On the Vegetative Biomass Partitioning of Seed Plant Leaves, Stems, and Roots

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Abstract: A central goal of comparative life-history theory is to derive the general rules governing growth, metabolic allocation, and biomass partitioning. Here, we use allometric theory to predict the relationships among annual leaf, stem, and root growth rates (GL, GS, and GR, respectively) across a broad spectrum of seed plant species. Our model predicts isometric scaling relationships among all three organ growth rates: GL ∝ GS ∝ GS R

Analyses of a large compendium of biomass production rates across diverse seed plant species provide strong statistical support for the predictions of the theory and indicate that reproductive investments may scale isometrically with respect to vegetative organ growth rates. The general rules governing biomass allocation as indexed by the scaling exponents for organ growth rates are remarkably indifferent to plant size and taxonomic affiliation. Yet, whether biomass partitioning abides by general “rules” transcending differences in organismic size, phyletic affiliation, habitat preference, or local environmental conditions remains contentious (Poorter 1989; Poorter and Lambers 1991; Marcelis 1996; Bultynck et al. 1999; Gross et al. 2000; Poorter and Nagel 2000).

Recently, however, allometric theory has provided a rapidly growing and robust framework with which to examine the scaling of plant form, function, and growth (Niklas 1992, 1994; Enquist et al. 1999; West et al. 1999; Niklas and Enquist 2001; Enquist and Niklas 2002). This framework focuses on how body size influences a variety of growth-related phenomena in terms of the general allometric equation log log Y2 = log β + α log Yn, where Y1 and Y2 are interdependent (size or growth) variables, β is the allometric constant, and α is the scaling exponent (Gould 1966; Peters 1983; LaBarbera 1986; Niklas 1994).

When approached in this manner, prior analyses demonstrate that, across 20 orders of magnitude of unicellular and metaphyte body size, overall plant growth (total biomass production per individual per year, which approximates the rate of net annual metabolic production) scales as the 3/4-power of body biomass and isometrically with respect to the light harvesting capacity of an individual (gauged by cell chlorophyll concentration or standing leaf biomass; Niklas and Enquist 2001).

Here, we take the same approach to derive analytically and test empirically the scaling exponents for the growth rates of seed plant vegetative organs (leaves, stems, and roots). Building on recent work (Niklas and Enquist 2001; Enquist and Niklas 2002), we first extend prior allometric models to derive the scaling exponents for the relationships among annual leaf, stem, and root biomass growth rates (GL, GS, and GR, respectively). We also derive mathematical expressions for the dimensionless “growth” quotients GL/

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How annual metabolic production and biomass production are used to maintain and construct the plant body on an annual basis has been a central focus of comparative life-history theory (Iwasa and Roughgarden 1984; Hunter and Lloyd 1987; Schieving 1988; Tilman 1988; Lloyd and Venable 1992; Venable 1996; Bazzaz and Grace 1997; Iwasa 2000). The relationships among metabolic production, growth, and biomass partitioning patterns are also pivotal to ecological and evolutionary theory, from the level of understanding the individual organism to that of predicting complex macroecological dynamics (Raich and Nadelhoffer 1989; Charnov 1993; Brown 1995; Enquist and Niklas 2001, 2002). Yet, whether biomass partitioning abides by general “rules” transcending differences in organismic size, phyletic affiliation, habitat preference, or local environmental conditions remains contentious (Poorter 1989; Poorter and Lambers 1991; Marcelis 1996; Bultynck et al. 1999; Gross et al. 2000; Poorter and Nagel 2000).

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With these assumptions, isometric scaling exponents for annual leaf, stem, and root growth ($G_l$, $G_s$, and $G_r$, respectively) are predicted as follows. The total annual biomass production in any year $G_t$ must equal the sum of annual leaf, stem, and root biomass production (vegetative “growth”):

$$G_t = G_l + G_s + G_r. \tag{1}$$

Prior derivations predict that $G_t$ scales isometrically with respect to total standing photosynthetic leaf biomass $M_l$ (Niklas and Enquist 2001):

$$G_t = \beta_t M_l, \tag{2}$$

where $\beta_t$ is an allometric constant whose numerical value depends on the rate of metabolic production per unit time $B$ that in turn reflects the efficiency of converting metabolite production into biomass $\beta_p$ (i.e., $\beta_t = \beta_p B$). Equation (2) has been empirically verified across 12 orders of magnitude of aquatic and terrestrial metaphyte body size (Niklas and Enquist 2001). However, the numerical value of $\beta_t$ can vary depending on whether a species is deciduous or nondeciduous. Even so, a generalized form for equation (2) is derived for all species as follows.

Deciduous species replace their entire set of leaves annually such that $G_t = \beta_t(M_l - M_i)$, where $\beta_t$ is an allometric constant (with units including yr$^{-1}$). Combining this relationship with equation (2) gives $G_t = (\beta_t/\beta_p) G_i$ that, in tandem with equation (1), yields

$$G_l = \left(\frac{\beta_t}{\beta_t - \beta_p}\right)(G_i + G_n) = \beta_t G_i, \tag{3}$$

where $\beta_t = [\beta_t/(\beta_t - \beta_p)]$ and $G_n = G_s + G_r$. Equation (3) predicts that annual leaf biomass production for deciduous species will scale isometrically with respect to the sum of annual nonphotosynthetic (stem and root) growth. This equation also shows that differences in the numerical value of $\beta_t$ can result in interspecific variation in the absolute amount of biomass allocated to leaf tissue construction.

In terms of nondeciduous species, some leaf biomass $M_i$ is retained from previous seasons of growth such that $G_l = \beta_t(M_i - M_i)$, where $\beta_t$ is yet another allometric constant (with units including yr$^{-1}$). With rare exceptions, we assume that $G_t$ will scale isometrically with respect to $M_i$ because leaf growth in any season is dependent on metabolic productivity in the previous growth season, which is dependent on the standing leaf biomass and growth conditions of the previous season (e.g., Andersson 1997; Nobel and Zhang 1997). Likewise, at the species level, the
functional life span of leaves is comparatively constant regardless of leaf phenology, even though significant differences exist across species (see Reich et al. 1997; Ackerly and Reich 1999). Thus, the quotient of retained and new leaf biomass is here simply assumed to be relatively constant for each species such that \( M_i = \beta_s M_l \), where the numerical value of \( \beta_s \) may nonetheless vary across species.

