**CANONICAL RULES FOR PLANT ORGAN BIOMASS PARTITIONING AND ANNUAL ALLOCATION**

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Here we review a general allometric model for the allometric relationships among standing leaf, stem, and root biomass (\(M_L\), \(M_M\), and \(M_R\), respectively) and the exponents for the relationships among annual leaf, stem, and root biomass production or "growth rates" (\(G_L\), \(G_M\), and \(G_R\), respectively). This model predicts that \(M_L = M^{0.7}M^{0.3} = M^{0.7}\) such that \(M_L \approx M_S\) and that \(G_L \approx G_S\). A large synoptic data set for standing plant organ biomass and organ biomass production spanning ten orders of magnitude in total plant body mass supports these predictions. Although the numerical values for the allometric "constants" governing these scaling relationships differ between angiosperms and conifers, across all species, standing leaf, stem, and root biomass, respectively, comprise 8%, 67%, and 25% of total plant biomass, whereas annual leaf, stem, and root biomass growth represent 30%, 57%, and 13% of total plant growth. Importantly, our analyses of large data sets confirm the existence of scaling exponents predicted by theory. These scaling "rules" emerge from simple biophysical mechanisms that hold across a remarkably broad spectrum of ecologically and phylogenetically divergent herbaceous and tree-sized monocot, dicot, and conifer species. As such, they are likely to extend into evolutionary history when tracheophytes with the stereotypical "leaf," "stem," and "root" body plan first appeared.

**Key words:** allometry; biomass allocation; organ biomass; plant growth.

How total standing biomass is partitioned among the three vegetative organs of the vascular plant body (leaves, stems, and roots) and how total growth in plant biomass is allocated annually to construct new organ tissues are important to a broad range of research agenda, spanning life-history theory and community dynamics to modeling global climate change and understanding plant evolutionary trends. Yet, whether canonical "rules" exist for these relationships across species differing in phylgetic affiliation, growth habit, or habitat preference remains highly controversial (Iwasa and Roughgarden, 1984; Hunter and Lloyd, 1987; Charnov, 1993; Iwasa, 2000). This paper attempts to address this issue, first, by reviewing an allometric model predicting the scaling exponents for vegetative organ biomass partitioning and growth, and, second, by testing whether the scaling exponents predicted by this theory comply with those observed for newly gathered data sets for plant organ biomass partitioning and annual allocation.

The model reviewed here rests on the general allometric equation \(Y_i = \log \beta + \alpha \log Y_o\), where \(Y_i\) and \(Y_o\) are interdependent (size or growth) variables, \(\beta\) is the allometric constant, and \(\alpha\) is the scaling exponent (Huxley, 1932; Gould, 1966; Peters, 1983; LaBarbera, 1986; Niklas, 1994; Enquist and Niklas, 2001, 2002; Niklas and Enquist, 2001, 2002). Previous theoretical and empirical studies using this formula have shown that, across 20 orders of magnitude of body size (ranging from unicellular algae to that of mature trees), total plant growth \(G_T\) (biomass production per plant per year) is proportional to the 3/4-power of body biomass \(M_T\) and that total plant growth scales isometrically with respect the capacity of an individual to capture sunlight \(H\) (i.e., \(G_T \propto M^{0.75}\) and \(G_T \propto H\), respectively; Enríquez et al., 1996; Niklas and Enquist, 2001).

Other recent developments in allometric theory have shed light on a broad spectrum of other ecological phenomena ranging from community dynamics to vascular plant hydraulics and other life-history traits (West, Brown, and Enquist, 1997, 1999; Enquist et al., 1999; Enquist and Niklas, 2001, 2002; Niklas and Enquist, 2002).

Here, with the aid of a few simple biophysical assumptions, we further elaborate on allometric theory that predicts standing leaf biomass will scale as the 3/4-power of stem (or root) biomass and that stem and root biomass will scale isometrically with respect to one another. We also review the model that predicts annual leaf, stem, and root biomass production (= organ growth) will each scale isometrically with respect to one another.

To test these predictions, we present statistical analyses of a large data base for organ biomass and growth representing a broad spectrum of seed plant species, which has been recently expanded to cover ten orders of magnitude in total body size. Using these data, we show that the scaling exponents predicted by our model comply statistically with those observed empirically. Although substantial variation in the allometric constants for these scaling relationships exists as a result of species-specific differences in ontogeny, anatomy, habitat preferences, and other important phenotypic and environmental features, the numerical values of empirically determined allometric constants can be used to calculate the standing organ biomass and the annual organ growth for an "average" plant across all species as well as an "average" angiosperm or conifer species.

