per plant across monocot, dicot, and conifer species differing by nine orders of magnitude in total body mass (19–21) [see supplemental data (22)]. Regression analyses (21) of these data show that all observed scaling exponents ($\alpha_{SMA}$) comply remarkably well with those predicted by the model (Table 1). For example, $M_S$ scales across species as the $1.99$ power (95% confidence interval (CI) = 1.90 $\leq \alpha_{SMA} \leq$ 2.07) of $D_L$ (Fig. 1) and does not differ significantly between angiosperm and conifer species (Table 1). Likewise, comparisons between angiosperm and conifer species reveal no statistically significant variation in the scaling exponents for standing $M_L$, $M_S$, and $M_R$, whereas the relation between $M_L$ and $M_R$ is nearly isometric for mature individuals, as predicted (i.e., $M_R = 3.88M_L^{1.9}$) (Fig. 2). Within the larger size ranges, statistical outliers are remarkably absent from all bivariable plots even when data from arborescent palm species, which lack a branched growth habit, are included (Figs. 1 and 2). However, our theory predicts a nonlinear log-log relation between $M_L$ and $M_R$ for plants less than 1 year old (16). This is not evident in our data for juvenile plants (i.e., less than 1 year old), which are best approximated by a linear log-log curve (Fig. 2). We attribute the departure of these data from theoretical expectations to the influence of nutrients provided by endosperm or megagametophyte tissues on the biomass partitioning pattern attending seedling establishment. Such a “maternal resource compartment” is expected to favor $M_R$ as opposed to $M_L$ (specifically leaf) accumulation.

The effect of plant size on the numerical values of scaling exponents was insignificant above the threshold of 1-year-old plants. When the data in the large size ranges were sorted into

Table 1. Statistical comparisons among standing $M_L$, $M_S$, and $M_R$ relations across seed plants and within angiosperm and conifer data sets. Scaling exponents and allometric constants are for reduced major axis regression ($\alpha_{SMA} \pm SE$ and $\beta_{SMA} \pm SE$) of log$_{10}$-transformed data (original units in kg of dry weight per plant). In all cases, $P < 0.0001$.

<table>
<thead>
<tr>
<th>$Y_1$ versus $Y_2$</th>
<th>$\alpha_{SMA} \pm SE$ (Observed)</th>
<th>95% CI</th>
<th>$\beta_{SMA} \pm SE$ (Observed)</th>
</tr>
</thead>
<tbody>
<tr>
<td>$M_L$ versus $M_S$</td>
<td>0.75 ± 0.008</td>
<td>0.73–0.76</td>
<td>0.12 ± 0.012</td>
</tr>
<tr>
<td>$M_L$ versus $M_R$</td>
<td>0.75 ± 0.006</td>
<td>0.70–0.78</td>
<td>0.41 ± 0.016</td>
</tr>
<tr>
<td>$M_S$ versus $M_R$</td>
<td>1.00 ± 0.009</td>
<td>1.05–1.13</td>
<td>2.59 ± 0.012</td>
</tr>
</tbody>
</table>

Angiosperm interspecific data sets

| $M_L$ versus $M_S$  | 0.75 ± 0.008                     | 0.71–0.74 | 0.13 ± 0.007                   | 0.924 622 7537 |
| $M_L$ versus $M_R$  | 0.75 ± 0.006                     | 0.74–0.79 | 0.30 ± 0.019                   | 0.920 217 2466 |
| $M_S$ versus $M_R$  | 1.00 ± 0.010                     | 1.08–1.12 | 2.61 ± 0.017                   | 0.977 221 9129 |

Conifer interspecific data sets

| $M_L$ versus $M_S$  | 0.75 ± 0.005                     | 0.74–0.81 | 0.34 ± 0.007                   | 0.863 350 2192 |
| $M_L$ versus $M_R$  | 0.75 ± 0.004                     | 0.79–0.92 | 0.76 ± 0.005                   | 0.802 108 689 |
| $M_S$ versus $M_R$  | 1.00 ± 0.010                     | 1.06–1.14 | 2.73 ± 0.002                   | 0.951 171 3282 |

Mean exponent of interspecific datasets

$M_R$ versus $M_A$  | $\alpha_{SMA} = 1.00$ | $\beta_{SMA} = 0.98 \pm 0.11$ | $0.885–1.09$ | 32 |

*To whom correspondence should be addressed. E-mail: benquist@u.arizona.edu
Plant biologists have long held the opinion that much idiosyncratic and site-specific variation in organ and biomass allocation shown in Figs. 1 through 3 is due to differences between Angiosperms and Gymnosperms.