Therefore, among nondeciduous species, we postulate that \( G_t = \beta_s (M_l - M_r) = \beta_s (1 - \beta_s) M_l = \beta_s M_l \), where \( \beta_s = \beta_s (1 - \beta_s) \) reflects the complex effects of annual leaf metabolic production and life span. Combining \( G_t = \beta_s M_l \) and equation (2) gives \( G_t = (\beta_s / \beta_p) G_r = \beta_s G_r \). Inserting this last relationship into equation (1) gives

\[
G_t = \frac{G_r}{\beta_p - 1} = \beta_p G_r. \tag{4}
\]

Importantly, the allometric constants \( \beta_p \) and \( \beta_s \) are mathematically equivalent (cf. eqq. [3]–[4]), such that, regardless of species-specific differences in leaf phenology,

\[
G_t = \beta_p (G_r + G_r) = \beta_p G_r, \tag{5}
\]

where \( \beta_p \) denotes either \( \beta_s \) or \( \beta_p \). However, since \( \beta_p \) is not equivalent numerically for deciduous and nondeciduous species, the \( y \)-intercepts for the isometric relationship between \( G_t \) and \( G_r \) are expected to differ, perhaps significantly across species differing in leaf phenology.

Isometric scaling exponents for the relationships among \( G_L \), \( G_S \), and \( G_R \) are predicted as follows. Since the water mass passing through the plant body per unit time must be conserved, it follows that the annual increase in average stem cross-sectional area is proportional to the increase in average root cross-sectional area (Murray 1927; Kramer 1983; West et al. 1999). Here, we note that the well-known four-power relationship between hydraulic conductivity and vessel diameter is largely irrelevant since this relationship holds for individual conducting cells but requires a summation of the frequency distribution of conducting cell diameters to evaluate the conductivity of an individual stem or root. In this regard, the assumption that stem and root cross-sectional areas scale isometrically is reasonable metabolically because the ability of new stem tissues to provide leaves with soil nutrients is dependent on the volume fraction of conducting stem (and root) cell types produced annually, which is, on average, a highly conserved (and time-averaged) anatomical feature for nonwoody and woody species, even those evincing ecomorphological plasticity (Carlquist 1975; Zimmerman 1983; Zobel and van Buijtenen 1989; Genard et al. 2001). Therefore, we explicitly assume the following relationship:

\[
D_s^7 = \beta_{10} D_s^5, \tag{6}
\]

where \( D_s^7 \) and \( D_s^5 \) reflect the average annual increase in root and stem cross-sectional area, respectively.

Although variation in tissue density is often correlated with differences in life-history traits among species, bulk organ tissue density is relatively constant for each species (see Niklas 1994; Enquist et al. 1999). Thus, from first principles, annual stem and root biomass growth equals the product of some allometric constant \( \beta \), the bulk density of new organ tissues \( \rho_s \), and the volume of new tissues produced per year, which is proportional to the cross-sectional area and the length of new stem or root biomass:

\[
G_s = \beta_{11} \rho_s D_s^5 L_s, \tag{7a}
\]

\[
G_r = \beta_{12} \rho_r D_r^5 L_r, \tag{7b}
\]

where \( L \) represents new stem or root length. Combining equations (5)–(7a) and solving for leaf growth with respect to stem growth gives

\[
G_s = \beta_{13} (\beta_{11} \rho_s D_s^5 L_s + \beta_{12} \rho_r D_r^5 L_r)
\]

\[
= \beta_{10} \rho_s + \alpha \beta_{10} \beta_{12} \rho_r D_r^5 L_r
\]

\[
= \beta_{10} \left( 1 + \frac{\beta_{10} \beta_{12} \rho_r}{\beta_{11} \rho_s} \right) G_r
\]

\[
G_s = \beta_{13} G_r, \tag{8}
\]

where \( \alpha = L_r / L_s \) and \( \beta_{13} = \beta_{10} [1 + \alpha (\beta_{10} \beta_{12} / \beta_{11}) (\rho_r / \rho_s)] \). (Note that the dimensionless parameter \( \alpha \) need not be constant across different growth seasons or species. Its numerical value simply designates the relationship between new root and stem extension in length on a season by season basis.)

Combining equations (5), (7b), and (8) and solving for \( G_s \) with respect to \( G_r \) obtains the relationship

\[
G_s = \left[ \frac{\beta_{10}}{\beta_{13} - \beta_{10}} \right] G_r = \beta_{14} G_r, \tag{9}
\]

where \( \beta_{14} = [\beta_{10} (\beta_{13} - \beta_{10})] \). Finally, combining equations (8) and (9) gives isometric scaling exponents for all three vegetative organ growth rates at the level of an individual plant:

\[
G_L = \beta_{13} G_S = \beta_{13} \beta_{14} G_R. \tag{10}
\]

From these relationships, shoot growth rates are predicted to scale isometrically with respect to root growth rates:

\[
G_L + G_R = \beta_{13} \beta_{14} G_R + \beta_{14} G_R = (\beta_{13} + 1) \beta_{14} G_R. \tag{11}
\]
These isometric scaling relationships are also compatible with the mechanical boundary condition set by elastic self-similarity among stems differing in size, which establishes the minimum theoretical scaling exponent for the relationship between plant height and stem diameter even for very small, nonwoody vertical stems that are principally supported by hydrostatic (turgor) pressure (Niklas 1992, 1994). Specifically, the critical buckling load \( P_c \) (i.e., the maximum load a new stem can support before it elastically deflects under the load) may be assumed to be proportional to the new leaf biomass. For a vertical support member (i.e., a new stem) with diameter \( D_s \) and length \( L_s \), this critical load is given by Euler’s formula \( P_c = 0.25 \pi^2 (EI_L^2) \), where \( E \) is Young’s elastic modulus (a material property of new stem tissues whose numerical value is constant for any species) and \( I \) is the axial second moment of area (a parameter reflecting the ability of a new stem to resist deformation as a property of the size and geometry of its cross section; McMahon 1973; Niklas 1992, 1994). For any stem with a terete cross section, engineering analysis shows that \( I \propto D_s^5 \). Provided that, for each taxon, stem deflections are minimized or held relatively constant across stems differing in size, the proportional relationship between stem length and diameter is \( L_s \propto D_s^{2/3} \) (i.e., elastic self-similarity across homologous stems differing in size; McMahon 1973; Niklas 1994). Proportionally, therefore, Euler’s formula takes the form \( P_c \propto EI_L^2 \propto D_s^{4/3} (D_s^{2/3})^2 \propto D_s^{8/3} \) (see Niklas 2000b). Noting that the new stem biomass \( m_s \) must be proportional to both stem growth \( G_s \) and to the 8/3-power of stem diameter \( D \) (i.e., \( m_s \propto G_s \propto D_s^2 L_s \propto D_s^{8/3} \)) and that the critical buckling load \( P_c \) must be isometrically proportional to new leaf biomass \( m_t \) (and thus \( G_t \)), it follows from \( P_c \propto D_s^{8/3} \) that \( G_t \propto G_s \). Since \( G_t \propto G_t + G_r \) (see eqs. [3]–[4]), we obtain \( G_t \propto G_s \propto G_r \) (see eq. [10]).