The model and analyses presented here identify a single canonical set of rules for the proportional relationships among organ biomass partitioning and allocation across a remarkably diverse spectrum of vascular land plant species. These rules provide a potentially powerful analytical tool for ecological
and evolutionary studies, especially since they likely extend into the fossil record when the stereotypical tracheophyte “leaf,” “stem,” and “root” body plan first evolved.

**ALLOMETRIC THEORY**

We here present the derivations for the scaling exponents governing standing organ biomass partitioning and the scaling exponents for annual organ biomass production at the level of an individual plant. Both sets of derivations are juxtaposed because “standing organ biomass” of plants less than 1 yr old is equivalent to “annual organ production.” Throughout these derivations, biomass allocation to reproductive effort is ignored, mainly due to lack of data and also because it can vary across growth seasons. In the context of our model we assume that reproductive effort is shared equally among the three vegetative organ types. Nevertheless, when compared to leaf, stem, and root biomass, reproductive allocation, in general, comprises a minor fraction of total biomass and biomass production. For convenience, allometric constants b in each set of derivations are numbered sequentially. Complex allometric constants are successively grouped and simplified in terms of their numerical designation.

**Standing organ biomass relationships**—The scaling exponents governing the relationships among standing leaf, stem, and root biomass (M_L, M_S, and M_R, respectively) are derived analytically based on the theoretical prediction and empirical observation that total annual plant growth G assumes scales as the 3/4-power of total plant biomass M (which equals the sum of standing leaf, stem, and root biomass; M_L, M_S, and M_R, respectively) and that it also scales isometrically with respect to M_T (Niklas and Enquist, 2001; see also Enriquez et al., 1996). Thus, G = \beta_L M_L^{10} = \beta_S (M_S + M_R)^{4/3} = \beta_R M_R, where the allometric constants \beta_L and \beta_S have units including per year. Simplifying this relationship gives M_L = \beta_L (M_S + M_R)^{4/3}, where \beta_L = \beta_S/\beta_R. Since M_T = B_L D_L L_T and M_R = B_R D_R L_T, where \rho is tissue bulk density, L is total organ length, and D is diameter, and since B_L, D_L, and B_R, D_R are roughly constant for each species (i.e., \beta_L = \beta_R = \beta_S = \beta, respectively), we obtain M_L = \beta_L (M_S + \beta S D_L^2 L_T + \beta R D_R^2 L_T)^{1/3}.

This last relationship can be solved for M_L because the total volume of water absorbed and transported by roots through stems to leaves per unit time must be conserved such that D_L^2 = D_R^2 and because, for metabolic as well as hydraulic reasons, M_L is predicted to be proportional to total stem and root diameters such that M_L = \beta_S D_L^2 = \beta_S D_R^2, where \beta_S and \beta_R are additional allometric constants (see Murray, 1927; Kramer, 1983; Zimmerman, 1983). Therefore, M_L = \beta_L [1 + (\beta_S/\beta_R) L_T + (\beta_R/\beta_S) L_T^3]. Provided that leaf and stem length scale isometrically such that L_T = \beta_L L, then M_L = \beta_L [1 / (1L_T^2) + (\beta_S/\beta_R) + (\beta_R/\beta_S)]^3. Noting that 1/L_T \to 0 with increasing growth in size, it is clear that M_L \sim \beta_L [1 + (\beta_S/\beta_R) + (\beta_R/\beta_S)]^3 
L_T = \beta_L L_T^3.

Allometric theory thus obtains M_L = \beta_L [1 + (\beta_S/\beta_R) + (\beta_R/\beta_S)] M_S = \beta_L M_S^{10/3} = \beta_R M_R^{10/3} = \beta_S M_S^{10/3} and, M_L = \beta_L M_S^{10/3} M_R^{10/3} or, in terms of simple proportional terms, M_S \propto M_L^{10/3} M_R^{10/3} M_R \propto M_S. Also, the relationship between standing shoot and root biomass is predicted to be M_L + M_S = (\beta_S/\beta_R) M_S + (M_R/\beta_S) M_R^{10/3}. Numerical simulations using different values for \beta_S and \beta_R indicate that M_L + M_R will, on average, scale in a near isometric way with respect to M_S. Importantly, these scaling relationships are expected to be invariant with respect to species phylogenetic affiliation provided that leaves are the sole or principal photosynthetic organs.

**Annual organ growth relationships**—The scaling exponents for leaf, stem, and root annual biomass production rates or annual “organ growth” (G_L, G_S, and G_R, respectively) are derived analytically by noting that total annual plant growth G_T must equal the sum of annual leaf, stem, and root growth and that total growth scales isometrically with respect to standing leaf biomass. Thus, G_T = G_L + G_S + G_R = \beta_T M_T, where the allometric constant \beta_T includes units of per year (see Niklas and Enquist, 2001, 2002).

