"Diminishing returns" in the scaling of functional leaf traits across and within species groups


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More than 5,000 measurements from 1,943 plant species were used to explore the scaling relationships among the foliar surface area and the dry, water, and nitrogen/phosphorus mass of mature individual leaves. Although they differed statistically, the exponents for the relationships among these variables were numerically similar among six species groups (ferns, graminoids, forbs, shrubs, trees, and vines) and within 19 individual species. In general, least one among the many scaling exponents was <1.0, such that increases in one or more features influencing foliar function (e.g., surface area or living leaf mass) failed to keep pace with increases in mature leaf size. Thus, a general set of scaling relationships exists that negatively affects increases in leaf size. We argue that this set reflects a fundamental property of all plants and helps to explain why annual growth fails to keep pace with increases in total body mass across species.

A. S. , B. S. , and I. J. W. contributed new reagents/analytic tools; and K. J. N. wrote the paper.

Author contributions: K. J. N. designed research; E. D. C. and U. N. performed research; P. B. R., A. S., B. S., and I. J. W. contributed new reagents/analytic tools; and K. J. N. wrote the paper.

The authors declare no conflict of interest.

Edited by James H. Brown, University of New Mexico, Albuquerque, NM, and approved April 13, 2007 (received for review February 8, 2007)

Size variations in foliar functional traits have received intense recent attention, because leaves are the principal photosynthetically active organs of the majority of plant species, because the manner in which foliar traits change within or across species as a function of differences in leaf size can profoundly affect plant growth, reproduction, and ecosystem function, and because standing leaf mass is a critical component in empirical and theoretical plant allometry models (1–14). Surprisingly, however, our knowledge about some very basic size-dependent (scaling) relationships is very incomplete, particularly in terms of how intra- and interspecific differences in mature leaf dry mass (MD) correlate with foliar water mass (MW), surface area (SA), and the nitrogen or phosphorus mass per leaf lamina (Nt and Pt, respectively), either within individual species or across taxonomically different species groups sharing the same life forms (and thus presumably similar foliar architectures and other functional traits).

The importance of quantifying size-dependent variations among functional traits is evident from the general scaling relationship X = β MDα, where X represents one among many functional traits influencing the physiological or mechanical functions of leaves (e.g., SA or MW) and where β and α are, respectively, the elevation and slope of the log-transformed X vs. MD regression curve. Noting that the change in X with respect to differences in mature leaf MD (i.e., ∂X/∂MD) equals β MDα−1, the magnitude of X will be independent of intra- or interspecific differences in MD when α = 1.0; it will increase disproportionately with increasing MD when α > 1.0; and it will fail to keep pace with intra- or interspecific increases in MD when α < 1.0. Among these three possibilities, the first and second do not a priori result in negative consequences as mature leaf mass increases intra- or interspecifically. The first is size-independent and results in a “break even” relationship, whereas the second yields “increasing returns.” In contrast, a relationship governed by α < 1.0 can have negative consequences, because increasing foliar MD investments yield “diminishing returns” in terms of gains in surface area.

Such negative consequences do not intrinsically limit maximum leaf size, provided that compensatory, functionally adaptive changes cooccur in other foliar traits. Nevertheless, some scaling relationships may be physically unavoidable. For example, the “materials” that serve as the principal stiffening agents in leaf laminae increase foliar MD without contributing directly or substantially to metabolism (e.g., cellulose, lignin, vascular fibers, and sclerenchyma). This phenomenology is demonstrated by the parameter called specific leaf area (SLA) (i.e., SA/MD) (15, 16). Because MD equals the product of SA, leaf thickness t, and bulk leaf-tissue density ρ, it follows that SLA = SA/MD = 1/(ρt). It also follows that 1/(ρt) will be constant (κ) for leaves differing in mature leaf size if the scaling exponent for SA vs. MD equals 1.0, whereas 1/(ρt) will decrease with increasing MD when α < 1.0, indicating a size-dependent increase in leaf-tissue bulk density or thickness or both.