**Derivation of the General Forms of the Allometric “Constants”**

Here, we show analytically that the numerical values of the allometric constants governing the relationships among the three organ annual growth rates reflect phenotypic features influencing how an individual plant occupies space and garners, transmits, and uses resources, which will vary across species. Regardless of leaf phenology or taxonomic affiliation, \( G_t \propto \rho_t S_t t \), where \( \rho_t \) is leaf bulk tissue density, \( S_t \) is total leaf surface area, and \( t \) is leaf thickness. Since \( G_t \propto \rho_t D_s^2 L_s \) (see eq. [7a]), the quotient of leaf and stem biomass growth can be expressed in proportional terms as

\[
\frac{G_t}{G_s} \propto \frac{S_t}{D_s^2 L_s} \rho_t \rho_s, \tag{12}
\]

Here, \( S_t \) gauges the ability of new leaf tissues to exchange mass (e.g., water, carbon dioxide, and oxygen) and energy (e.g., light and heat) with their environment, whereas \( D_s^2 \) reflects the ability of new stem tissues to conduct nutrients and provide mechanical support (since mechanical stresses are inversely proportional to \( D_s^2 \) and since \( I \propto D_s^4 \)).

For roots, we also see that \( G_r \propto \rho_r S_r D_r \) (see eq. [7b]), where \( S_r \) is new root surface area, which is proportional to \( D_r L_r \). Therefore,

\[
\frac{G_t}{G_r} \propto \frac{S_t}{D_r L_r} \rho_t \rho_r, \tag{13}
\]

Here, \( S_t/S_r \) reflects the relative capacities of new leaf and root tissues to exchange mass and energy with their respective environments. Note that root length is allometrically related to both root diameter and surface area such that equation (13) can be cast in terms of root length, which may be a better proxy for root absorption capacity (see Nye and Tinker 1969). Finally, since hydraulic and metabolic considerations predict that \( D_r^2 \propto D_s^4 \) (see eq. [6]), we see that

\[
\frac{G_r}{G_s} \propto L_r \rho_s \rho_r, \tag{14}
\]

which indicates that the capacity of new stems and roots to occupy three-dimensional space (measured in terms of their annual extension in length) is proportionally equivalent.

Anatomical features also influence the numerical values of these allometric constants. Data from a variety of sources indicate that \( \rho_t < \rho_r < \rho_s \) across vascular plants (see Tendelenburg and Mayer-Wegelin 1955; Zobel and van Buijenen 1989; Niklas 1992, 1994). Therefore, low values for \( G_t/G_s \) and \( G_r/G_s \) may reflect allocational differences in tissue density reflecting the general case that \( \rho_t/\rho_s \ll 1 \) and \( \rho_r/\rho_s \ll 1 \) across species, especially those that produce woody stems or roots.

**Allocation Trade-offs and Variation in the γ-Intercept**

Here, we draw further attention to interspecific variation among the allometric constants when isometric scaling exponents govern biomass allocation patterns. For simplicity, we consider a purely hypothetical plant consisting of two body compartments (e.g., cacti lacking foliage) in...
terms of the consequences of partitioning a finite amount of biomass between two equally important body compartments (e.g., stems and roots). In doing so, we do not advocate the perspective that biomass partitioning complies with an optimization process per se but merely that it necessitates a trade-off in allocation that involves allometric relationships (see Iwasa and Roughgarden 1984; Iwasa 2000).

Let \( P \) represent the total metabolic cost (or functional performance) of constructing the entire plant body and let \( P_1 \) and \( P_2 \) represent the construction costs (or performance) of each of the two body compartments. Also, let \( k \) denote a quantity of interest (annual biomass allocation) that interrelates \( P_1 \) and \( P_2 \) in terms of the scaling exponents \( m \) and \( n \) and the allometric constants \( a \) and \( b \). For the purpose of this treatment, we specify the following relationships among all of these variables:

\[
P = P(k) + P_2(k) = \frac{a}{k^m} + bk^n. \tag{15}
\]

Under these circumstances, differentiating \( P \) with respect to \( k \) and setting the result equal to zero (to obtain the extremum) obtains the minimum biomass “investment” \( k^* \) and the minimum “cost” function \( P^* \):

\[
k^* = \left(\frac{ma}{nb}\right)^{\frac{1}{m+n}} \tag{16}
\]

and

\[
P^* = \frac{a(m + n)}{n(k^*)^n}. \tag{17}
\]

Equations (15)–(17) show that the annual partitioning of a finite amount of biomass between even two organ types is invariably governed by the constants \( a \) and \( b \) when the exponents \( m \) and \( n \) are invariant within or across species (see fig. 1 for the case where \( m = n = 1 \)). As the number of organ types increases, more allocation trade-offs are required and the ways they can be reconciled increases. Importantly, if \( m \) and \( n \) are invariant as predicted by our theory, then \( a \) and \( b \) are the only parameters that can be varied to achieve these trade-offs. Under these circumstances, intraspecific allometric trends will share the same scaling exponents but manifest different \( y \)-intercepts that produce “scatter” in bivariate plots of annual organ growth rates.

Material and Methods

Data Sets

The data sets compiled by Cannell (1982) and Karl J. Niklas (see below in this section) for annual biomass production for herbaceous and tree-sized dicots, monocots, and conifers were used to establish empirically the numerical values of the scaling exponents and allometric constants for \( G_L \), \( G_S \), and \( G_R \) relationships. Each of the Cannell data sets is based on a 1.0-ha sample of \( \sim 600 \) sites worldwide, published in a standardized tabular format that includes the primary citation and (whenever provided 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 dry matter per year). The reported values for annual stem wood, bark, foliage, and so forth, production reflect as much as possible annual losses of dry matter due to mortality, litter fall, decay, and consumption (Cannell 1982).

For the majority of the Cannell data sets, organ biomass and productivity was determined from direct measurements of fully dissected representative plants from each site (typically \( \geq 5 \) individuals) and regression of the resulting data to estimate total organ biomass per 1.0-ha community sample. We rejected all data based on estimated regression variables; that is, all values for standing or annual organ biomass production are based on empirical information (available in the online edition of the American Naturalist). Most of the published Cannell data

Figure 1: Total and individual cost functions \((P, P_1, \text{and } P_2, \text{respectively})\) plotted against the parameter of interest \((k, \text{“biomass”})\) for a hypothetical plant consisting of two vegetative body compartments. The minimum cost function and biomass investment, denoted by \( P^* \) and \( k^* \), respectively, are indicated for the special case \( m = n = 1 \), where \( m \) and \( n \) are scaling exponents.
sets are from even-aged conspecific stands \((n = 600\) out of 880 complete data sets). Likewise, 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 is likely comparatively small and annual production rates are more representative of “normal” than idiosyncratic growth seasons. However, it is reasonable to assume that most of the Cannell data sets underestimate root biomass and root biomass production, particularly those of fine and small roots, which are more difficult to excavate completely for increasingly larger root systems. Indeed, based on a small data set, we found that the sum of fine and small root biomass scales as the \(1.89\)-power \((\pm 0.18)\) of large root biomass \((n = 20, r^2 = 0.798, F = 71.03, p < .0001)\).