For deciduous species, annual leaf biomass production is directly proportional to standing leaf biomass such that G_L = \beta_L M_L (Enriquez et al., 1996; Niklas and Enquist, 2001). Therefore, G_L = \beta_L (G_L + G_R) = \beta_L G_R, where G_R denotes annual non-photosynthetic biomass production. However, for nondeciduous species, leaf growth is proportional to the difference between the standing leaf biomass and the leaf biomass retained from previous growth seasons, denoted here as M_L. That is, G_L = \beta_L (M_L - M_T). For metabolic and life-history reasons (i.e., leaf phenology; see Ackerly and Reich, 1999), we assume that the leaf biomass retained from previous seasons is directly proportional to the standing leaf biomass in any growth season. If so, then M_L = \beta_L M_T, from which it follows that G_L = \beta_L (1 - \beta_L) M_T = \beta_L M_T and G_L = (\beta_L/\beta_T) G_T = \beta_L G_T. Thus, G_L = (1 - \beta_L)^{-1} (G_L + G_R) = \beta_L G_T. Thus, regardless of leaf phenology, an isometric relationship is predicted for annual leaf biomass production and the sum of annual stem and root biomass production. That is, G_T = \beta_T (G_L + G_R), where \beta_T = \beta_S or \beta_R.

This last scaling relationship may now be used to derive the scaling exponents relating leaf growth to stem and root growth for all species as follows. Stem (or root) growth may be modeled such that the bulk density of newly formed organ tissues \rho, and organ volume, which for stems or roots equals \pi D^2 L, is conserved such that \beta_S = \beta_L = \beta_R. Since G_L = \beta_L D_L^2 L_T and G_S = \beta_S D_S^2 L_T, such that G_L = \beta_L (\beta_S D_S^2 L_T + \beta_S D_S^2 L_T), the relationships among standing leaf, stem, and root biomass (Niklas, 1994). Assuming that annual root and stem extension in length is relatively constant for any particular species such that \rho D_L L_T = \beta_L N, we see that G_L = \beta_L (1 + \beta_S) D_S^2 L_T = \beta_S D_S^2 L_T. Since D_S^2 L_T is proportional to G_L, leaf and stem growth will scale isometrically with respect to one another: G_L = \beta_T (G_L + G_R) = \beta_T G_T. Leaf growth will also scale isometrically with respect to root growth: G_R = \beta_R (G_L + G_R) = \beta_R G_T. Thus, stem and root growth are predicted to scale isometrically: G_L = \beta_T (G_L + G_R) = \beta_T G_T. Finally, annual shoot biomass production (i.e., the sum of leaf and stem growth, G_L + G_S) is predicted to scale isometrically with respect to root growth: G_T = G_L + G_S = \beta_T (G_L + G_R) = \beta_T G_T. Thus, in simple proportional terms, our model predicts G_L \propto G_T, G_T \propto G_T, and G_T \propto G_T. These exponents are expected to be invariant with respect to species phylogenetic affiliation provided that leaves are the sole or principal photosynthetic organs.

**MATERIALS AND METHODS**

**Data sets**—To assess the predictions of our model, data for standing organ biomass and annual organ growth were gathered from the primary literature. For the majority of tree species, the bulk of these data comes from Cannell (1982) who compiled data sets for tree-sized dicot, monocot, and conifer species as well as a limited number of bamboo species. Each of the Cannell data sets is standardized to 1.0 ha and represents ~600 sites worldwide, published in a standardized tabular format that provides the primary citation and, when supplied by authors, longitude, elevation, the age of the dominant species (or conspecific in the case of monotypic managed stands), the number of plants per 1.0 ha (“plant density”), height, total basal stem cross-sectional area, and the standing biomass and net biomass production of stem wood, bark, branches, fruits, foliage, and roots (in units of metric tons of dry matter per year). The reported values for annual stem wood, bark, foliage, etc., production reflect as much as possible annual losses of dry matter due to mortality, litter-fall, decay, and consumption (see Cannell, 1982).

Organ biomass and productivity were determined by authors from direct measurements of fully dissected representative plants (typically ≤5 individuals) for the majority of the Cannell sites. Authors regressed these data to estimate total organ biomass per 1.0 ha community sample. Data based on estimated regression variables were rejected when entering the
Cannell data sets into computer memory. Importantly, most of these data sets are for even-aged conspecific stands \((n = 600\) out of 880 usable data sets), and biomass production values are typically averaged values for two or more years. Therefore, for each site used in our analyses, the variance in standing organ biomass and biomass production was assumed to be comparatively small and annual production rates were considered representative of “normal” rather than idiosyncratic growth seasons.

