

RESEARCH ARTICLE

Simultaneous 3/4-power scaling of leaf mass and 2/3-power scaling of leaf area with stem mass in plants

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Abstract

Background: Plant allometry theory developed in the last century focused on 2/3-power scaling, determined by light interception considerations. More recently, 3/4-power scaling based on the properties of vascular distribution networks has been proposed.

Methods: We assembled 812 observations on plant height, leaf area, leaf mass, stem mass, and total mass for eight species groups and spanning eight orders of magnitude for total mass to empirically explore which scaling theory best defines plant allometry.

Results: The data confirmed that the relationship between leaf mass and stem mass follows 3/4-power scaling. However, leaf area–total (leaf plus stem) mass relationships follow 2/3-power scaling. Previously reported non-1:1 scaling of specific leaf area:stem diameter and associated lower specific leaf area of larger plants emerges as a mechanism whereby 3/4-power scaling of organ mass for resource distribution and 2/3-power scaling of leaf area for light capture are reconciled in one body plan. In our data set, scaling coefficients of leaf area:total mass in smaller plants tend toward 1:1, which is intuitively logical where stems provide only leaf–root connection without leaf support for light capture.

Conclusions: A unified theory of plant allometry would integrate 3/4-power scaling of organ mass for resource distribution, 2/3-power scaling of leaf area for light capture, scaling near 1:1 for small plants, provision for increased allocation to stem mass for mechanical strength in larger trees and provision for variation reflecting ‘tactical’ species-specific body plan configuration.

KEYWORDS

2/3-power scaling, 3/4-power scaling, allometry, light capture, plant body plan

INTRODUCTION

In the late 1990s, West et al. (1997) and Enquist et al. (1998) published a generalized derivation of a resource allocation rule for allometric scaling in biology. Specifically, this work explored the fractal geometry and constraints of vascular systems at different body sizes and derived a “universal” allometric exponent of $-4/3$ for allometry of body mass components in biological systems. Notably, whereas $-4/3$ allometry had previously been recognized in animals, Enquist et al. (1998) extended the concept to plants, providing both a theoretical derivation of the universal $-4/3$ -power allometric exponent and an empirical confirmation using 272 observations of individual plant mean above-ground total mass (M_T) and density (d). In this validation,

the included observations ranged in average mass from 10^{-4} to 10^7 g and were drawn from a range of published studies for different plant species; density was taken as the number of discrete plants per m^2 in a monospecific stand and ranged from $<10^{-2}$ to $>10^6$ m^{-2} . Furthermore, while the empirical validation by Enquist et al. (1998) was confined to examination of data for $M_T:d$, these authors extrapolated that as their $-3/4$ -power universal allometric scaling relationship was derived from a general equation:

$$Y = Y_0 M^b, \quad (1)$$

where Y can represent any one of a range of attributes and b is an allometric exponent, their empirically

confirmed $-4/3$ -power $M_T \cdot d$ relationship (or, equivalently, the related $1/4$ -power scaling of other structural, functional, and ecological attributes) should be also applicable to allocation of mass to specific organs within plants (e.g., allocation between leaf mass and stem mass) and be invariant with plant size across the plant kingdom, thus “promising to provide a general framework for explaining many features of biological diversity.” We will hereafter refer to this $-4/3$ plant scaling theory as the WBE model (Coomes, 2006).