An important concern regarding the Cannell data sets is that many reflect the biometry of mixed stands of species rather than monotypic sites. However, \(~62\%\) of the data sets used in our analyses are from monotypic sites \((i.e., 300 monotypic sites/487 sites \times 100\% = 61.8\%\) ). Preliminary statistical comparisons between the trends evident in the monotypic and mixed site data sets also revealed little or no significant differences in the numerical values of scaling exponents. Thus, both kinds of data sets were pooled and analyzed.

With these caveats in mind, we computed annual leaf, stem, and root growth rates \((G_L, G_S, \text{ and } G_R)\), the sum of stem and root growth \((G_S)\), aboveground “shoot growth” \((G_L + G_S = G_{\text{shoot}})\), and total annual plant growth \((G)\) for an “average plant” from each of the Cannell sites using the quotient of total community annual leaf, stem (= trunk, branches, and bark), or root biomass production and plant density. Six orders of magnitude of \(G_L, G_S, \text{ and } G_R\) are

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**Table 1: Predicted and observed scaling exponents \((\alpha_{\text{RMA}} \pm SE)\) for growth and biomass relationships (based on reduced major axis regression of log_{10}-transformed data)**

<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>Across all data sets:</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>(G_L) vs. (G_S)</td>
<td>1.00</td>
<td>.97 ± .01</td>
<td>.95–.99</td>
<td>.983</td>
<td>278</td>
<td>15,649</td>
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<tr>
<td>(G_L) vs. (G_R)</td>
<td>1.00</td>
<td>1.00 ± .01</td>
<td>.98–1.01</td>
<td>.988</td>
<td>229</td>
<td>18,108</td>
</tr>
<tr>
<td>(G_S) vs. (G_R)</td>
<td>1.00</td>
<td>.93 ± .01</td>
<td>.92–.95</td>
<td>.985</td>
<td>598</td>
<td>16,677</td>
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<tr>
<td>(G_L) vs. (G_R)</td>
<td>1.00</td>
<td>1.06 ± .01</td>
<td>1.04–1.08</td>
<td>.973</td>
<td>281</td>
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<tr>
<td>(G_S) vs. (G_R)</td>
<td>1.00</td>
<td>1.17 ± .01</td>
<td>1.14–1.18</td>
<td>.981</td>
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<tr>
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<td>1.01 ± .05</td>
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<tr>
<td>(G_L) vs. (G_R)</td>
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<td>(G_S) vs. (G_R)</td>
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<td>1.01 ± .04</td>
<td>.92–1.11</td>
<td>.842</td>
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<td>Across angiosperm data sets:</td>
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<tr>
<td>(G_L) vs. (G_S)</td>
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<td>.97–1.02</td>
<td>.981</td>
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<td>(G_L) vs. (G_R)</td>
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<td>(G_S) vs. (G_R)</td>
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<td>(G_S) vs. (G_R)</td>
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<td>1.06 ± .06</td>
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<td>.590</td>
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<td>(G_L) vs. (G_S)</td>
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<td>.98 ± .04</td>
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<td>Across conifer data sets:</td>
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<tr>
<td>(G_L) vs. (G_S)</td>
<td>1.00</td>
<td>.94 ± .01</td>
<td>.92–.96</td>
<td>.986</td>
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</tr>
<tr>
<td>(G_L) vs. (G_R)</td>
<td>1.00</td>
<td>1.03 ± .02</td>
<td>.99–1.06</td>
<td>.958</td>
<td>131</td>
<td>2,923</td>
</tr>
<tr>
<td>(G_S) vs. (G_R)</td>
<td>1.00</td>
<td>.97 ± .01</td>
<td>.95–1.00</td>
<td>.973</td>
<td>260</td>
<td>9,187</td>
</tr>
<tr>
<td>(G_L) vs. (G_S)</td>
<td>1.00</td>
<td>1.04 ± .01</td>
<td>1.02–1.06</td>
<td>.986</td>
<td>160</td>
<td>10,453</td>
</tr>
<tr>
<td>(G_L) vs. (G_R)</td>
<td>1.00</td>
<td>1.19 ± .01</td>
<td>1.17–1.21</td>
<td>.990</td>
<td>160</td>
<td>15,420</td>
</tr>
<tr>
<td>(G_S) vs. (G_R)</td>
<td>...</td>
<td>1.02 ± .11</td>
<td>.85–1.38</td>
<td>.358</td>
<td>57</td>
<td>30.64</td>
</tr>
<tr>
<td>(G_L) vs. (G_S)</td>
<td>...</td>
<td>.99 ± .12</td>
<td>.80–1.37</td>
<td>.375</td>
<td>46</td>
<td>26.28</td>
</tr>
<tr>
<td>(G_L) vs. (G_R)</td>
<td>...</td>
<td>1.04 ± .19</td>
<td>.50–1.59</td>
<td>.590</td>
<td>14</td>
<td>17.27</td>
</tr>
</tbody>
</table>

Note: \(G_L\) = annual leaf biomass production, \(G_S\) = combined annual stem and root biomass production, \(G_R\) = annual stem biomass production, \(G_S\) = annual root biomass production, \(G_S\) = total plant growth, \(G_R\) = annual reproductive biomass production (no predicted exponents; empirical values based on small sample sizes). For all vegetative growth rate relationships, \(p < .0001\).

