''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, at 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.

foliar traits | plant allometry | scaling relations

Size variations in foliar functional traits have received intense recent attention, because leaves are the principal photosynthetic 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 (M_D) correlate with foliar water mass (M_W), surface area (SA), and the nitrogen or phosphorus mass per leaf lamina (N_L and P_L, 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 $X = \beta M_D^{\alpha}$, where X represents one among many functional traits influencing the physiological or mechanical functions of leaves (e.g., SA or M_W) and where β and α are, respectively, the elevation and slope of the log-transformed X vs. M_D regression curve. Noting that the change in X with respect to differences in mature leaf M_D (i.e., $\partial X/\partial M_D$) equals $\alpha \beta M_D^{\alpha-1}$, the magnitude of X will be independent of intra- or interspecific differences in M_D when $\alpha = 1.0$; it will increase disproportionately with increasing M_D when $\alpha > 1.0$; and it will fail to keep pace with intra- or interspecific increases in M_D when $\alpha < 1$. 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 $\alpha < 1.0$ can have negative consequences, because increasing foliar M_D 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 M_D 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/M_D) (15, 16). Because M_D equals the product of SA, leaf thickness t, and bulk leaf-tissue density ρ, it follows that $SLA = SA/M_D = 1/(\rho t)$. It also follows that $1/(\rho t)$ will be constant (κ) for leaves differing in mature leaf size if the scaling exponent for SA vs. M_D equals 1.0, whereas $1/(\rho t)$ will decrease with increasing M_D when $\alpha < 1.0$, 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. Garnier, 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, M_W, N_L, P_L, and M_D 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, M_W, N_L, and P_L) 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

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Abbreviations: α, slope of SMA curve (''scaling exponent''); C.I., confidence interval; log β, Y intercept of SMA curve (''elevation''); M_D, dry mass; M_W, foliar water mass; N_L, nitrogen mass; P_L, phosphorus mass; SA, lamina surface area; SLA, specific leaf area.

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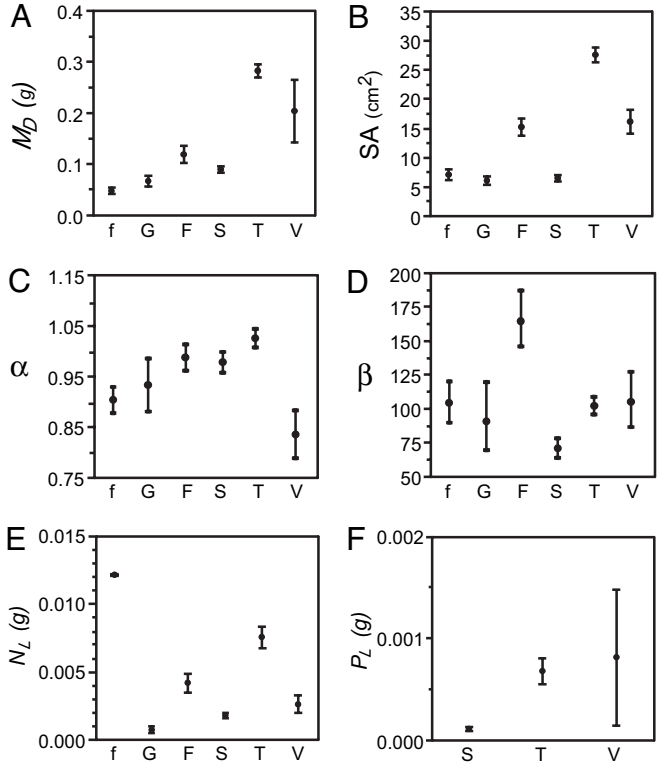

Fig. 1. Comparisons of leaf M_D, SA, M_D vs. SA regression slopes, and elevations ($\alpha$and log β, respectively; see Table 1), and N_L and P_L among fern (f), graminoid (G), forb (F), shrub (S), tree (T), and vine (V) species groups. (*A*) Mean (± SE) M_D. (*B*) Mean (± SE) SA. (*C*) Regression slopes (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.