The emergence of the WBE model asserting a general $-4/3$ exponent for plant allometry was something of a watershed in thinking, because up to this point, the exponent reported in plant allometry studies, especially between the 1960s and 1980s, was typically $-3/2$ (Westoby, 1984; Yoda et al., 1963; Zeide, 1987). The work of Yoda et al. (1963) focused on a process termed “self-thinning” whereby density in monospecific plant stands decreases due to the death of smaller plants from shading by larger plants, as mean plant size increases with time. In self-thinning, the coordinates for mean single plant above-ground mass within the stand and survivor plant density were typically observed to follow a $-3/2$ trajectory as plants grew over time. Westoby (1984) further showed that a similar $-3/2$ slope emerged when $\log(\text{size})$ and $\log(\text{density})$ data from stands of different plant species at a particular point in time were aggregated into a multi-species plot of plants spanning a wide size range. Self-thinning at a $-3/2$ slope mathematically defines an increase of stand biomass with time. Based on the fact that stem mass is a trait with cubic dimensions and leaf area has dimensions of size squared (Hardwick, 1987, see below), this can be intuitively understood as the increase in stem mass needed to hold leaves to the light as plants increase in size. In certain circumstances in mature stands, mortality can continue at constant (or declining) herbage mass with $M_T \cdot d$ slope therefore observed at (or less steep than) -1 (Matthew et al., 1995). In clonal plants, self-thinning is usually presumed to occur at the genet level, rather than the whole plant level (see e.g., Davies, 1988). Because:

$$\text{Stand biomass} = M_T \times d, \quad (2)$$

it can be shown mathematically that $-3/2$ self-thinning defines a $-1/2$ -power relationship between $\log(\text{stand biomass})$ and $\log(d)$.

During the 1960–1980 period, empirical confirmation of self-thinning predominated over theoretical understanding, and one commentary (Hutchings, 1983) referred to this $-3/2$ -power relationship as “ecology’s law in search of a theory.” However, both Yoda et al. (1963) and Zeide (1987) presented theoretical derivations for $-3/2$ plant allometry, which identically assumed similarity of plant shape for plants of the same species, irrespective of size and habitat, and self-thinning operating in response to canopy closure or to regulate the plant canopy to provide 100% ground cover, as plants increase in size. Hardwick (1987) provided an alternative theoretical derivation of a $-3/2$ power plant size–density relationship based on plants comprising a metabolically active skin with dimension l^2 and an inactive core with dimension l^3 , where l represents plant size. From the

1990s onward, an increasing number of studies noted systematic lack of fit to a $-3/2$ allometric exponent, and the fundamental usefulness and validity of the self-thinning relationship began to be questioned (Lonsdale, 1990). It has also been noted (Pretzsch & Mette, 2008) that plant shape can change with growth, thus calling into question the theoretical basis for expecting $-3/2$ -power self-thinning as implied by considerations mentioned above.

In parallel with this questioning of the generality of $-3/2$ plant allometry, others explored how light capture considerations might explain deviation from $-3/2$ power self-thinning. Westoby and Howell (1982) documented the biomass–density trajectories for pots containing subterranean clover (*Trifolium subterraneum* L.) seedlings transferred from light to shade or vice versa. They found that shade moved the self-thinning line downward, but that prior history of the plants also affected the path of their biomass–density trajectories. Similarly, Matthew et al. (1995) conceptualized the self-thinning line as a light-determined environmental carrying capacity for leaf area. Any systematic variation in a factor affecting the leaf area index (LAI) of a plant stand along the size–density continuum (such as changing canopy LAI or non-isometry of plant shape) could then be modeled as a slope correction to a presumed underlying $-3/2$ slope. Matthew et al. (1995) therefore calculated slope corrections for decreased LAI caused by increased grazing intensity in shorter grass swards compared to longer swards, and systematic changes in plant shape with sward height. Higher grazing intensity extracts comparatively more energy from the system than lower grazing intensity and, in a manner analogous to lower light levels in the study of Westoby and Howell (1982), results in lower LAI. Hence, tiller size–density compensation across a series of swards continuously grazed or regularly defoliated at different heights was observed by Matthew (1995) to assume a slope steeper than $-3/2$ and near $-5/2$. In this sense, Matthew (1995) saw the self-thinning rule as a particular expression of a more fundamental plant allometry of size, governed by light capture considerations. However, it is evident that the dynamics of self-thinning in plant stands is extremely complex. For example, Stoll et al. (2002) demonstrated that where plasticity of individuals reduces population size–asymmetry during competition for light, density-dependent mortality will be less than in a comparable population with greater size–asymmetry.