* Denotes scaling exponents that numerically deviate from those predicted.
were computed using the formulas and

**Table 2:** Scaling exponents ($\alpha_{RMA} \pm SE$) over different magnitude intervals of $G_s$, $G_o$, and $G_h$ values (kg dry weight/plant/year)

<table>
<thead>
<tr>
<th>Minimum$^c$</th>
<th>Maximum$^c$</th>
<th>$\alpha_{RMA} \pm SE$</th>
<th>95% CI</th>
<th>$r^2$</th>
<th>$n$</th>
<th>$F$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$Y_1 = G_s$; $Y_2 = G_o$; $Y_3 = G_h$; $Y_4 = G_h$</td>
<td>$10^{-6}$</td>
<td>$10^{-3}$</td>
<td>$1.15 \pm .07$</td>
<td>1.00–1.31</td>
<td>.781</td>
<td>63</td>
</tr>
<tr>
<td>$10^{-3}$</td>
<td>$10^0$</td>
<td>$1.07 \pm .02$</td>
<td>1.01–1.11$^b$</td>
<td>.886</td>
<td>213</td>
<td>1,647</td>
</tr>
<tr>
<td>$10^{-2}$</td>
<td>$10^0$</td>
<td>$1.03 \pm .01$</td>
<td>1.00–1.06</td>
<td>.922</td>
<td>430</td>
<td>5,057</td>
</tr>
<tr>
<td>$10^0$</td>
<td>$10^0$</td>
<td>.75 $\pm .03$</td>
<td>.86–1.00</td>
<td>.857</td>
<td>322</td>
<td>714.4</td>
</tr>
<tr>
<td>$Y_1 = G_s$; $Y_2 = G_o$</td>
<td>$10^{-6}$</td>
<td>$10^{-3}$</td>
<td>$1.23 \pm .16$</td>
<td>.69–1.78</td>
<td>.377</td>
<td>37</td>
</tr>
<tr>
<td>$10^{-3}$</td>
<td>$10^0$</td>
<td>$1.10 \pm .03$</td>
<td>1.09–1.22$^b$</td>
<td>.922</td>
<td>112</td>
<td>1,296</td>
</tr>
<tr>
<td>$10^{-2}$</td>
<td>$10^0$</td>
<td>$1.08 \pm .04$</td>
<td>.99–1.17</td>
<td>.746</td>
<td>197</td>
<td>573.4</td>
</tr>
<tr>
<td>$10^0$</td>
<td>$10^0$</td>
<td>$1.25 \pm .03$</td>
<td>.99–1.48</td>
<td>.471</td>
<td>115</td>
<td>100.7</td>
</tr>
<tr>
<td>$Y_1 = G_s$; $Y_2 = G_h$</td>
<td>$10^{-6}$</td>
<td>$10^{-3}$</td>
<td>.85 $\pm .07$</td>
<td>.69–1.00</td>
<td>.708</td>
<td>51</td>
</tr>
<tr>
<td>$10^{-3}$</td>
<td>$10^0$</td>
<td>$1.28 \pm .02$</td>
<td>1.23–1.33$^b$</td>
<td>.962</td>
<td>112</td>
<td>2,819</td>
</tr>
<tr>
<td>$10^{-2}$</td>
<td>$10^0$</td>
<td>$1.03 \pm .02$</td>
<td>.99–1.08</td>
<td>.898</td>
<td>197</td>
<td>1,718</td>
</tr>
<tr>
<td>$10^0$</td>
<td>$10^0$</td>
<td>$1.18 \pm .05$</td>
<td>1.06–1.30$^b$</td>
<td>.770</td>
<td>115</td>
<td>378.8</td>
</tr>
</tbody>
</table>

Note: In all cases, $p < .0001$.

$^c$ Minimum < $G_s$, $G_o$, and $G_h$ values

$^b$ Denotes scaling exponents that numerically deviate from those predicted.

$G_h$ (in units of kilograms dry weight per plant per year) each were obtained.

To expand the range of data and increase the statistical robustness of regression analyses, additional data were gathered by K. J. Niklas from the primary literature published between 1984 and 2001. Since the Cannell data sets emphasize plants with large body sizes, special emphasis was placed on collecting data reported for small species (e.g., *Arabidopsis*, *Bromus*, *Lactuca*, *Lycopersicum*, *Plantago*, *Spartina*), seedlings, and juveniles of tree species (e.g., *Betula*, *Quercus*, and *Thuja*). These additional data, which expanded the number of species in the collective data set from 307 to 358, came from laboratory or field studies of plants grown under normal field or experimental conditions (e.g., elevated CO$_2$, UV-B radiation, salinity, or soil micronutrient levels). Every attempt was made to select data evincing little variance per treatment as gauged by the standard errors reported for biomass production. The quotient of total standing organ biomass and the product of plant density and age was used to compute annual organ growth rates per plant. With these additional data, the range of annual organ growth rates was expanded to eight or more orders of magnitude each.

**Data Analyses**

Model Type II (reduced major axis, RMA) regression analysis was used to determine scaling exponents ($\alpha_{RMA}$) and allometric constants ($\beta_{RMA}$). The values for $\alpha_{RMA}$ and $\beta_{RMA}$ were computed using the formulas $\alpha_{RMA} = \alpha_{OLS}/r$ and $\text{log} \beta_{RMA} = \text{log} \ Y_1 - \alpha_{RMA} \text{log} \ Y_2$, where $\alpha_{OLS}$ is the ordinary least squares scaling exponent (slope), $r$ is the OLS correlation coefficient, and $Y$ denotes the mean value of $Y$ (Sokal and Rohlf 1981; Niklas 1994). This regression procedure is recommended when the variables of interest are biologically interdependent, subject to unknown measurement error (Rayner 1985; McArdle 1988), and when functional rather than predictive relationships are sought (Sokal and Rohlf 1981; Harvey and Mace 1982). Importantly, the numerical values of $\alpha_{RMA}$ and $\beta_{RMA}$ differ little from those obtained from Model Type I (ordinary least squares regression) analyses whenever $r^2 \geq 0.95$ (Sokal and Rohlf 1981; Niklas 1994). Since $r^2 > 0.95$ was found for all empirically determined interspecific $G_s$, $G_o$, and $G_h$ relationships (see table 1), the selection of regression model is arguably moot.

Paired comparisons of untransformed $G_s$, $G_o$, and $G_h$ values evinced linear trends when plotted on log-log scales (based on analyses of residuals and smoothing spline-regression models with different $\lambda$-values). All of the growth rates 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 comparisons. To reduce the resulting effects of heteroscedasticity, the raw data were log$_{10}$-transformed for subsequent Model Type II regression analyses. This protocol is recommended for functional analyses of biological growth variables (Sokal and Rohlf 1981). Attempts to approximate trends in the log-transformed data with nonlinear regression curves either failed to improve or reduced the goodness of fit (based on anal-
Plant Biomass Partitioning

Figure 2: Bivariate plot of log₁₀-transformed data for leaf versus stem growth rates (Gₗ vs. Gₛ) and leaf versus total plant growth rates (Gₗ vs. Gᵢ; A and B, respectively) measured in kilograms dry weight per plant per year across angiosperm and conifer species (see insert). Solid line, reduced major axis (RMA) regression curve; dashed lines, 95% confidence intervals. Statistical parameters for scaling exponents (αᵣ₉ₐ) given in table 1.

yses 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 obtain interspecific trends, on the angiosperm and conifer data sets separately to determine the effect of phylectic affiliation on regression parameters, and on individual species for which data were sufficient to determine intraspecific scaling relationships. Also, since the magnitude of organ growth correlates with total standing biomass (i.e., across species, on average, $G \propto M^{1/3}$; see Niklas and Enquist 2001), paired organ growth rates were regressed over different ranges of their magnitude to determine the effect of plant size on the numerical values of scaling exponents. Because some primary sources did not report sufficient data to calculate all $Gₗ$, $Gₛ$, and $Gᵢ$ values, sample sizes $n$ varied across statistical comparisons. The effect of sample size on regression parameters was determined using analyses of residuals.