This kind of limitation can operate at different levels, e.g., across leaves differing in mature size drawn from different individuals of the same species, or from individuals of diverse species sharing the same life-forms but differing in mature leaf size. In this paper, we demonstrate the existence of “diminishing returns” in both the intra- and interspecific comparisons. Using a recently compiled database composed of >5,000 paired measurements for 1,943 species, drawn from the published and unpublished studies (refs. 17–44 and D. Ackerly, H. Cornelissen, E. Garner, P. Groom, B. Lamont, M.-L. Navas, J. Overton, H. Poorter, C. Roumet, R. Villar, and C. Vriesendrop, unpublished work), we show that at least one of the exponents governing the relationships among SA, MW, Nt, Pt, and MD is statistically less than unity for the majority of 19 individual species, within each of six different functional species groups (ferns, vines, graminoids, forbs, shrubs, and trees), and across all 1,943 species in our data set.

The four foliar traits used to gauge foliar functions (i.e., SA, MW, Nt, and Pt) were selected as indirect measures of photosynthetic and general metabolic capacity, because direct measurements of physiological rates on the majority of the species used in our analyses have not been reported (and are dependent on local ambient conditions that undoubtedly vary among habitats). Nevertheless, prior studies show that lamina surface area is a good measure of the ability to intercept light and that foliar water, nitrogen, and phosphorus mass per leaf lamina are strongly correlated with metabolic capacity (1, 4, 5, 14). Using the scaling relationships among these surrogate measures of
Foliar functions, we show that scaling exponents are, on average, numerically $<1.0$, and we argue that this likely reduces the advantages gained by intra- and interspecific increases in leaf size. This general “constraint” at the level of light-harvesting, which may reflect the ancestral (metabolic, anatomical, and morphological) traits shared by diverse nonvascular plants and all tracheophytes (45), helps to explain why total annual growth fails to keep pace with increases in body mass across plant species.

Results

Leaf $M_D$ and SA. All pairwise comparisons indicated significant differences in $M_D$ and SA among the six species groups (Fig. 1A and B). Ferns, graminoids, and shrubs had the smallest leaves among the six groups (either in terms of $M_D$ or SA); vine and tree species had the largest leaves. Across species and within each species group except trees, SA and $M_D$ were highly correlated ($0.810 < r^2 < 0.945$; Fig. 2A), with SA generally scaling less than $M_D$ across species. This general “constraint” at the level of light-harvesting, which may reflect the ancestral (metabolic, anatomical, and morphological) traits shared by diverse nonvascular plants and all tracheophytes (45), helps to explain why total annual growth fails to keep pace with increases in body mass across plant species.

![Fig. 1. Comparisons of leaf $M_D$, SA, $M_D$ vs. SA regression slopes, and elevations (and log β, respectively; see Table I), and $N_L$ and $P_L$, among fern (F), graminoid (G), forb (F), shrub (S), tree (T), and vine (V) species groups. (A) Mean (± SE) $M_D$. (B) Mean (± SE) SA. (C) Regression slopes (and 95% C.I.s) for $M_D$ vs. SA. (D) Antilogs of log β (and 95% C.I.s) for $M_D$ vs. SA. (E) Mean (± SE) $N_L$. (F) Mean (± SE) $P_L$.](#)

![Fig. 2. Log–log bivariate relationship for SA vs. $M_D$ and changes in SA with respect to increasing $M_D$ (i.e., $SA/M_D$). Original units: SA = cm$^2$; $M_D$ = g per leaf lamina. (A) Across all species (regression curve in bold) and within 19 individual species (regression curves in hairlines). (B) Regression curves for fern (f), graminoid (g), forb (f), shrub (s), tree (t), and vine (v) species groups. Lines in A and B are standardized major axis regression curves. (C) $SA/M_D$ vs. $M_D$.](#)