This paper arises primarily from an interest of the authors to empirically test the finding of a universal $-4/3$ -power allometric scaling relationship across the entire plant kingdom, governing the mass relationships between plants and plant organs of differing sizes, as specified in the WBE model. We found it disconcerting that the WBE model predicting widespread $-4/3$ -power allometry for both mass–mass and mass–density relationships in plants sits alongside many published studies reporting $-3/2$ -power allometry for size–density relationships, with the discrepancy largely unresolved. In planning how to approach such a test, we considered that plant density data might often reflect stand management history rather than plant response to canopy closure and

so render an inconsistent and unreliable signal of factors governing plant allometry. Instead, we hypothesized that the reverse approach of compiling a data set to explore the allometry of biomass allocation between plant organs, particularly leaves and stems, and of the allometry of leaf area change with plant size, might allow theoretical insight of expectation for variation of allometric exponents in plant stands, by empirically testing the assumptions for internal plant allometry that are held to underpin the theoretical expectation for $-4/3$ or $-3/2$ mass–density relationships, respectively. We therefore pursued the assembly of a data set spanning at least 6 orders of magnitude of plant size and including the traits: plant height, leaf mass, leaf area, stem mass, and total mass, respectively, h (m), M_L (kg), A_L (m²), M_S (kg), and M_T (kg). Intuitive expectations for the allometric exponents of trait pairs from these five traits under different scaling models have been published by Price et al. (2009) and Pretzsch (2019) (Table 1).

Our research question was: will a set of empirical data, representative of plants in general, confirm the internal plant allometric relationships predicted by the WBE scaling model: namely a universal allometric exponent of $-4/3$, invariant with plant size, and relationships for other trait pairs as in the fractal model of Table 1, or will some other reality emerge?

MATERIALS AND METHODS

Data compilation

The bulk of the data set was assembled in 2003 while the first author was a visiting researcher at Technische Universität München (Technical University of Munich, TUM), on study leave from Massey University. Criteria

TABLE 1 Intuitively predicted allometric exponents for plant component traits in classic $-3/2$ -power self-thinning (i.e., the Euclidean model) and under the fractal geometry vascular distribution-constrained scaling model ($-4/3$ -power scaling of plant above ground mass with plant density as proposed by Enquist et al., 1998).

	Height, h	Total mass, M_T	Stem mass, M_S	Leaf mass, M_L
Euclidean model				
A_L	2	2/3	2/3	1
M_L	2	2/3	2/3	
M_S	3	1		
M_T	3			
Fractal model of Enquist et al. (1998)				
A_L	3	3/4	3/4	1
M_L	3	3/4	3/4	
M_S	4	1		
M_T	4			

Note: For a plant of size “ l ,” it can be assumed that h is proportional to l ; A_L and M_L are proportional to l^2 , and M_S and M_T are proportional to l^3 in classic self-thinning. A_L denotes leaf area. Exponents come from Table 2.1 of Pretzsch (2019); entries in bold are also found in Price et al. (2009).

for inclusion were that a datum came from observation of a crowded stand rather than from plants growing in isolation, and that data collection had included measures of the five plant traits discussed above, h , M_L , A_L , M_S , and M_T .

For smaller plants, we drew 228 observations from data collected in the course of several research projects conducted at the Lehrstuhl für Grünlandlehre (Institute of Grassland Science, TUM), comprising sunflower (*Helianthus annuus* L., 98 observations), four forage grass species (82 observations), and alfalfa (*Medicago sativa* L., 48 observations). Because the 88 grass observations are from four species, we use the term “species groups” rather than “species” when exploring what is essentially inter-specific variation in the data set. These 228 data points ranged from a smallest aboveground plant size, M_T , of 57 mg dry weight (DW) to a largest DW of 130 g.