The ability to predict the absolute amounts of $M_L$, $M_S$, or $M_R$ at the level of both the individual plant or an entire community is limited, because significant variation exists in the numerical values of allometric "constants" across species. For example, although both angiosperm and gymnosperm $M_L$ scales as the 3/4 power of $M_T$ (Table 1), the corresponding allometric constants ($b_{MAL}$, values of the intercepts) significantly differ from each other (i.e., 0.13 ± 0.075 and 0.34 ± 0.074, respectively) (Table 1). Thus, for equivalent $M_A$, conifers have, on average, 2.6 times more $M_L$ than do angiosperms. This observation resonates with the fact that conifers typically retain three cohorts of leaves that have less well-developed aerenchymatous mesophyll as compared with angiosperm leaves. Yet, even though conifer wood tends to be less dense than angiosperm wood, angiosperms and gymnosperms do not differ in the allometric relation between total $M_T$ and $M_L$ nor with the scaling of plant density and $M_T$ (Figs. 2 and 3).  

Recent biologists have long held the opinion that many idiosyncratic and site-specific variation exists in biomass allocation both within and across plant taxa, especially during ontogeny (23). Taxon and site-specific variation in biomass allocation is well known in response to differential selection for adaptations to different environmental conditions (e.g., species adapted to arid and hot conditions tend to have reduced $M_L$ with respect to $M_S$ or $M_R$ (23, 24). Nevertheless, when viewed across a large range of plant sizes, the about 10-fold variation in biomass allocation shown in Figs. 1 through 3 is slight as compared with the striking invariance observed (and predicted) for the scaling exponents of $M_T$, $M_L$, and $M_R$ across diverse communities differing in latitude and elevation. Traditionally, this variation has been indexed by ratios (e.g., stem:leaf, root:shoot, etc.). How-
ever, ratios fail to capture the actual functional relations characterizing biomass allocation among organ types. In contrast, our model and empirical findings quantitatively define the numerical limits on plant allocation strategies, which incidentally accord well with the observation that $M_s$ and $M_R$ are not significantly correlated with site age, absolute latitude, elevation, or number of species within the community. Furthermore, expressing allocation in terms of functional allometric relation provides a baseline by which to assess residual variation. For example, residual variation in biomass allocation between roots and shoots is significantly, although very weakly, correlated with plant height ($P < 0.0001, r^2 = 0.058, n = 271$) and local productivity ($P = 0.007, r^2 = 0.04, n = 178$).

Our model provides strong bridges to more detailed biometric analyses of individual plants within and across communities (10, 25). Furthermore, in conjunction with the allometric relation predicted by a growing body of allometric theory (12–15, 26), a general allometric framework directly pertains to developing quantitative models for global climate as well as a variety of other important ecological and evolutionary phenomena including the approximate boundary conditions for difficult-to-measure $M_R$ (1–10). Also, by identifying fundamental biomass partitioning rules, the model helps to identify the biophysical constraints acting on allocation tradeoffs in plant biology that potentially extend into the fossil record when seed plants first evolved. Allometric theory therefore holds great promise as a powerful quantitative tool with which to predict past and present-day plant structure-function relation at the level of the individual, community, or entire ecosystem (26).

### References and Notes

16. Noting that $B = \beta_1 M + \beta_2 M^2$ and $B = \beta_1 M + \beta_2 M^2$ where $\beta_1$ and $\beta_2$ include units of years $^{-1}$, we obtain $M_s = \beta_1 M + \beta_2 M^2$ and $M_s = \beta_1 M + \beta_2 M^2$. Because, for any species, $M_s = \beta_1 M_d L_2 + M_s = \beta_2 M_d L_2$, where $p$ is stem or root tissue bulk density, $L$ is organ length, and $D_2$ is root diameter, and because $\beta_1$ and $\beta_2$ are constant (i.e., denoted by $\beta_1$ and $\beta_2$, respectively), we also see that $M_s = \beta_1 M_d L_2 + \beta_2 M_d L_2$ and $M_s = \beta_1 M_d L_2$. This relation can be solved for $M_s$ by imposing a minimum "cost" constraint so that the total volume of water absorbed and transported by roots through stems per unit time is conserved so that $D_2$ is proportional to $D_2$ (17, 18, 27). Thus, $M_s = B_{D_2}^2$ and $M_s = B_{D_2}^2$ where $\beta_1$ and $\beta_2$ are additional allometric constants reflecting the proportional allocation to root and shoot biomass. These scaling relations give $M_s = B_{D_2}^2 + B_{D_2}^2 [M_{D_2}^2 (M_{D_2}^2)]^{1/2}$ and $M_s = B_{D_2}^2 + B_{D_2}^2 [M_{D_2}^2 (M_{D_2}^2)]^{1/2}$. Another way to express this is $M_s = B_{D_2}^2 + B_{D_2}^2 [M_{D_2}^2 (M_{D_2}^2)]^{1/2}$, where $\beta_1$ and $\beta_2$ are additional allometric constants reflecting the proportional allocation to root and shoot biomass. These scaling relations give $M_s = B_{D_2}^2 + B_{D_2}^2 [M_{D_2}^2 (M_{D_2}^2)]^{1/2}$ and $M_s = B_{D_2}^2 + B_{D_2}^2 [M_{D_2}^2 (M_{D_2}^2)]^{1/2}$.
Enzyme Dynamics During Catalysis