Living and Structural Mass Components. The living, metabolically active mass component of mature leaves was estimated on the basis of foliar water mass $M_W$ (i.e., $M_W = M_D - M_D$). Data for fresh foliar mass ($M_F$) and thus $M_W$ were unavailable for the majority of fern, graminoid, and vine species. However, the data for forb, shrub, and tree species show that $M_W$ scales with respect to $M_D$ differently among the three groups but that $α < 1.0$ for each group. This finding indicates that increases in $M_W$ fail to keep pace with increasing $M_D$ (Table 1 and Fig. 3A). Within each of the three groups, $M_W$ scaled either nearly isometrically (in the case of forbs) or increased disproportionately with increasing SA (Table 1 and Fig. 3C). By inference, these trends collectively imply that increases in the foliar metabolically active mass component fail to keep pace with increasing leaf $M_D$ (but can increase with increasing surface area) across species.

[N/P Stoichiometry. All pairwise comparisons indicated that the species groups differed in their mean $N_L$ or $P_L$ (Fig. 1E and F). However, $P_L$ and $N_L$ were highly correlated across species ($r^2 = 0.903, n = 350$) (Fig. 4A), for which $P_L$ increases disproportionately with increasing $N_L$ (i.e., $α = 1.05, r^2 = 0.940, P < 0.0001$).](#)
Statistically significant differences in the scaling of $N_L$ (or $P_L$) with respect to $M_D$ were observed among groups (Table 2 and Fig. 4 B and C), e.g., the $\alpha$ values for $N_L$ vs. $M_D$ do not differ statistically among graminoids, shrubs, trees, or vines, but the elevations of the $N_L$ vs. $M_D$ regression curves for these groups differ statistically (Table 2).

$P_L$ and $N_L$ were, on average, more tightly correlated with SA than with $M_D$ (Table 2 and Fig. 5 A and B). Significant differences in the scaling of either $P_L$ (or $N_L$) with respect to SA were observed among the species groups because of differences in $\alpha$ (or, if not $\alpha$, then $\log \beta$). For example, the $N_L$ vs. SA relationships for forbs and shrubs shared the same scaling exponents but differed statistically in their elevations (Table 2). Shrubs and vines shared statistically indistinguishable $P_L$ vs. SA regression curve parameters (Table 2). However, inspection of $\partial P_L/\partial$ SA vs. SA log–log plots for these two groups shows that $P_L$ increases more rapidly for vines than shrubs with increasing SA (Fig. 5 C). Finally, although the data were insufficient to examine the scaling relationships for foliar nitrogen and phosphorus vs. lamina $M_D$ for individual species or most species groups, $N_L$ and $P_L$ scaled as the 0.952 and 1.00 power of $M_D$, respectively, across 144 tree species ($r^2 = 0.942$ and 0.880, respectively) and the 95% confidence intervals (C.I.s) of both exponents include values $<1.00$.

### Table 1. Standardized major axis regression slopes and elevations ($\alpha$ and $\log \beta$, respectively) for log–log linear relationships among $M_D$, $M_W$, and SA for different species groups