For sunflower, the experiment from which the data were taken used variation in planting density (50 or 400 plants m⁻²) to provide data for less or more crowded plants, respectively, and variation in planting date and plant nutrition to create differences in hierarchical position in the canopy; namely, dominant plants and subordinate plants at either high or low nutrition. Destructive harvests were carried out from 14 to 50 days of age. Data from the isolated plants and from plants less than 3 weeks of age were not included in the data set for determining allometric exponents. Data for alfalfa came from an experiment in which treatments included a factorial combination of high and low light and two N-nutrition levels (Lötscher et al., 2004).

A further 12 observations representing larger crop plants were derived from plants of different cultivars in a New Zealand maize variety field trial.

For trees, 543 observations were collated by staff at the TUM Lehrstuhl für Waldwachstumkunde (Chair of Forest Growth Science). In collating the tree data, observations with one or more measurements determined indirectly from allometric formulae were generally rejected, although in some cases data with one measure determined allometrically were included after first checking that the allometrically determined data lay within a cloud of points for directly measured data. The tree species were Norway spruce (*Picea abies* (L.) H. Karst., 280 observations), European beech (*Fagus sylvatica* L., 145 observations), Scots pine (*Pinus sylvestris* L., 50 observations), and sessile oak (*Quercus petraea* (Mattuschka) Liebl., 68 observations).

The smallest tree DW was 81 mg (a seedling) and the largest weighed 7670 kg (a mature tree). Hence, in total, the data from the TUM Institutes of Grassland Science and Forest Science and from New Zealand provided a base data set of 783 observations (D783) for all five target variables, spanning eight orders of magnitude. Here, we explore the linear coefficients of all 10 pairwise logarithmic relationships (i.e., allometries) between them.

Finally, we also included a group of 29 observations for tropical trees of mixed species (Ketterings et al., 2001), which expanded the data set to 812 observations (D812). These observations lacked A_L data and were used in this study for more detailed investigation of $M_L:M_S$ allometry. The data appear in Table S1a–c;

further information on data sources is provided in Table S2.

Statistical analysis

To proceed, we assumed that the 783 or 812 observations for single plants described above could be taken as “representative” of plants in general when growing under crowded conditions. Our data set comprised a range of species groups, and we also included multiple observations within species groups to allow some discernment of within- and between-species effects. All data were log-transformed (base 10) and “global” allometric exponents for trait pairs across the plant size range were determined as the reduced major axis (RMA) slope (Niklas, 1994) for the 10 trait pair combinations available in D783 (Regression model 1).

Since M_L and M_S data were judged to be more precisely and independently measured than h and A_L data, allometry of $M_L:M_S$ was investigated in more detail using D812, to cover a slightly more diverse plant species range. First, since visual inspection of data suggested differences in allometric trait relationships between large and small plants, a break point was introduced at the visual point of inflexion; the data were divided into separate sets for large and small plants and separate allometric slopes calculated. When dividing a data set in this way, the number of degrees of freedom (DF) is reduced by two compared to the single regression line. These two degrees of freedom were then assigned: 1 DF for the sums of squares accounted for by fitting two parallel lines for large and small plants (i.e., an intercept separation, IS), and 1 DF to the sums of squares accounted for by fitting a line of different slope for small plants (i.e., a slope difference, SD). The calculation of IS and SD sums of squares was achieved by multiple regression with dummy variables for IS and SD (Table S1d). It was noted that the allocation of sums of squares between IS and SD was sensitive to the order in which the terms were fitted to the model, with both terms having a larger sum of squares when fitted first than when fitted second. Hence, for a conservative test of the significance of the slope change at the break point, we fitted IS first and SD second in the multiple regressions. As a check, we used the “AOVO” command of Minitab (a one-way analysis of variance (ANOVA) on two groups) to calculate the sums of squares attributable to the mean separation between large and small plants, to which was added the separate sums of squares for the separate regressions of M_L for large and small plants (or other traits of interest) on M_S . In this way, the increase in the sum of squares explained by fitting two lines instead of one line was the same as the sum of the terms IS and SD in the multiple regression model. The position of the break point for dividing the data into two groups was progressively moved from right to left to find the break point at which multiple regression error sum of squares was minimized. Considering both minimization of the error sum of squares and visual inspection of data plots, a regression break point of $\log(M_S) = -2.0$ (M_S measured in kg) was selected. For comparison, Regression Model 2