Standing leaf, stem, and root biomass per “average” plant was computed for each of the Cannell sites using the quotient of total community standing organ biomass and plant density. Annual leaf, stem, and root production rates were similarly calculated using the quotient of annual organ type production per hectare sample and plant density. However, we note that most of the Cannell data sets probably underestimate standing root biomass and biomass production, particularly those of fine and small roots, because these are more difficult to excavate completely for increasingly larger root systems and because these root-size categories are reported to increase with increasing plant size \((e.g.,\) Powell and Day, 1991). Thus, numerically higher scaling exponents than those predicted were anticipated for any regression analysis using root biomass or biomass production as the \(Y_2\) variable.

Since the Cannell data sets emphasize mature and large plant body sizes, additional data were recently gathered by K. J. Niklas from the primary literature published between 1990 and 2001 \(\text{(data available on request)}\) for species with comparatively small mature body sizes \(\text{(e.g., Arabidopsis, Bromus, Lactuca, Lycopersicum, Plantago, Sparrtina)}\) or for seedlings and saplings of tree species \(\text{(e.g., Betula, Quercus, and Thuja)}\). These additional data, which span 51 species not represented in the Cannell data sets, are from laboratory or field studies of plants grown under normal field or experimental conditions \(\text{(e.g., elevated CO}_2,\text{ UV-B radiation, salinity, or soil micro-nutrient levels)}\). Every attempt was made to select data evincing little variance per treatment as gauged by the standard errors reported for standing biomass or biomass production. For these plants, standing organ biomass and annual organ biomass production were calculated as for the Cannell data sets.

### Statistical analyses—Model Type II (reduced major axis, RMA) regression analysis was used to determine scaling exponents \(\alpha_{\text{RMA}}\) and allometric constants \(\beta_{\text{RMA}}\). The values for \(\alpha_{\text{RMA}}\) and \(\beta_{\text{RMA}}\) were computed using the formulas \(\alpha_{\text{RMA}} = \alpha_{\text{OLS}}/r\) and \(\log \beta_{\text{RMA}} = \log Y_1 - \alpha_{\text{RMA}} \log Y_2\), where \(\alpha_{\text{OLS}}\) is the ordinary least squares \(\text{(OLS)}\) regression exponent, \(r\) is the OLS correlation coefficient, and \(Y_1\) denotes the mean value of \(Y_1\) or \(Y_2\) \(\text{(Sokal and Rohlf, 1981; Niklas, 1994)}\). This regression procedure is recommended when the variables of interest are biologically interdependent, subject to unknown measurement error, and when functional rather than predictive relationships are sought \(\text{(Sokal and Rohlf, 1981; Harvey and Mace, 1982; Rayner, 1985; McArindle, 1988)}\). The numerical values of \(\alpha_{\text{RMA}}\) and \(\beta_{\text{RMA}}\) differ little from those obtained from Model Type I \(\text{(OLS regression)}\) analyses whenever \(r^2 \geq 0.95\) \(\text{(Sokal and Rohlf, 1981; Niklas, 1994)}\). Since \(r^2 > 0.95\) was found for most of the empirically determined interspecific relationships, the selection of regression model is arguably moot.

Paired comparisons of the untransformed data evinced linear trends when plotted on log-log scales \(\text{(based on analyses of residuals and smoothing spline-regression models with different } \lambda \text{ values)}\). However, all of the values computed for the Cannell data sets come from populations differing in plant density and, given the nature of these data sets, the variance about the “mean” values for each growth variable could not be determined, yet undoubtedly differed across community sites. To reduce the resulting effects of heteroscedasticity, the raw data were log10-transformed for subsequent Model Type II regression analyses. This protocol is recommended for functional analyses of biological growth variables \(\text{(Sokal and Rohlf, 1981)}\). Attempts to approximate trends in the log-transformed data with log-curvilinear regression models either failed to improve or reduced the goodness of fit \(\text{(based on analyses of residuals, bivariate normal ellipse protocol estimates, or the correlation coefficients of spline-smoothing regression curves)}\).

Regression analyses were performed on the pooled data sets to determine interspecific trends, on the angiosperm and conifer data sets separately to determine the effect of phyletic affiliation on regression parameters, and on individual species for which data were sufficient to determine intraspecific scaling relationships. Also, since the magnitude of many variables correlate with total standing biomass, paired values for organ biomass and growth rates were regressed over different ranges of their magnitude to determine the effect of plant size on the numerical values of scaling exponents. Since some primary sources did not report all the data needed to calculate values for all variables of interest, sample sizes \(n\) varied across statistical comparisons. The effect of \(n\) on regression parameters was determined using analyses of residuals.