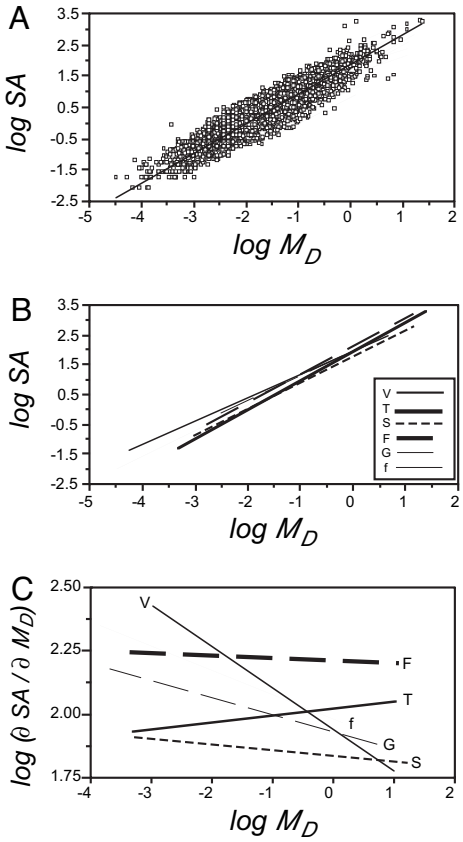

Fig. 2. Log–log bivariate relationship for SA vs. M_D and changes in SA with respect to increasing M_D (∂SA/∂M_D). Original units: SA = cm^2; M = g per leaf lamina. (*A*) Across all species (regression curve in bold) and within 19 individual species (regression curves in hairlines). (*B*) Regression 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.

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. 1 *A* 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 ($0.810 < r^2 \leq 0.945$; Fig. 2*A*), with SA generally scaling less than one to one with increasing M_D. Statistical analyses (see *Materials and Methods*) indicated that all species groups differed in the numerical values of α (or, if not α, then log β) (Table 1 and Fig. 1 *C* and *D*). These group differences were also evident from inspection of log–log plots of SA vs. M_D and ∂SA/∂ M_D vs. M_D, e.g., increases in M_D result in disproportionately smaller gains in SA across ferns, graminoids, and vines compared with forbs or shrubs, whereas increasing M_D results in proportionally larger gains in SA gains across tree species because $\alpha > 1.0$ (Table 1 and Fig. 2 *B* and *C*). Because SLA equals $\beta M_D{}^{\alpha-1}$, it follows that SLA decreases with increasing M_D in all species groups other than trees.

The exponents governing the SA vs. M_D relationship were also, on average, < 1.0 for 19 individual species for which sufficient data were available (Fig. 2*A*), The exponents for individual species ranged between 0.468 for *Tilia cordata* (n = 121 leaves, r^2 = 0.610) and 1.09 for *Populus tremula* (n = 223 leaves, r^2 = 0.566). Only three of the 19 species had $\alpha \geq 1.00$, and each of these had 95% confidence intervals for which $\alpha < 1.00$ (i.e., *Populus tremula*, *Hypericum calycinum*, and *Cercis occidentalis*).

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., $M_W = M_F - M_D$). 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 $\alpha < 1.0$ for each group. This finding indicates that increases in M_W fail to keep pace with increasing M_D (Table 1 and Fig. 3*A*). 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. 3*C*). 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. 1 *E* and *F*). However, P_L and N_L were highly correlated across species (r^2 = 0.903, n = 350) (Fig. 4*A*), for which P_L increases disproportionately with increasing N_L (i.e., α = 1.05, r^2 = 0.940, $P < 0.0001$).

Table 1. Standardized major axis regression slopes and elevations (α and log β, respectively) for log–log linear relationships among M_D, M_W, and SA for different species groups

Species group	α	95% C.I.s	Log β	95% C.I.s	r^2
Log SA vs. log M_D					
Ferns (n = 275)	0.904	0.880, 0.929	2.02	1.96, 2.09	0.945
Graminoids (n = 173)	0.933	0.881, 0.985	1.96	1.85, 2.08	0.810
Forbs (n = 601)	0.989	0.963, 1.02	2.22	2.16, 2.27	0.882
Shrubs (n = 1,066)	0.978	0.958, 0.999	1.85	1.81, 1.89	0.865
Trees (n = 1,038)	1.03	1.01, 1.05	2.02	1.99, 2.04	0.887
Vines (n = 140)	0.836	0.790, 0.883	2.02	1.94, 2.11	0.853
All species (n = 3,356)	0.979	0.968, 0.990	2.01	1.98, 2.03	0.918
Log M_W *vs. log* M_D					
Forbs (n = 120)	0.868	0.833, 0.903	0.293	0.218, 0.369	0.822
Shrubs (n = 217)	0.965	0.926, 1.00	0.398	0.368, 0.427	0.821
Trees (n = 329)	0.869	0.851, 0.886	0.114	0.090, 0.134	0.919
All species (n = 666)	0.982	0.964, 1.00	0.299	0.277, 0.320	0.905
Log M_W *vs. log SA*					
Forbs (n = 120)	0.997	0.986, 1.01	−1.47	−1.48, −1.45	0.981
Shrubs (n = 217)	1.22	1.19, 1.26	−2.30	−2.41, −2.19	0.893
Trees (n = 329)	1.06	1.04, 1.08	−1.60	−1.63, −1.57	0.780
All species (n = 666)	1.05	1.04, 1.07	−1.92	−1.95, −1.89	0.932

Original units: SA = cm^2; M = g.