**Results**

**Scaling Exponents**

Based on analyses of residuals and 95% confidence intervals (CIs), the scaling exponents governing organ growth rates were either statistically indistinguishable from an isometric hypothesis or so numerically dissimilar from alternative power-functions (e.g., 3/4, 4/5, 7/8, 8/7, or 6/5) that an isometric hypothesis was the most parsimonious functional relationship (tables 1, 2). The scaling relationship between annual leaf biomass production $Gₗ$ and combined annual stem and root biomass production $Gᵢ$ was best approximated by the formula $Gₗ = 0.322Gᵢ^{0.32}$ across all species, whereas $Gᵢ$, which must correlate with overall plant growth $Gᵢ$, scaled isometrically with respect to this parameter, i.e., $αᵣ₉ₐ = 1.00 \pm 0.01$ (fig. 2). Likewise, the annual partitioning of total growth among the three organ types was expressed by the regression formulas $Gₗ = 0.532Gᵢ^{0.26}$, $Gₛ = 2.27Gᵢ^{0.26}$, and $Gᵢ = 4.66Gᵢ^{1.17}$ (fig. 3). At the interspecific level of comparison, the scaling exponent relating leaf to stem growth rates was lower than predicted, whereas the scaling exponents relating leaf and root growth rates and stem and root growth rates were higher than predicted.

The numerical deviations between the predicted and observed scaling exponents for leaf, stem, and root growth rates were attributed to size-dependent effects on the measurement errors of leaf and root growth rates. If, with increasing plant size, annual leaf biomass production is
systematically underestimated (either as a consequence of defoliation or herbivory), the scaling exponent relating leaf to stem growth rates is expected to have a lower numerical value than unity. Likewise, if annual root biomass production is systematically underestimated with increasing plant size (owing to the difficulties of excavating and measuring fine or small root growth), the scaling exponent relating leaf or stem growth rates to root growth rates is expected to be larger than predicted.

An additional factor influencing the scaling exponents of organ growth rates was the phyletic effects on the y-intercepts (allometric “constants”) of regression curves. For example, although the interspecific exponent for the relationship between leaf and stem growth rates is lower than predicted, the exponents observed for angiosperm and conifer leaf and stem growth rates deviated little from the predicted value of unity (table 1).

By the same token, the numerical values of the scaling exponents for organ growth rates varied from unity in only four of 12 comparisons across different ranges of growth rate magnitudes (table 2). For example, across angiosperm and conifer species, the scaling exponent for $G_L$ versus $G_S$ ranged between 0.75 ± 0.03 for $0 < \log G_S \leq 2$ and 1.15 ± 0.07 for $-6 < \log G_S \leq -3$. However, the corresponding 95% CI for each exponent included unity (table 2). The most significant deviation from unity was observed for the comparison between stem and root growth rates within the size range of $-3 < \log G_R \leq 0$ (95% CI = 1.23 to 1.33), which could be attributed to a shift in the y-intercept within this region of the interspecific regression curve ($p = .001$). Since organ growth rates correlate with total plant biomass (see Niklas and Enquist 2001), these results indicated that interspecific scaling exponents were, overall, numerically indifferent to absolute plant size.

Importantly, isometric scaling exponents were also evident at the level of individual species for which sufficient data were available. Parallel regression curves with isometric scaling exponents were observed for each of these species (fig. 4). For example, for the conifer Cryptomeria japonica, $G_L$ scaled as the $1.08 \pm 0.05$–power of $G_S$ (95% CI = 0.963 to 1.19, $r^2 = 0.828$, $n = 71$, $F = 332.5$, $p < .0001$) and as the $1.06 \pm 0.04$–power of $G_R$ (95% CI = 0.964 to 1.15, $r^2 = 0.890$, $n = 66$, $F = 519.3$, $p < .0001$), whereas $G_S$ scaled as the $0.99 \pm 0.03$–power of $G_R$ (95% CI = 0.920 to 1.05, $r^2 = 0.936$, $n = 66$, $F = 935.8$, $p < .0001$; fig. 5).
Finally, shoot growth \( G_s + G_r \) scaled in a reasonably isometric way with respect to root growth across all species and within the angiosperm and conifer data sets. Across all species, \( G_s + G_r \) scaled as the \( 1.10 \pm 0.01 \)–power of \( G_r \) (95% CI = 1.08 to 1.12, \( r^2 = 0.981 \), \( n = 302 \), \( F = 15,151 \), \( p < .0001 \)). Angiosperm and conifer shoot growth scaled as the \( 1.12 \pm 0.02 \)– and \( 1.11 \pm 0.01 \)–power of root growth, respectively. That these exponents were higher than predicted was attributable to a shift in the \( y \)-intercept at \( \log G_r \approx -1.5 \). When the data for \( G_s + G_r \) were regressed against \(-6 < \log G_r \leq -1.5 \) and \( G_r > -1.5 \), shoot growth scaled as the \( 1.00 \pm 0.03 \)– and \( 1.04 \pm 0.03 \)–power of \( G_r \), respectively (fig. 6).

### Allometric “Constants” (“Growth” Quotients)

Since the most statistically parsimonious hypothesis across all comparisons of organ growth rates was the null hypothesis (i.e., isometric exponents), the numerical value of the biomass production quotient for each scaling relationship designates roughly the relevant allometric constant (i.e., the absolute amount of biomass partitioned annually to construct new organ tissues with respect to that of another organ type: \( G_x/G_y \sim \beta _{\text{RMA}} \)). In this respect, across all data sets, \( G_s/G_r = 0.532 \pm 0.01 \) (\( r^2 = 0.965 \), \( n = 598 \), \( F = 16,677 \), \( p < .0001 \)), \( G_s/G_r = 2.27 \pm 0.02 \) (\( r^2 = 0.973 \), \( n = 281 \), \( F = 9,948 \), \( p < .0001 \)), and \( G_s/G_r = 4.66 \pm 0.02 \) (\( r^2 = 0.981 \), \( n = 278 \), \( F = 14,454 \), \( p < .0001 \); table 3). Therefore, on average, \( 53\% \) less biomass is annually allocated to new leaf than new stem tissue production, roughly twice as much biomass is used to produce new leaf tissues compared to new root tissues, and substantially more biomass is allocated to new stem than new root tissue production.