<table>
<thead>
<tr>
<th>Species group</th>
<th>$\alpha$</th>
<th>95% C.I.s</th>
<th>$\log \beta$</th>
<th>95% C.I.s</th>
<th>$r^2$</th>
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<tbody>
<tr>
<td>Log SA vs. $\log M_D$</td>
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<tr>
<td>Forbs (n = 120)</td>
<td>0.868</td>
<td>0.833, 0.903</td>
<td>0.293</td>
<td>0.218, 0.369</td>
<td>0.822</td>
</tr>
<tr>
<td>Shrubs (n = 217)</td>
<td>0.965</td>
<td>0.926, 1.00</td>
<td>0.398</td>
<td>0.368, 0.427</td>
<td>0.821</td>
</tr>
<tr>
<td>Trees (n = 329)</td>
<td>0.869</td>
<td>0.851, 0.886</td>
<td>0.114</td>
<td>0.090, 0.134</td>
<td>0.919</td>
</tr>
<tr>
<td>All species (n = 666)</td>
<td>0.982</td>
<td>0.964, 1.00</td>
<td>0.299</td>
<td>0.277, 0.320</td>
<td>0.905</td>
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<tr>
<td>Log $M_W$ vs. $\log M_D$</td>
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</tr>
<tr>
<td>Forbs (n = 120)</td>
<td>0.997</td>
<td>0.986, 1.01</td>
<td>-1.47</td>
<td>-1.48, -1.45</td>
<td>0.981</td>
</tr>
<tr>
<td>Shrubs (n = 217)</td>
<td>1.22</td>
<td>1.19, 1.26</td>
<td>-2.30</td>
<td>-2.41, -2.19</td>
<td>0.892</td>
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<tr>
<td>Trees (n = 329)</td>
<td>1.06</td>
<td>1.04, 1.08</td>
<td>-1.60</td>
<td>-1.63, -1.57</td>
<td>0.780</td>
</tr>
<tr>
<td>All species (n = 666)</td>
<td>1.05</td>
<td>1.04, 1.07</td>
<td>-1.92</td>
<td>-1.95, -1.89</td>
<td>0.932</td>
</tr>
</tbody>
</table>

Original units: SA $= \text{cm}^2; M = \text{g}$. 

![Fig. 3](image-url) Log–log bivariate relationships among $M_D$, $M_W$, and SA for forb (F), shrub (S), and tree (T) species groups. Original units: SA $= \text{cm}^2; M = \text{g}$ per leaf lamina. Lines are standardized major axis regression curves. See Table 1 for regression statistics.

![Fig. 4](image-url) Log–log bivariate relationships among $N_L$ and $P_L$ and leaf $M_D$ for graminoid (G), forb (F), shrub (S), tree (T), and vine (V) species groups. Original units: SA $= \text{cm}^2; M = \text{g}; N_L$, and $P_L = \text{g}$ per leaf lamina. Lines are standardized major axis regression curves. See Table 2 for regression statistics.
Discussion

Our analyses show that different species and different species groups have foliar allometries that theoretically have functionally negative consequences (gauged indirectly by their affects on tissue nutrient content or the potential to capture light) as mature leaf MD increases. We have shown that at least one among the many scaling relationships for the functional traits known to influence the capacity of leaves to intercept sunlight and mechanically support laminae has a scaling exponent less than unity. This finding agrees with a concurrent study showing among the many scaling relationships for the functional traits (or both) increase as mature leaf

changes in SA fail to keep pace with increasing MD. Thus, increases in leaf water content that, in turn, fails to keep pace with increases in leaf MD. It is not unreasonable to assume, therefore, that the living mass component of leaves (as gauged by either \( N_L \) or \( M_W \), or both) disproportionately decreases as \( M_D \) increases across these species.

The diminishing returns resulting from scaling relationships such as these might be circumvented by increasing leaf longevity. However, prior studies indicate that the fraction of total \( N_L \) invested in cell wall construction likely disproportionately increases with leaf longevity, resulting in a decline in metabolically active leaf nitrogen content (see ref. 45). Also, our data indicate that no simple “rule” governs the relationship between leaf longevity and the numerical values for the scaling exponent governing SA vs., \( M_D \). For example, two “evergreen” species in our data set (\( Picea abies \) and \( Pinus sylvestris \)) have numerically and statistically very different SA vs. \( M_D \) scaling exponents (i.e., 0.608 and 0.951, respectively), whereas a deciduous dicot species (\( Tilia cordata \)) has the numerically lowest scaling exponent among the remaining 17 deciduous species (i.e., 0.468).