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 α 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 α (or, if not α, then log β). 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_W for individual species or most species groups, N_L and P_L scaled as the 0.952 and 1.00 power of M_W, 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.

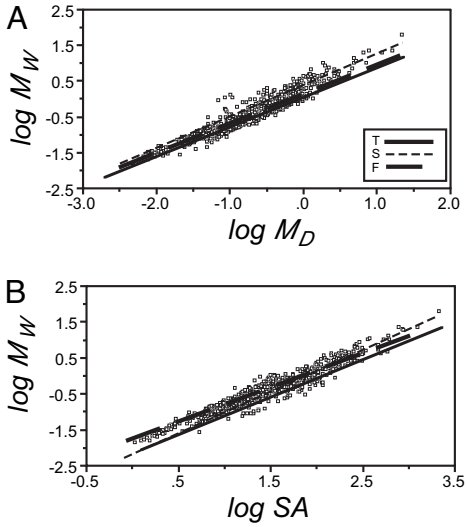

Fig. 3. Log–log bivariate relationships among M_D, M_W, and SA for forb (F), shrub (S), and tree (T) species groups. Original units: SA = cm^2; M = g per leaf lamina. Lines are standardized major axis regression curves. See Table 1 for regression statistics.

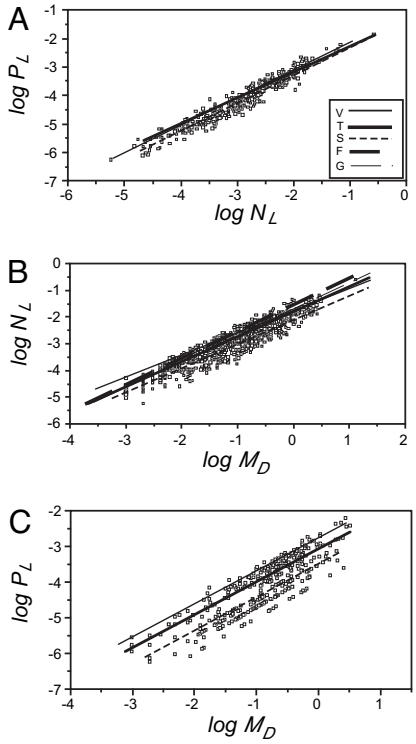

Fig. 4. Log–log bivariate relationships among N_L and P_L and leaf M_D for graminoid (G), forb (F), shrub (S), tree (T), and vine (V) species groups. Original units: SA = cm^2; M, N_L, and P_L = g per leaf lamina. Lines are standardized major axis regression curves. See Table 2 for regression statistics.

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

Species group	α	95% C.I.s	Log β	95% C.I.s	r^2
Log N_L vs. log M_D					
Graminoids (n = 42)	0.980	0.949, 1.01	−1.96	−2.02, −1.89	0.981
Forbs (n = 141)	1.03	1.00, 1.06	−1.22	−1.28, −1.16	0.957
Shrubs (n = 312)	0.979	0.945, 1.01	−1.43	−1.51, −1.36	0.838
Trees (n = 414)	0.998	0.978, 1.02	−1.45	−1.48, −1.42	0.917
Vines (n = 10)	0.897	783, 1.01	−5.12	−1.46, −1.66	0.856
All species (n = 919)	1.02	1.00, 1.04	−1.27	−1.30, −1.23	0.881
Log P_L vs. log M_D					
Shrubs (n = 209)	1.08	1.01, 1.14	−3.14	−3.25, −3.04	0.690
Trees (n = 137)	0.950	0.905, 0.996	−2.84	−2.90, −2.79	0.877
Vines (n = 6)	0.871	0.769, 0.973	−2.87	−3.01, −2.73	0.986
All species (n = 352)	1.17	1.12, 1.22	−2.84	−2.91, −2.77	0.743
Log N_L vs. log SA					
Graminoids (n = 42)	1.14	1.08, 1.19	−4.03	−4.08, −3.98	0.951
Forbs (n = 141)	0.947	0.900, 0.994	−3.49	−3.54, −3.44	0.888
Shrubs (n = 312)	1.01	0.990, 1.04	−3.29	−3.31, −3.26	0.920
Trees (n = 414)	0.914	0.896, 0.932	−3.36	−3.38, −3.33	0.927
Vines (n = 10)	0.953	0.793, 1.11	−3.52	−3.74, −3.31	0.760
All species (n = 919)	0.988	0.973, 1.00	−1.92	−1.95, −1.89	0.923
Log P_L vs. log SA					
Shrubs (n = 209)	1.06	1.02, 1.10	−5.06	−5.10, −5.01	0.876
Trees (n = 137)	0.908	0.874, 0.943	−4.83	−4.90, −4.76	0.925
Vines (n = 6)	1.15	1.07, 1.24	−5.12	−5.28, −4.97	0.990
All species (n = 352)	1.02	0.996, 1.05	−5.02	−5.06, −4.98	0.923

Original units: N_L , P_L , and M_D = g; SA = cm^2.