was also applied to D783 data for $A_L:M_S$ (break point again $\log(M_S) = -2.0$).

Third, a “design matrix” was introduced and multiple regression performed to fit a common slope but separate intercepts for each of the plant species groups, which is a test for species differences in partitioning of M_T between M_L and M_S (Regression Model 3). When fitting separate intercepts for n different groups, $n - 1$ groups are defined in the design matrix, making the undefined group the reference with intercept zero. We used maize, located near the data centroid, as the reference species.

Fourth, we were interested to know to what extent allometric ratios indicative of plant species differences in ecological strategy could explain lack of fit to the global allometric relationship in the $M_L:M_S$ relationship, as an alternative to fitting separate intercepts for the different species groups. We therefore explored the behavior of three derived parameters calculated from the collected data: (i) specific leaf area (A_L/M_L , $\text{m}^2 \text{kg}^{-1}$, the reciprocal of leaf mass per unit area, one of the intercorrelated traits in the worldwide leaf economic spectrum (LES); Wright et al., 2004); (ii) a measure of allocation of body mass to gaining height, “allometric height” (h_a) ($\log_{10}(h/(M_T)^{0.292})$)—the exponent 0.292 was used here as the mean of Euclidian and fractal expectations, 0.333 and 0.250, respectively; and (iii) a measure of allocation of body mass to gaining leaf area, the area:volume ratio, R [A_L , m^2 / (volume, m^3)^{2/3}] of Matthew et al. (1995). To calculate R , volume in m^3 was taken as M_T (kg)/850 (Matthew et al., 1995). The parameter R with units m^2 per m^2 is dimensionless, which confers mathematical advantages in modeling of this type (Louie et al., 1998). These indices (Table S1e) were then added to the regression model in place of the design matrix specifying unique species intercepts, to gain further ecological insight (Regression model 4). Based on the proportion of the total sums of squares in Regression models 3 and 4 accounted for by fitting intercepts for each species group or ecological indicator, respectively, data variation of data points around the global regression line was assigned to between- or within-species effects in each case.

Finally, a principal component analysis (PCA) was performed on D783 to investigate whether different superimposed allometry patterns within the data set would be revealed. Principal component (PC) scores were subjected to one-way ANOVA to determine if any of the PCs differentiated between plant species, thereby providing information on the ecological strategy of the species or species groups in our data set.

The majority of analyses were carried out using the Minitab® 10.51 statistics package (Minitab Inc, 1995). In all analyses, the five variables were $\log_{10}$ transformed, but not standardized.

RESULTS

“Global” allometric exponent

In our data, M_S was found to scale at near 1:1 with M_T as expected, and $M_L:M_S$ scaled close to 0.75 as predicted by