We freely acknowledge that the numerical values of scaling exponents are notoriously dependent on the taxonomic or life form composition of any data set. This concern is undoubtedly true for the scaling exponents reported here, because shrub and tree species comprise >60% of the database used in our study. A related concern emerges when comparing intraspecific with interspecific scaling exponents. The allometry determined for leaves differing in size drawn from a single individual plant undoubtedly reflects the phenotypic plasticity of that individual and the particular ambient environmental conditions attending growth and development, whereas the allometry determined for leaves differing in size drawn from numerous conspecifics (which describes the kind of data used in our study) reflects a much broader range of environmental conditions, genotypes, and phenotypic reaction norms.

A conservative interpretation of intra- and interspecific trends is therefore warranted. However, because the allometry observed for the majority of individual species is consistent with that observed for each of six very different functional species

Table 2. Standardized major axis regression slopes and elevations (\( \alpha \) and \( \log \beta \), respectively) for log–log linear relations among \( N_L \), \( P_L \), \( M_D \), and SA across different species-groups

<table>
<thead>
<tr>
<th>Species group</th>
<th>( \alpha )</th>
<th>95% C.I.s</th>
<th>( \log \beta )</th>
<th>95% C.I.s</th>
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<tr>
<td>( \log N_L ) vs. ( \log M_D )</td>
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<tr>
<td>Graminoids (( n = 42 ))</td>
<td>0.980</td>
<td>0.949, 1.01</td>
<td>–1.96</td>
<td>–2.02, –1.89</td>
<td>0.981</td>
</tr>
<tr>
<td>Forbs (( n = 141 ))</td>
<td>1.03</td>
<td>1.00, 1.06</td>
<td>–1.22</td>
<td>–1.28, –1.16</td>
<td>0.957</td>
</tr>
<tr>
<td>Shrubs (( n = 312 ))</td>
<td>0.979</td>
<td>0.945, 1.01</td>
<td>–1.43</td>
<td>–1.51, –1.36</td>
<td>0.838</td>
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<tr>
<td>Trees (( n = 414 ))</td>
<td>0.998</td>
<td>0.978, 1.02</td>
<td>–1.45</td>
<td>–1.48, –1.42</td>
<td>0.917</td>
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<tr>
<td>Vines (( n = 10 ))</td>
<td>0.897</td>
<td>0.783, 1.01</td>
<td>–5.12</td>
<td>–4.16, –1.66</td>
<td>0.856</td>
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<tr>
<td>All species (( n = 919 ))</td>
<td>1.02</td>
<td>1.00, 1.04</td>
<td>–1.27</td>
<td>–1.30, –1.23</td>
<td>0.881</td>
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<tr>
<td>( \log P_L ) vs. ( \log M_D )</td>
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<tr>
<td>Shrubs (( n = 209 ))</td>
<td>1.08</td>
<td>1.01, 1.14</td>
<td>–3.14</td>
<td>–3.25, –3.04</td>
<td>0.690</td>
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<tr>
<td>Trees (( n = 137 ))</td>
<td>0.950</td>
<td>0.905, 0.996</td>
<td>–2.84</td>
<td>–2.90, –2.79</td>
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<tr>
<td>Vines (( n = 6 ))</td>
<td>0.871</td>
<td>0.769, 0.973</td>
<td>–2.87</td>
<td>–3.01, –2.73</td>
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<tr>