The numerical values of \( G_s/G_r \) for angiosperms and conifers were statistically indistinguishable, whereas the values of \( G_s/G_r \) and \( G_s/G_r \) differed between the seed plant groups (table 3). For angiosperms and conifers, \( G_s/G_r = 0.54 \pm 0.02 \) (\( r^2 = 0.964 \), \( n = 338 \), \( F = 9,053 \), \( p < .0001 \), and \( 0.54 \pm 0.02 \), \( r^2 = 0.973 \), \( n = 260 \), \( F = 9,187 \), \( p < .0001 \), respectively). The biomass allocated to leaf versus stem new tissue construction was thus equivalent for both seed plant groups. However, for angiosperms, \( G_s/G_r = 3.39 \pm 0.05 \) (\( r^2 = 0.963 \), \( n = 121 \), \( F = 3,066 \), \( p < .0001 \)) and \( G_s/G_r = 6.92 \pm 0.04 \) (\( r^2 = 0.976 \), \( n = 118 \), \( F = 4,671 \), \( p < .0001 \)), whereas for conifers, \( G_s/G_r = 1.39 \pm 0.02 \) (\( r^2 = 0.986 \), \( n = 160 \), \( F = 10,453 \), \( p < .0001 \)) and \( G_s/G_r = 2.84 \pm 0.01 \) (\( r^2 = 0.990 \), \( n = 160 \), \( F = 15,420 \), \( p < .0001 \)). The allometric constants likewise varied across species, for example, for \( C. japonica \), \( G_s/G_r \sim 0.6 \) and \( G_s/G_r \sim 2 \). The relatively low values for \( G_s/G_r \) and \( G_s/G_r \) observed across angiosperm and conifer species was attributed to low leaf tissue density with respect to bulk stem or root tissue density (see eqq. [12]–[13]).

Interspecific differences in the numerical values of allometric “constants” accounted for most of the “scatter” in bivariate plots of organ growth. Significantly less scatter was attributable to environmental conditions attending growth, and that which was observed resulted from data collected from plants growing naturally under low light or soil nutrients or under stressful experimental conditions (e.g., elevated salt or UV-B). Another significant factor, was taxon-specific differences in leaf phenology. As noted, the standing leaf biomass \( M_L \) of nondeciduous plants equals the sum of \( G_s \) and the leaf biomass produced and retained from previous growth seasons \( M_L \) (see “Extension of Allometric Theory”). In this respect, among evergreen species, \( G_s = 0.274 M_L^{0.98} (a_w \text{CI } 0.93 \text{ to } 1.03, r^2 = 0.891, n = \ldots \)
Figure 6: Bivariant plot of log_{10}-transformed data for shoot growth rate ($G_{\text{shoot}} = G_s + G_p$) versus root growth rate ($G_r$) measured in kilograms dry weight per plant per year. Each of the four interspecific reduced major axis regression curves (solid lines) for angiosperms and conifers over the range $-6 < \log G_r = -1.5$ and $\log G_s > -1.5$ have statistically indistinguishable slopes (see text).

201, $F = 1.633, p < .0001$). Although some degree of autocorrelation must exist between standing leaf biomass and annual leaf biomass production rates (fig. 7), nondeciduous species add, on average, 33% new leaf biomass with respect to the leaf biomass retained from previous seasons; that is, $M_t = G_t + M_i = 0.274M_t + M_i$ such that $M_i = 0.726M_t$.

Reproductive Annual Production

The data for annual reproductive biomass production $G_r$ were limited. However, for the sake of completeness, we report that, across all species, $G_r$ scaled isometrically with respect to leaf, stem, and root annual growth (table 1). The strongest correlation between reproductive effort and any of the three vegetative growth variables was for root growth, both across species ($r^2 = 0.872$) and within the angiosperm and conifer data sets ($r^2 = 0.849$ and 0.590, respectively).

No significant difference was observed between the exponents for angiosperms and conifers. For example, the scaling exponent for $G_r$ versus $G_s$ was $1.00 \pm 0.04$ (95% CI = 0.89 to 1.10, $r^2 = 0.728, n = 144, F = 380.3, p < .0001$) and $0.99 \pm 0.12$ (95% CI = 0.60 to 1.37, $r^2 = 0.375, n = 46, F = 26.38, p < .0001$) for angiosperms and conifers, respectively. Across all species, $G_r/G_s = 0.28 \pm 0.07$ ($r^2 = 0.608, n = 201, p < .0001$), $G_r/G_p = 0.18 \pm 0.06$ ($r^2 = 0.714, n = 190, p < .0001$), and $G_r/G_R = 0.29 \pm 0.06$ ($r^2 = 0.842, n = 92, F = 479.9, p < .0001$; table 3). Thus, on average, within and across species, significantly less biomass is allocated annually to construct reproductive tissues than to construct new leaf, stem, or root tissues.

The reproductive quotients of angiosperms and conifers based on small data sets were statistically indistinguishable but had comparatively large standard errors. With these caveats in mind, angiosperms were found to allocate more biomass annually to the construction of reproductive organs (in comparison to leaf, stem, or root tissue construction) than conifer species. For example, $G_r/G_s$ for angiosperms was $0.22 \pm 0.08$ ($r^2 = 0.728, n = 114, F = 380.3, p < .0001$), whereas, $G_r/G_s$ for conifers was $0.16 \pm 0.09$ ($r^2 = 0.375, n = 46, p < .0001$; table 3). These differences are magnified by the preponderance in our data sets of conifer species typically bearing three cohorts of ovulate cones per season of which only the most recently formed contribute to the calculation of $G_r$ (e.g., Pinus spp.).

Discussion

Our allometric derivations predict isometric inter- and intraspecific relationships among annual leaf, stem, root, and shoot growth that can manifest significant variation in their respective allometric constants. Accordingly, bivariate plots of annual leaf, stem, or root growth are expected to have parallel slopes but potentially significant variation in their $y$-intercepts (reflecting differences in the absolute amounts of biomass allocated to construct the three different vegetative organ types that will manifest as data “scatter”).

Analyses of synoptic data sets for annual organ biomass production across a diverse spectrum of seed plant species
Many different species from the same geographical area will have different rates of growth of their photosynthetic and respiratory tissues. At the level of interspecific comparisons, the isometric scaling hypothesis predicts that the biomass allocation between organs isometrically related (e.g., leaf, stem, and root) would be comparable across all species. However, empirical studies have shown that the scaling exponents for biomass allocation are not always isometric, indicating that allocation patterns may vary significantly among species and environmental conditions.

One important caveat about rejecting any null hypothesis for a scaling relationship is that an empirically observed pattern across extant spermatophytes regardless of phyletic affiliation. An important caveat about rejecting any null hypothesis for a scaling relationship is that an empirically observed pattern across extant spermatophytes regardless of phyletic affiliation.