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 M_D 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 that (*i*) leaf area fails to keep pace with leaf M_D within each of 85 species (R. Milla and P.B.R., unpublished work); (*ii*) specific leaf area SLA varies among individual species and within species groups sharing the same life-form (15, 16); and (*iii*) studies reporting strong correlations among functional foliar morphological, anatomical, and stoichiometric traits (1, 5, 6, 9–51), e.g., a single principal component captures 74% of the total variance in six key foliar traits in the Global Plant Trait Network (GLOPNET) database (5).

Specifically, within all but one species group (i.e., trees) and within most of the 19 individual species for which sufficient data were available, the exponent governing SA vs. M_D is <1.0. Thus, changes in SA fail to keep pace with increasing M_D such that SLA is neither constant for the majority of the species examined nor within five of the six species groups differing in life form, suggesting that either bulk leaf-tissue density or lamina thickness (or both) increase as mature leaf M_D increases. Although M_D allocations for the mechanical support of photosynthetic tissues may come at little cost to plants, our analyses reveal additional constraints on the size of mature leaves. For example, across tree species, although lamina surface area scales isometrically with foliar M_D, leaf N_L scales as the 0.952 power of M_W that in turn scales as the 0.869 power of M_D. Because $\alpha < 1.0$ for both of these scaling relationships, increases in N_L fail to keep pace with increases in leaf water content that, in turn, fails to keep pace with increases in leaf M_D. 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

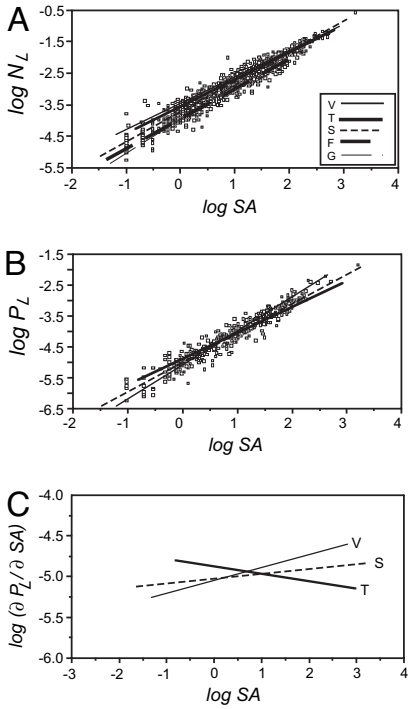

Fig. 5. Log–log bivariate relationships for foliar N_L and P_L, SA, and changes in P_L with respect to increasing SA (i.e., $\partial P_L/\partial$SA). Original units: SA = cm^2; N_L and P_L = g per leaf lamina. (*A*) Across all species. (*B*) Within graminoid (G), forb (F), shrub (S), and tree (T) species groups. Lines in *A* and *B* are standardized major axis regression curves. (*C*) $\partial P_L/\partial$SA vs. SA.

groups, it is reasonable to suggest that a general (albeit noncanonical) phenomenology exists that constrains increases in the mature leaf size at both the level of individual species and the level of functional species groups. This phenomenology 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. M_D 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 indifferent to increases in M_D across these species (i.e., ∂ SA/∂ $M_D \approx \beta$). However, our analyses also indicate that increases in the leaf water content of forbs fail to keep pace with increasing foliar M_D. Thus, by inference, the metabolically active mass component in leaves fails to increase at the same rate as the M_D component (see Table 1).

This general phenomenology 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., $G \propto M_L \propto M_T^{3/4}$ (7, 8, 14, 50). Noting that M_L equals the number of leaves per plant (n) times M_D, it follows that $M_T \propto n^{4/3}\,\mathrm{SA}^{4/3\alpha}$, where α is the scaling exponent for SA vs. M_D. Thus, when $\alpha \leq 1.0$, 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 phenomenology 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_W. 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 ≈50% are "evergreen"). No species group is monophyletic, e.g., "ferns" include microphyllous lycopod and megaphyllous lepto- and eusporangiate ferns.

Statistical Protocols. Standardized major axis (SMA) (also known as reduced major axis) slopes and intercepts (α and log β, 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 $P \approx 0.05$. As in standard analyses of covariance (ANCOVA), when slope homogeneity was observed, differences in log β were tested for. SMATR analyses were checked using closed-form 95% C.I. formulas (53). In all cases, comparisons of α and log β 95% C.I.s

to determine slope or elevation differences agreed with the results of SMATR.

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