<td>All species (( n = 352 ))</td>
<td>1.17</td>
<td>1.12, 1.22</td>
<td>–2.84</td>
<td>–2.91, –2.77</td>
<td>0.743</td>
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<td>( \log N_L ) vs. ( \log SA )</td>
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<td>Graminoids (( n = 42 ))</td>
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<td>–4.03</td>
<td>–4.08, –3.98</td>
<td>0.951</td>
</tr>
<tr>
<td>Forbs (( n = 141 ))</td>
<td>0.947</td>
<td>0.900, 0.994</td>
<td>–3.49</td>
<td>–3.54, –3.44</td>
<td>0.888</td>
</tr>
<tr>
<td>Shrubs (( n = 312 ))</td>
<td>1.01</td>
<td>0.990, 1.04</td>
<td>–3.29</td>
<td>–3.31, –3.26</td>
<td>0.920</td>
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<tr>
<td>Trees (( n = 414 ))</td>
<td>0.914</td>
<td>0.836, 0.932</td>
<td>–3.38, –3.33</td>
<td>–3.36</td>
<td>0.927</td>
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<td>Vines (( n = 10 ))</td>
<td>0.953</td>
<td>0.793, 1.11</td>
<td>–3.52</td>
<td>–3.74, –3.31</td>
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<td>All species (( n = 919 ))</td>
<td>0.988</td>
<td>0.973, 1.00</td>
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<td>–1.95, –1.89</td>
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<tr>
<td>( \log P_L ) vs. ( \log SA )</td>
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</tr>
<tr>
<td>Shrubs (( n = 209 ))</td>
<td>1.06</td>
<td>1.02, 1.10</td>
<td>–5.06</td>
<td>–5.10, –5.01</td>
<td>0.876</td>
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<tr>
<td>Trees (( n = 137 ))</td>
<td>0.908</td>
<td>0.874, 0.943</td>
<td>–4.83</td>
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<tr>
<td>Vines (( n = 6 ))</td>
<td>1.15</td>
<td>1.07, 1.24</td>
<td>–5.12</td>
<td>–5.28, –4.97</td>
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<tr>
<td>All species (( n = 352 ))</td>
<td>1.02</td>
<td>0.996, 1.05</td>
<td>–5.02</td>
<td>–5.06, –4.98</td>
<td>0.923</td>
</tr>
</tbody>
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Original units: \( N_L \), \( P_L \), and \( M_D \) = g; SA = cm\(^2\).
groups, it is reasonable to suggest that a general (albeit noncanonical) phenomenon exists that constrains increases in the mature leaf size at both the level of individual species and the level of functional species groups. This phenomenon undoubtedly operates in different ways for different taxa or species groups as indicated by the statistically significant differences among the numerical values observed for the allometric constants (regression curve elevations) and the extent to which the scaling exponents for different relationships deviate from unity. For example, forbs have an SA vs. SA scaling relationship with an exceptionally large β value (i.e., log β = 2.22) linked to a nearly isometric scaling exponent (i.e., α = 0.989). Changes in SA therefore are largely different from increases in MD across these species (i.e., SA/MD ≈ 1). However, our analyses also indicate that increases in the leaf water content of forbs fail to keep pace with increasing foliar MD. Thus, by inference, the metabolically active mass component in leaves fails to increase at the same rate as the MD component (see Table 1).