A related concern about testing the isometric hypothesis is that differences in the intercepts of the regression lines can provide misleading evidence for or against isometry. To address this concern, we have calculated the intercepts for each species and compared them to the overall mean intercept. If the intercepts are not significantly different from the overall mean, this suggests that the scaling relationships are isometric.

Table 3: Mean and SE for biomass production quotients \(\beta_{\text{ALL}}\ ± SE\) across and within angiosperm and conifer species

<table>
<thead>
<tr>
<th>Quotient</th>
<th>Across all species</th>
<th>Within angiosperms</th>
<th>Within conifers</th>
</tr>
</thead>
<tbody>
<tr>
<td>(G_r/G_s)</td>
<td>0.53 ± 0.01 (598)</td>
<td>0.54 ± 0.02 (338)</td>
<td>0.54 ± 0.01 (260)</td>
</tr>
<tr>
<td>(G_r/G_m)</td>
<td>2.27 ± 0.02 (281)</td>
<td>3.39 ± 0.05 (121)</td>
<td>1.39 ± 0.02 (160)</td>
</tr>
<tr>
<td>(G_m/G_s)</td>
<td>4.66 ± 0.02 (278)</td>
<td>6.92 ± 0.04 (118)</td>
<td>2.84 ± 0.01 (160)</td>
</tr>
<tr>
<td>(G_m/G_i)</td>
<td>0.28 ± 0.07 (201)</td>
<td>0.30 ± 0.10 (144)</td>
<td>0.27 ± 0.08 (57)</td>
</tr>
<tr>
<td>(G_i/G_s)</td>
<td>0.18 ± 0.06 (190)</td>
<td>0.22 ± 0.08 (144)</td>
<td>0.16 ± 0.09 (46)</td>
</tr>
<tr>
<td>(G_i/G_m)</td>
<td>0.29 ± 0.08 (92)</td>
<td>0.31 ± 0.09 (78)</td>
<td>0.24 ± 0.16 (14)</td>
</tr>
</tbody>
</table>

Note: Sample sizes \(n\) given in parentheses; see Table 1 for additional statistical parameters.

Although allometric models can be used to derive analytically the scaling relationships for any particular species (provided that organ functions and types are specified), they cannot currently predict a priori the numerical values of the corresponding allometric constants. In part, this limitation is a result of insufficient information about physiological, morphological, and anatomical features that influence the numerical values of constants (see eqq. [12]–[14]). These differences clearly have a bearing on reports that allometric constants vary in species-specific and local environmental ways (e.g., Gary et al. 1998; Waring et al. 1998; Cornelissen 1999; Enquist et al. 1999).

Additional variation in the numerical values of allometric constants comes from the lack of information about some critical metabolic production sinks and biomass allocation pathways. One such important allocation pathway is the potentially sizable metabolic commitment to mycorrhizal associations, which typically goes unreported by many authors and which change as a function of soil nutrient levels (see Grierson et al. 1981; Vogt et al. 1982; Högberg et al. 2001; Schultz et al. 2001).
root biomass annually lost to herbivory is typically unreported. This loss is neither invariably large nor necessarily correlated with differences in leaf phenology (e.g., Marquis et al. 2001). Yet herbivory can account for an important fraction of biomass production; for example, folivorous vertebrates on Barro Colorado Island, Panama, consume an estimated \( \sim 300 \) kg dry foliage ha\(^{-1}\) yr\(^{-1}\) (Leigh 1999). We have also drawn repeated attention to the underestimation of fine and small root biomass production, which becomes increasingly more problematic with increasing plant size (see Makkonen and Helmissar 2001). There is also considerable evidence that the fine “feeder roots” produced by suberized (old) roots atrophy annually such that annual root growth may be further underestimated (Niklas et al. 2002). The failure to consider these and other growth compartments will bias estimates of annual root biomass production and alter leaf, stem, and root scaling exponents as well as the corresponding allometric constants since the amount of “missing” root biomass production will increase with increasing plant size and thus elevate scaling exponents whenever \( G_R \) is used as the “independent” variable in functional (regression) analyses.

Perhaps the most obvious “missing” allocation pathway is reproductive effort, which can vary widely over the course of ontogeny and change in response to a variety of abiotic and biotic environmental factors (Bierzychudek 1981; Reekie and Bazzaz 1987; Hemborg and Larlsson 1998; Gardner and Mangel 1999; Ronce et al. 2000). Additional complications result from the fact that reproductive effort is often quantified in a variety of noninterchangeable ways (e.g., number, size, or biomass of ovulate cones, flowers, seeds, or fruits) and that some reproductive organs photosynthetically contribute to their own growth in biomass during some or all of their ontogeny (Bazzaz et al. 1997).

For simplicity, we assumed that the biomass allocated to reproduction was either negligible with respect to total annual vegetative growth or that it scales isometrically with respect to total growth and equally with respect to leaf, stem, and root growth (see Enquist et al. 1999). The data available to us support an isometric relationship between yearly reproductive effort and vegetative organ growth, both across and within angiosperm and conifer species. However, we have emphasized that these data are extremely limited and thus unreliable in terms of drawing statistical inferences, especially in terms of the allometric relationship between conifer reproductive and vegetative growth.

Nonetheless, the most plausible statistical hypothesis is that isometric scaling exponents govern vegetative organ growth rates across a remarkably diverse constellation of seed plant species. We believe that this biomass allocation pattern reflects the existence of biophysical constraints that have uniformly influenced the partitioning of net metabolite and biomass production within the highly conserved “stereotypical” body plan of seed plants (Vogellehner 1981; Niklas 1997, 2000a). At the level of the individual plant, our analyses certainly suggest that the partitioning of a finite amount of biomass among functionally interrelated and equally important body compartments necessitates “trade-offs” in annual allocation. Whether these have been reconciled optimally remains contentious (for different perspectives, see Reynolds and Chen 1996 and Iwasa 2000). However, the persistence of isometric or near-isometric scaling exponents for vegetative organ growth across and within phylogenetically and ecologically vastly different species suggests that vegetative biomass allocation has been
reconciled in similar proportional ways, from seedling to reproductive maturity (see Jurado and Westoby 1992).

The general absence of variation in scaling exponents across diverse species provides strong evidence that vegetative growth in biomass is, on average, independent of plant size and species phyletic affiliation and surprisingly conservative with respect to the effects of many abiotic environmental factors. Future advances in allometric models and additional empirical analyses of other large data sets are clearly required to explore the derivations advanced here. However, our mechanistic theory highlights as never before the quantitative allometric rules underlying how metabolic production is allocated to construct the basic seed plant body plan, which appears to have remained remarkably uniform throughout much of seed plant evolution. Our model, therefore, offers a potentially powerful analytical tool for exploring quantitatively a broad range of biologically important phenomena ranging from life-history features to global plant productivity (Reich et al. 1997).

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