the WBE model and measured by Enquist and Niklas (2002). However, $A_L:M_S$ scaled at 0.636 and $A_L:M_T$ at 0.670, both fitting the Euclidean rather than the WBE model, and the latter being statistically indistinguishable from 0.66 (Table 2). The $A_L:M_T$ allometry can be subdivided into multiplicative components $A_L:M_L$ and $M_L:M_T$ with an intuitive expectation that $A_L:M_L$ will be 1 and $M_L:M_T$ will match $A_L:M_T$ as either 0.75 in the fractal model or 0.66 in the Euclidean model (Table 1). However, in our data, the $M_L:M_T$ allometric exponent of 0.805 was larger than the Euclidean or fractal model predictions of 0.66 and 0.75, respectively. Similarly, the $A_L:M_L$ allometric exponent of 0.832 was lower than the model prediction of unity. Multiplication of the two exponents yielded the value 0.669, the Euclidean model exponent for $A_L:M_T$. In this way, a general decrease in $A_L:M_L$ from larger to smaller plants provides a mechanism whereby $M_L:M_S$ scales at 0.75 while $A_L:M_T$ simultaneously scales at 0.66. Meanwhile, allometries with h neither fitted the Euclidean nor the fractal model, but were intermediate between them (Table 2). Scatterplots for visualization of the data are provided in Figure S1.

Variation of the allometric exponent with plant size

We noted in our compiled data in many of the biplots (Figure S1) a subtle visual impression of a steeper slope for smaller plants and selected the relationship of $M_L:M_S$ in our D812 data set for further investigation of linearity across the range of plant sizes in the data set. We tested for linearity of the allometric relationship by introducing dummy variables for IS and SD as described above (Table 3; Figure 1). The term SD was significant at $p < 0.001$ (Table 3). The equivalent calculation for the D783 data set is provided in Table S3, and the use of the D783 data set is also provided for linearity testing of allometry of A_L (Table 4).

Consistent with WBE theory, the $M_L:M_S$ allometric exponent was statistically indistinguishable from 0.75 for large plants, but contrary to WBE theory was statistically indistinguishable from 1.0 for plants with $\log(M_S) < -2.0$, while the $A_L:M_S$ allometric exponent for large plants was statistically indistinguishable from 0.66 and $A_L:M_T$ had an allometric exponent intermediate between 0.66 and 0.75, and statistically different from both of them (Table 4). $A_L:M_S$ and $A_L:M_T$ allometric exponents for smaller plants were both close to 0.84, presumably reflecting the implications of the $A_L:M_L$ allometric exponent being less than 1 (Table 1).

Modeling of unique species-group intercepts and ecological indicators

On fitting unique intercepts for the species groups in the $M_L:M_S$ relationships (Regression model 3), the residual sum of squares was greatly reduced, falling from 118.1 to 41.59 (Table 5), and there were highly significant

TABLE 3 Analysis of variance table comparing models fitting a single line for the regression of M_L on M_S or two lines with an intercept separation (IS) and slope difference (SD) for small plants compared to large plants in data set D812.

Source of variation	DF	SS	MS	F	p
Regression of M_L on M_S	1	2997	2997	20 156	***
Error	810	120.4	0.1453		
Total sum of squares	811	3117.3			
Regression of M_L on M_S	1	2997	2997	21 315	***
IS	1	2.5	2.5		
SD	1	4.3	4.3	30.6	***
Error	808	113.6	0.1406		
Total sum of squares	811	3117.3			

Note: Both models have the same total sum of squares, but fitting two lines significantly reduces the error sum of squares. The two-line model was fitted by multiple regression in Minitab, using dummy variables (Table S1d) to represent IS and SD.

*** $p < 0.001$.

TABLE 2 Reduced major axis regression (RMA) slope coefficients (i.e., allometric exponents) with standard errors and confidence intervals in parentheses and r^2 values (%). A_L denotes leaf area.

	Height, h	Total mass, M_T	Stem mass, M_S	Leaf mass, M_L
A_L	2.180 (0.0209) (2.141–2.220) 93.5%	0.670 (0.0040) (0.662–0.678) 97.2%	0.636 (0.0042) (0.627–0.643) 96.7%	0.832 (0.0032) (0.826–0.838) 98.9%
M_L	2.621 (0.0258) (2.570–2.671) 92.4%	0.805 (0.0051) (0.794–0.814) 96.8%	0.764 (0.0054) (0.753–0.774) 96.2%	
M_S	3.431 (0.0180) (3.396–3.466) 97.9%	1.054 (0.0015) (1.051–1.056) 99.9%		
M_T	3.256 (0.0184) (3.220–3.292) 98.7%			