This general phenomenon of “diminishing returns” in one or more scaling relationships may reflect the results of an evolutionary tradeoff among the many ancestral metabolic, morphological, and anatomical traits shared by all vascular plants and many nonvascular taxa (45). If true, this may help to explain why annual growth rate G scales as the 3/4 power of total body size $M_T$ (51) and why G scales isometrically with respect to total dry leaf mass $M_L$ across otherwise very different plant species, i.e., $G \propto M_L^{3/4}$ (7, 8, 14, 50). Noting that $M_L$ equals the number of leaves per plant $n$ times $M_D$, it follows that $M_T \propto \alpha^{3/4} \propto n^{3/4}$. Where α is the scaling exponent for SA vs. $M_D$. Thus, when $\alpha \approx 1.0$, $M_T$ increases at a faster pace than total leaf surface area because the capacity to harvest sunlight and grow annually, on average, declines as $M_T$ increases. We propose that this “diminishing returns” results from the accumulation of metabolically “inert” mass components, which increase body size, and that this phenomenon is a fundamental attribute of all photoautotrophs.

Materials and Methods

Data Sets. The data used in this study comes predominately from the GLOPNET database but includes published and unpublished data sets contributed by the authors and their colleagues (refs. 17–44 and D. Ackerly, H. Cornelissen, E. Garnier, P. Groom, B. Lamont, M.-L. Navas, J. Overton, H. Poorter, C. Roumet, R. Villar, and C. Vriesendrop, unpublished work). The paired measurements from GLOPNET used in our analyses span 127 families and 1,190 species. These data, which are for a species subset for which leaf size and surface area measurements were available, are not included in the online version of GLOPNET. Approximately 600 species entries include data for $M_D$, SA, and $M_T$. The data provided by colleagues add $>100$ families and $>750$ additional species, yielding a collective data set representative of all vegetated continents, a wide range of vegetation types (arctic tundra to tropical rainforest), and a spectrum of abiotic conditions (see ref. 5).

More than 5,000 measurements of the six variables of interest were available for a total of 1,943 species, including 307 species for which data for all six variables were available. A complete list of these species is available upon request. Most genera are represented by one species; some by as many as 42 species (i.e., Hakea). The combination SA and $M_D$ had the largest paired measurements (3,356); the combination $P_L$ and $M_D$ had the fewest paired measurements (352). Each datum is a mean for the variable of interest per leaf (or leaflet, for species with compound leaves); the maximum number of observations (leaves) per species to produce mean values is 50. In addition, data from conspecifics of 19 individual species were available to study intraspecific scaling relationships (raw data are available upon request), including those of three gymnosperms (Ginkgo biloba, Picea abies, and Pinus sylvestris). The variables $M_D$, $M_W$, SA, $N_L$, and $P_L$ were measured, in the majority of cases, using standard techniques under laboratory conditions; these techniques are detailed in the primary literature (e.g., for $N_L$ and $P_L$, analyses, see ref. 14).

Species were sorted into one of the six functional groups on the basis of the life-form classifications provided by colleagues, with the exception of 17 epiphytic or parasitic taxa, which were used in “all species” analyses (or, in the case of epiphytic ferns, in the fern species group). Among the six groups, vines were represented by 6 species; shrubs and trees were represented by 650 and 619 species, respectively (of which $\approx$50% are “evergreen”). No species group is monophyletic, e.g., “ferns” include microphyllous lycopod and megaphyllous lept- and euphorangiate ferns.

Statistical Protocols. Standardized major axis (SMA) (also known as reduced major axis) slopes and intercepts ($\alpha$ and log $\beta$, respectively) were calculated before and after sorting species into six functional species groups. Preliminary regression analyses showed that all bivariate relationships were log–log linear; all subsequent statistical analyses used log$_{10}$-transformed data. These parameters and their respective 95% C.I.s were computed using the software package Standardized Major Axis Tests and Routines (SMATR), version 2 (statistical routines described by ref. 52).

SMATR was also used to determine whether a common slope fit the data for all species; the significance test for slope heterogeneity was $P > 0.05$. If $P > 0.05$, a common slope was used in subsequent analyses. Because permutation tests are used to calculate $P$ values, the mean $P$ value for several reruns is reported for cases in which the initial analysis indicated $P = 0.05$. As in standard analyses of covariance (ANCOVA), when slope homogeneity was observed, differences in log $\beta$ were tested for. SMATR analyses were checked using closed-form 95% C.I. formulas (53). In all cases, comparisons of $\alpha$ and log $\beta$ 95% C.I.s

![Fig. 5. Log–log bivariate relationships for foliar $N_L$ and $P_L$, SA, and changes in $P_L$ with respect to increasing SA (i.e., $P_L$ vs. SA). Original units: SA = cm$^2$; $N_L$ and $P_L$ per leaf lamina. (A) Across all species. (B) Within graminoid (G), forb (F), shrub (S), and tree (T) species groups. Lines in A and B are standardized major axis regression curves. (C) $P_L$ vs. SA.](image-url)
to determine slope or elevation differences agreed with the results of SMATR.

We thank all of our colleagues, particularly David Ackerly, Hans Cornelissen, Eric Garnier, Phil Groom, Byron Lamont, Marie-Laure