### RESULTS

A critical assumption made in our derivations is that standing leaf biomass will scale as the 2-power of stem diameter. Across all species, \(M_L\) scaled as the 1.99 \((\pm 0.038)\)-power of stem diameter \(\text{(95% CI = 1.90} \sim 2.07; n = 593, r^2 = 0.786, F = 2165, P < 0.0001)}\). For the angiosperm and conifer data sets, \(M_L\) scaled as the 1.86 \((\pm 0.047)\)-power \(\text{(95% CI = 1.76} \sim 1.96; n = 281, r^2 = 0.823, F = 1297, P < 0.0001)}\) and as the 1.93 \((\pm 0.042)\)-power of stem diameter \(\text{(95% CI = 1.84} \sim 2.03; n = 312, r^2 = 0.852, F = 1778, P < 0.0001)}\), respectively. Therefore, our data were consistent with the assumption that \(M_L \approx D_s^2\).

Another critical assumption was that annual leaf biomass production scales as the 2-power of stem diameter. Across all species, \(G_L\) scaled as the 1.89 \((\pm 0.041)\)-power of \(D_s\) \(\text{(95% CI = 1.80} \sim 1.98; n = 410, r^2 = 0.809, F = 1728, P < 0.0001)}\). For angiosperms, \(G_L\) scaled as the 1.79 \pm 0.053 power of \(D_s\) \(\text{(95% CI = 1.67} \sim 1.90; n = 172, r^2 = 0.852, F = 977.9, P < 0.0001)}\). For conifers, the scaling exponent was 1.97 \pm 0.058 \(\text{(95% CI = 1.85} \sim 2.10; n = 235, r^2 = 0.802, F = 941.5, P < 0.0001)}\). Therefore, our data were consistent with the assumption that \(G_L \approx D_s^x\).

The scaling exponents observed for standing biomass relationships did not significantly differ from those predicted by theory and bivariate plots had remarkably few statistical outliers \(\text{(Fig. 1)}\). Based on analyses of regression residuals and the 95% confidence intervals of log-log linear regression curves, standing leaf biomass scaled, on average, as the 3/4-power of stem biomass, both across all species and within the angiosperm and conifer data sets \(\text{(Table 1)}\). Likewise, stem and root biomass scaled isometrically with respect to each other.

The 95% confidence intervals of the scaling exponent for
the relationship between leaf and root biomass exceeded the predicted value of $3/4$ both across species and within the angiosperm and conifer data sets (Table 1). However, this was not considered a serious departure from the predictions of our model, because the data responsible for the higher than expected exponent were those collected from juvenile individuals ($\approx 1$–2 yr old) whose “standing” organ biomass is equivalent to annual organ biomass production (e.g., $M_L \approx G_L$). For these plants, allometric theory predicts a scaling exponent of 1.0 rather than 0.75. This was demonstrated by regression and statistical comparisons between leaf biomass vs. stem (or root) biomass within the small and the large size ranges of data collected from juvenile and older plants (i.e., $10^{-6} < M_{\text{Leaf}} \leq 10^{-3}$ and $10^{-3} < M_{\text{Leaf}} \leq 10^{-1}$ kg dry mass/plant, respectively). Within the small stem (or root) biomass range (data from juveniles), leaf biomass scaled isometrically, as predicted when “standing” biomass equals annual organ growth. In contrast, leaf biomass scaled as the $3/4$-power within the large size range of stem or root biomass (data from mature individuals), as predicted by theory (Table 2).

Another prediction of our model is that standing shoot biomass will scale in a nearly isometric manner with respect to root biomass and that annual shoot biomass and root biomass production will scale isometrically with respect to each other. Across all our data sets, $M_L + M_S$ scaled as the 1.07 ($\pm 0.005$)-power of $M_S$ ($95\%$ CI = 1.06–1.08; $n = 1050$, $r^2 = 0.975$, $F = 40915$, $P < 0.00001$), whereas $G_L + G_S$ scaled as the 1.11 ($\pm 0.009$)-power of $G_S$ ($95\%$ CI = 1.09–1.13; $n = 324$, $r^2 = 0.977$, $F = 13522$, $P < 0.0001$) (Fig. 2). These scaling exponents were somewhat higher than predicted by our model. This was ascribed to an underestimation of standing (fine and small) root biomass or annual root biomass production with increasing plant size resulting from difficulties in excavating the peripheral elements of progressively larger root systems.