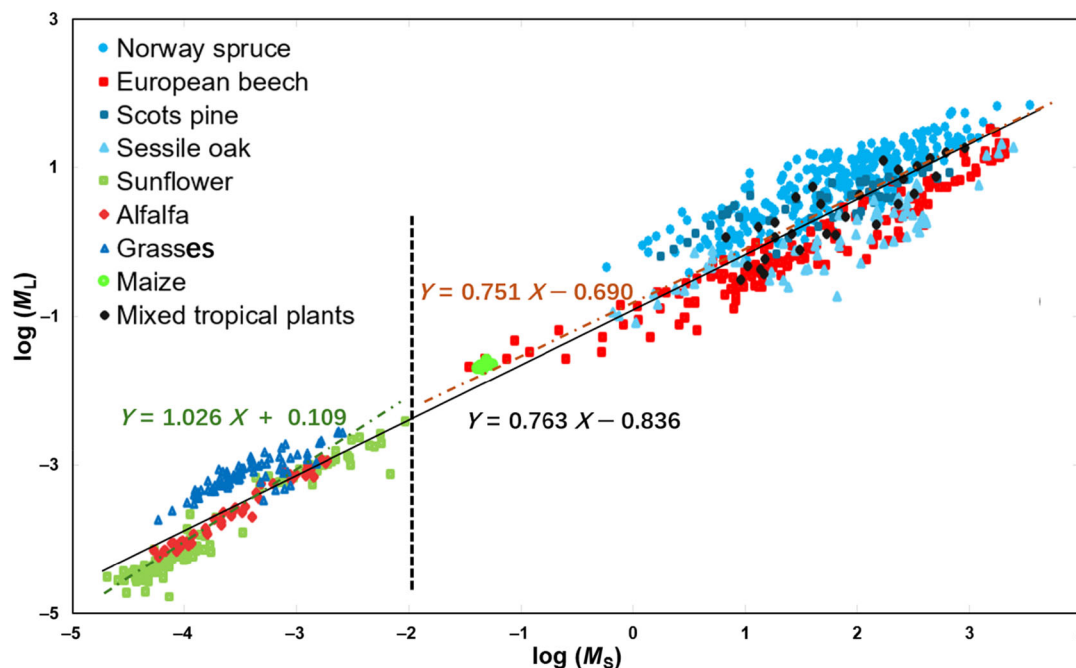


FIGURE 1 Allometric scaling between M_L and M_S in 812 observations on plant shoots ranging in size from grass tillers to mature trees and spanning eight orders of magnitude in M_S measured in kg. Across the whole data set (black equation and unbroken line), and for large plants (red-brown equation and broken line), allometric exponents fitted the 3/4-power scaling model of Enquist et al. (1998). For small plants (dark green equation and broken line), allometry was statistically indistinguishable from 1:1. See text for further explanation. Equations are determined as the reduced major axis slope (Niklas, 1994) through the data centroid.

TABLE 4 Reduced major axis regression slopes and their 95% confidence intervals (CI) when fitting separate regression lines for large and small plants, together with break points and statistical significance (F statistic and p -value) of the reduction in error sum of squares accounted for by sum of squares for slope difference in smaller plants when fitting two lines.

Variables	Slope 1 (95% CI)	Slope 2 (95% CI)	Break point	F (d.f.)	p
D812 $M_L:M_S$	0.751 (0.718–0.777)	1.026 (0.963–1.090) ^a	$M_S = -2.0$	30.6 (1,808)	<0.001
D783 $M_L:M_S$	0.775 (0.741–0.801)	1.026 (0.963–1.090) ^a	$M_S = -2.0$	30.85 (1,779)	<0.001
D783 $A_L:M_S$	0.685 (0.658–0.712)	0.836 (0.788–0.885)	$M_S = -2.0$	17.4 (1,779)	<0.001
D783 $A_L:M_T$	0.707 (0.680–0.734)	0.842 (0.804–0.879)	$M_T = -1.70$	20.7 (1,779)	<0.001

^aThe same small-plant data are common to both data sets.

differences between species group intercepts (as would be expected from visual inspection of Figure 1). The intercepts ranged from +0.44 (s.e. 0.077) for Norway spruce to −0.70 (s.e. 0.076) for sunflower (Tables 6 and S4).