Elan Zohar Eisenmesser,1 Daryl A. Bosco,1 Mikael Akke,2 Dorothee Kern1*

Internal protein dynamics are intimately connected to enzymatic catalysis. However, enzyme motions linked to substrate turnover remain largely unknown. We have studied dynamics of an enzyme during catalysis at atomic resolution using nuclear magnetic resonance relaxation methods. During catalytic action of the enzyme cyclophilin A, we detect conformational fluctuations of the active site that occur on a time scale of hundreds of microseconds. The rates of conformational dynamics of the enzyme strongly correlate with the microscopic rates of substrate turnover. The present results, together with available structural data, allow a prediction of the reaction trajectory.

Although classical enzymology together with structural biology have provided profound insights into the chemical mechanisms of many enzymes (1), enzyme dynamics and their relation to catalytic function remain poorly characterized. Because many enzymatic reactions occur on time scales of micro- to milliseconds, it is anticipated that the conformational dynamics of the enzyme on these time scales might be linked to its catalytic action (2). Classically, enzyme reactions are studied by detecting substrate turnover. Here, we examine enzyme catalysis in a nonclassical way by characterizing motions in the enzyme during substrate turnover. Dynamics of enzymes during catalysis have previously been detected with methods such as fluorescent resonance energy transfer, atomic force microscopy, and stopped-flow fluorescence, which report on global motions of the enzyme or dynamics of particular molecular sites. In contrast, nuclear magnetic resonance (NMR) spectroscopy enables investigations of motions at many atomic sites simultaneously (3, 4). Previous NMR studies reporting on the time scales, amplitudes, and energetics of motions in proteins, have provided information on the relation between protein mobility and function (5–15). Here, we have used NMR relaxation experiments to advance these efforts by characterizing conformational exchange in an enzyme, human cyclophilin A (CypA), during catalysis.

CypA is a member of the highly conserved family of cyclophilins that are found in high concentrations in many tissues. Cyclophilins are peptidyl-prolyl cis/trans isomerases that catalyze the interconversion between cis and trans conformations of X-Pro peptide bonds, where “X” denotes any amino acid. CypA operates in numerous biological processes (16, 17). It is the receptor for the immunosuppressive drug cyclosporin A, is essential for HIV infectivity, and accelerates protein folding in vitro by catalyzing the rate-liming cis/trans isomerization of prolyl peptide bonds (18, 19). However, its function in vivo and its molecular mechanism are still in dispute. X-ray structures of CypA in complex with different peptide ligands show cis X-Pro bonds (20, 21), except for a trans conformation in the CypA/HIV-1 capsid complex (22, 23). In each case, only one conformer was observed in the crystal, even though both isomers must bind to CypA for catalysis of cis/trans isomerization to occur.

We characterized motions in CypA during catalysis with the use of 15N spin relaxation experiments with and without the substrate Suc-Ala-Phe-Pro-Phe-4-NA (24). Longitudinal (R1) and transverse (R2) auto-relaxation rates, transverse cross-correlated cross-relaxation rates (νM), and (1H)-15N nuclear Overhauser enhancements (NOE) were measured for all backbone amides in CypA (25). Though all parameters are sensitive to “fast” motions (pico- to nanoseconds), only R2 is sensitive to “slow” conformational exchange (micro- to milliseconds) (3–8). A progressive substrate-induced shift for several CypA amide resonances (Fig. 1) indicates catalysis-linked motions. It shows (i) that these amides experience different magnetic environments in free CypA (E) and in CypA bound to substrate (ES) and (ii) that the

---

1Department of Biochemistry, Brandeis University, Waltham, MA 02454, USA. 2Department of Biophysical Chemistry, Lund University, Post Office Box 124, SE-221 00 Lund, Sweden.

*To whom correspondence should be addressed. E-mail: dkern@brandeis.edu

---

**Fig. 1.** Chemical shift changes of the amide signals in CypA upon titration with the substrate Suc-Ala-Phe-Pro-Phe-4-NA. (A) At a constant CypA concentration of 0.43 mM, spectra were recorded at 0 mM (blue), 0.38 mM (orange), 1.01 mM (green), and 2.86 mM (red) substrate. The signal of V139 is progressively shifting upon addition of increasing amounts of substrate, indicating fast conformational exchange during catalysis. The observed chemical shifts are population-weighted averages of E and ES, and thus shift towards the position of the ES complex with increasing amounts of substrate. In contrast, the signal of V139 is not affected by catalysis. (B) The chemical shift differences between free CypA and in the presence of 2.86 mM substrate were mapped onto the structure (1RMH) with the use of a continuous color scale.