Importantly, isometric scaling exponents were observed for all annual biomass production relationships both across and within species comparisons (Fig. 3). Based on analyses of regression residuals and the 95% confidence intervals for the slopes of log-log linear regression curves, the scaling exponents for annual leaf, stem, or root growth were, on average, indistinguishable from unity (Table 3). The observed scaling exponent for annual stem and root biomass production, however, was slightly higher than that predicted for all comparisons (Table 1). Once again, this feature was attributed to the increasing difficulty of excavating and measuring fine and small roots with increasing overall plant size. Also, the biomass of these root size classes are reported to increase with increasing plant size (see Powell and Day, 1991; Makkonen and Helmissar, 2001). These features are expected to elevate

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**Table 1.** Statistical comparisons between predicted and observed scaling exponents for standing leaf, stem, and root biomass ($M_L$, $M_S$, and $M_R$, respectively) relationships across seed plants and within angiosperm and conifer data sets. Scaling exponents are for reduced major axis regression ($a_{rMA} \pm SE$) of log$_{10}$-transformed data (original units in kilograms of dry mass per plant). In all cases, $P < 0.0001$.

<table>
<thead>
<tr>
<th></th>
<th>Predicted</th>
<th>Observed</th>
<th>95% CI</th>
<th>$r^2$</th>
<th>$n$</th>
<th>$F$</th>
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<tr>
<td>Across all data sets</td>
<td></td>
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<tr>
<td>$M_L$ vs. $M_S$</td>
<td>0.75</td>
<td>0.76 $\pm$ 0.004</td>
<td>0.75–0.77</td>
<td>0.964</td>
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<td>$M_L$ vs. $M_R$</td>
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<td>0.84 $\pm$ 0.008</td>
<td>0.82–0.85</td>
<td>0.951</td>
<td>568</td>
<td>10 877</td>
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<td>$M_R$ vs. $M_S$</td>
<td>1.00</td>
<td>1.12 $\pm$ 0.006</td>
<td>1.11–1.13</td>
<td>0.985</td>
<td>560</td>
<td>35 450</td>
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<td>Across angiosperm data sets</td>
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<td>1.13 $\pm$ 0.007</td>
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<td>0.78 $\pm$ 0.015</td>
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<td>$M_L$ vs. $M_R$</td>
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<td>0.951</td>
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Table 2. Statistical comparisons between predicted and observed scaling exponents for leaf biomass relationships for different size-ranges of $M_L$ and $M_R$ across all species. Scaling exponents are for reduced major axis regression ($\theta_{RMA} \pm SE$) of log$_{10}$-transformed data (original units in kilograms of dry mass per plant). In all cases, $P < 0.0001$.

<table>
<thead>
<tr>
<th>$Y_1$ vs. $Y_2$</th>
<th>Predicted</th>
<th>Observed</th>
<th>95% CI</th>
<th>$r^2$</th>
<th>$n$</th>
<th>$F$</th>
</tr>
</thead>
<tbody>
<tr>
<td>log $M_L$ vs. log $M_R$</td>
<td>$-6 &lt; \log M_L$</td>
<td>$-3$</td>
<td>1.00</td>
<td>$0.94 \pm 0.010$</td>
<td>0.92–0.96</td>
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<td>$0.75 \pm 0.008$</td>
<td>0.73–0.76</td>
<td>0.910</td>
</tr>
<tr>
<td>log $M_L$ vs. log $M_R$</td>
<td>$-6 &lt; \log M_L$</td>
<td>$-3$</td>
<td>1.00</td>
<td>$1.00 \pm 0.024$</td>
<td>0.95–1.05</td>
<td>0.862</td>
</tr>
<tr>
<td></td>
<td>$-3 &lt; \log M_R$</td>
<td>$+4$</td>
<td>0.75</td>
<td>$0.79 \pm 0.016$</td>
<td>0.76–0.82</td>
<td>0.861</td>
</tr>
</tbody>
</table>

The slope of any regression curve with root biomass production plotted on the abscissa, which was evident throughout all statistical comparisons (see Tables 1–3).

Yet another prediction of our model is that the same scaling exponents will hold true within as well as across species comparisons. Although large intraspecific data sets ($n \geq 25$) were limited in number, this prediction was consistent with the allometry of those species for which sufficient sample sizes existed (Fig. 4). For example, for the conifer Cryptomeria japonica, the standing leaf biomass scaled as the $0.74 (\pm 0.031)$-power of stem biomass (95% CI = 0.64–0.77; $n = 59$, $r^2 = 0.854$, $F = 335.0$, $P < 0.0001$) and as the $0.72 (\pm 0.041)$-power of root biomass (95% CI = 0.64–0.81; $n = 30$, $r^2 = 0.913$, $F = 292.7$, $P < 0.0001$). Standing stem biomass also scaled as the $0.99 (\pm 0.016)$-power of root biomass (95% CI = 0.93–1.0; $n = 30$, $r^2 = 0.992$, $F = 3543$, $P < 0.0001$). The exponents for these scaling relationships were statistically indistinguishable from those predicted by theory (i.e., $3/4$, $3/4$, and 1, respectively). Also, for C. japonica, annual leaf biomass production scaled as the $1.08 (\pm 0.05)$-power of annual stem biomass production (95% CI = 0.963–1.19, $r^2 = 0.828$, $n = 71$, $F = 332.5$, $P < 0.0001$) and as the $1.06 (\pm 0.04)$-power of annual root biomass production (95% CI = 0.964–1.15, $r^2 = 0.890$, $n = 66$, $F = 519.3$, $P < 0.0001$). Stem biomass production scaled as the $0.99 (\pm 0.03)$-power of root biomass production (95% CI = 0.920–1.05, $r^2 = 0.936$, $n = 66$, $F = 935.8$, $P < 0.0001$). These scaling exponents did not differ from 1.0, as predicted by our model.

![Fig. 2](image1.png)  
(A) Standing shoot (M_L + M_S) biomass vs. standing root biomass (M_R). Original units in kilograms of dry mass per plant. (B) Annual shoot biomass production (G_L + G_S) biomass vs. annual root biomass production (G_R). Original units in kilograms of dry mass per plant per year.

![Fig. 3](image2.png)  
(A) Leaf biomass production vs. stem biomass production. (B) Leaf biomass production vs. root biomass production. (C) Stem biomass production vs. root biomass production. See Table 3 for regression parameters across all species and within angiosperm and conifer data sets.
respectively. Since there is a total of 3.33 kg/yr (5 kg/yr)/2.27 5 1.0 kg/yr), there are (1.0 kg/yr)/0.53 6 2.27, respectively (Table 4). Thus, for each of standing leaf biomass (i.e., M_L), which constitute 5%, 70%, and 25% of total plant biomass, whereas for conifers, the values are 16%, 61%, and 23%, respectively. That conifers tend to have roughly three times more leaf biomass than angiosperms likely reflects the fact that conifers typically retain three leaf cohorts each year (see Ackerly and Reich, 1999). That angiosperm stem and root biomass, on average, slightly exceeds that of conifers resonates with the higher densities of angiosperm woods with respect to those of most

### DISCUSSION

Currently, we are unable to predict a priori the numerical values of the allometric constants for scaling relationships due to insufficient information about species-specific differences in ontogeny, organ bulk tissue density, and other phenotypic factors that dictate the absolute amounts of standing organ biomass or organ biomass production for a particular species. These factors are known to influence these “constants” significantly (Andersson, 1997; Bazzaz and Grace, 1997; Cornelissen, 1999; Poorter and Nagel, 2000). However, the dimensionless organ growth quotients G_L/M_L and G_R/M_R, which equal the respective allometric “constants” for these scaling relationships, can be used to calculate empirically the percentage of leaf, stem, and root growth with respect to total annual growth.

For example, across all species, the quotients G_L/M_L and G_R/M_R equal 0.53 and 2.27, respectively (Table 4). Thus, for each 1.0 kg of leaf biomass produced per year per plant (i.e., G_L = 1.0 kg/yr), there are (1.0 kg/yr)/0.53 = 1.89 kg/yr and (1.0 kg/yr)/2.27 = 0.44 kg/yr of stem and root growth in biomass, respectively. Since there is a total of 3.33 kg/yr (=1.0 kg/yr + 1.89 kg/yr + 0.44 kg/yr) annual biomass production, the percentages of leaf, stem, or root annual growth are 30% ([1.0 kg/yr]/3.33 kg/yr] × 100%), 57% ([1.89 kg/yr]/3.33 kg/yr] × 100%), and 13% ([0.44 kg/yr]/3.33 kg/yr] × 100%), respectively (Fig. 5A). Using the same procedure, annual angiosperm leaf, stem, and root biomass growth respectively equals 32%, 59%, and 9% of total plant growth, whereas for conifers, the respective values are 48%, 35%, and 17%. On average, conifers appear to “invest” slightly less annual growth in the construction of new root tissues compared to the majority of angiosperm species.

In terms of the percentages of standing leaf, stem, and root biomass, statistical analyses show that M_L = 0.195 M_S 0.8 and M_L = 0.407 M_S 0.64 across all species. Therefore, for any 1.0 kg of standing leaf biomass (i.e., M_L = 1.0 kg), there are 8.84 kg (1.0 kg/0.195 0.8) and 3.32 kg (1.0 kg/0.407 0.64) of stem and root biomass, respectively, giving a total of 13.2 kg of standing biomass per average plant. Thus, standing leaf, stem, and root biomass, on average, respectively equal 8% (1.0 kg/13.2 × 100%), 67% (8.84 kg/13.2 × 100%), and 25% (= 3.32 kg/13.2 × 100%) of total plant biomass (Fig. 5B). Similar calculations indicate that angiosperm leaf, stem, and root biomass constitute 5%, 70%, and 25% of total plant biomass, whereas for conifers, the values are 16%, 61%, and 23%, respectively. That conifers tend to have roughly three times more leaf biomass than angiosperms likely reflects the fact that conifers typically retain three leaf cohorts each year (see Ackerly and Reich, 1999). That angiosperm stem and root biomass, on average, slightly exceeds that of conifers resonates with the higher densities of angiosperm woods with respect to those of most

### Table 3. Predicted and observed scaling exponents (a_{all} 6 SE) for annual organ biomass growth relationships based on reduced major axis regression of log_{10}-transformed data (original units in kilograms of dry). In all cases, P 6 0.0001.

<table>
<thead>
<tr>
<th>Quotient</th>
<th>Across all data sets</th>
<th>Within angiosperms</th>
<th>Within conifers</th>
</tr>
</thead>
<tbody>
<tr>
<td>G_L/G_S</td>
<td>0.97 6 0.01 (338)</td>
<td>0.95 6 0.01 (278)</td>
<td>0.99 6 0.01 (338)</td>
</tr>
<tr>
<td>G_S/G_R</td>
<td>1.08 6 0.02 (121)</td>
<td>1.09 6 0.02 (121)</td>
<td>1.10 6 0.02 (121)</td>
</tr>
<tr>
<td>G_R/M_R</td>
<td>1.14 6 0.02 (118)</td>
<td>1.14 6 0.02 (118)</td>
<td>1.15 6 0.02 (118)</td>
</tr>
</tbody>
</table>

Fig. 4. Bivariate plots of log_{10}-transformed data for Cryptomeria japonica standing leaf, stem, and root biomass (M_L, M_S, and M_R, respectively) and annual leaf, stem, and root biomass production or “growth” (G_L, G_S, and G_R, respectively). Solid line is reduced major axis regression curve; dashed lines are 95% confidence intervals of regression curve. (A) and (C) Standing organ biomass relationships (original units in kilograms of dry mass per plant). (B) Annual organ biomass production relationships (original units in kilograms of dry mass per plant per year).

At the level of individual species, the differences in the numerical values of allometric constants account for much of the “data spread.” This is a direct reflection of species-specific differences in anatomy, morphology, and ontogeny (see Niklas and Enquist, in press). Nonetheless, the regression curves for individual species share the same slopes (scaling exponents). When seen from this broad interspecific perspective, a single invariant pattern for organ biomass partitioning and annual biomass allocation to organ construction is identified by both our model and statistical analyses of large data sets. Remarkably, this pattern holds across a minimum of ten orders of magnitude of total body size and at least eight orders of magnitude in organ growth rates. It is indifferent to species phylogenetic affiliation, since angiosperms and conifers manifest the same scaling exponents, and it is largely insensitive to local environmental conditions, since data were gathered from plants growing under normal as well as some strikingly stressful conditions (e.g., low light levels, elevated UV-B, varying soil salinity, impoverished soil nutrients, or drought).

This invariance suggests that the partitioning of a finite amount of biomass produced per year (among three functionally equally important organ types) necessitates tradeoffs that are governed at least in part by the inexorable operation of biophysical phenomena (e.g., the conservation of water mass flowing from roots through stems to leaves and the mechanical relationship between leaf biomass and the stresses it produces in subtending stems). Whether these tradeoffs are resolved optimally over the course of an individual’s ontogeny or over the evolutionary history of each species remains conjectural (see Hunter and Lloyd, 1987; Schieving, 1988; Poorter, 1989; Lloyd and Venable, 1992; Iwasa, 2000; Niklas and Enquist, 2002). Yet, it is clear that otherwise widely different seed plant species are convergent in terms of the allometry of biomass partitioning and allocation.

This convergence provides a potentially powerful analytical tool for macroecological and evolutionary analyses of plant communities. For example, our data and model indicate that root biomass can be predicted with reasonable accuracy based on aboveground biomass measurements. This has obvious implications to modeling global climate change affected by standing plant biomass (see Raich and Nadelhoffer, 1989). Likewise, there is good reason to suspect that the pattern of biomass partitioning and allocation extends throughout the evolutionary history of vascular plants possessing a stereotypical “leaf,” “stem,” and “root” body plan (Niklas, 1997). If so, then root biomass may be estimated provided that aboveground biomass can be measured or reasonably estimated from morphological data.

Additional theoretical and empirical insights are required, especially in terms of reproductive biomass allocation, which can vary from year to year. But it is becoming increasingly clear that allometric theory is rapidly developing and holds much promise to shed considerable light on virtually every aspect of plant life, past and present.

**LITERATURE CITED**


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