When codes for unique species group intercepts were replaced in the regression analysis with the ecological indicators h_a , A_L/M_L , and R (Regression model 4), the residual sum of squares was even more reduced to 23.71. Across plant species groups, allometric height ranked: Norway spruce, oak > Scots pine, beech > maize > grasses, sunflower, and alfalfa. Conversely, specific leaf area ($m^2 kg^{-1}$) generally decreased with increasing plant size such that the correlation between the two was -0.854 ($p < 0.001$). The dimensionless area:volume ratios of species groups ranged from 309 in maize to 73 in oak (Table 6). For comparison, the dimensionless area:volume ratio of a cube is 6.

Based on the regression ANOVAs, the data scatter around the universal regression line; 63% of data variation was explained by modeling a unique intercept for each species (Table S4) and 79% was explained by including the three ecological indices in the regression (Table S5; 59.5%,

19.6%, and 1.0% for R , A_L/M_L and h_a , respectively). Meanwhile, ANOVA to distinguish between- and within-species variation for these indices showed variation in R and A_L/M_L to be 32% and 72%, respectively, attributable to between-species effects.

PCA

PCA of the D783 dataset yielded a “size” PC (Matthew, 2025) as PC1, explaining 98.4% of data variation and with the four loading coefficients for A_L , h , M_L , and M_S all within the range -0.497 to -0.502 . Despite the extremely small proportion of variation explained, all three of the remaining PCs on ANOVA of their scores displayed highly statistically significant species group effects ($p < 0.001$ in all cases), which can be logically interpreted as elucidating species group body plan or ecological strategy differences. PC2 identified a trade-off between increased h and decreased M_L and A_L with Norway spruce, grasses, and Maize low-scoring and

TABLE 5 Progressive increase in sums of squares explained on introducing additional terms in the regression model to explain variation in leaf mass (M_L) across 783 observations spanning 8 orders of magnitude for plant stem mass (M_S).

Term in model	Regression model			
	1	2	3	4
Sum of squares explained by M_S	2950.7***	2957.6***	2950.7***	2950.7***
Norway spruce			48.56***	
European beech			1.62***	
Scots pine			8.49**	
Sessile oak			0 ^a	
Sunflower			10.83***	
Lucerne			6.84***	
Grasses			n.s.	
$h: M_T^{0.292a}$				9.62***
$A_L: M_L$				24.41***
$\text{Log}_{10}(R)$				60.33***
Residual sum of squares	118.1	111.1	41.59	23.71
F -statistic (model)	19 518	20 742	7042	24 978
Residual mean square	0.150	0.143	0.054	0.0304
Total sum of squares	3068.7	3068.7	3068.7	3068.7
r^2	96.10%	96.38%	98.60%	99.23%

Note: The exponent 0.292 was used here as the mean of Euclidean and fractal geometry exponents, 1/3 and 1/4, respectively (Table 1); use of exponents 0.25 or 0.33 did not substantially change the result.

Model 1: Regression of M_L on M_S to determine the global allometric exponent. Model 2: Separate slopes fitted for large and small plants. Model 3: Separate intercepts fitted for each of seven plant groups. Maize was used as the reference species and therefore does not appear as a term in this model. Model 4: Separate intercepts in Model 3 replaced with the derived allometric indices: allometric height (h_a) ($h: M_T^{0.292}$), specific leaf area (A_L m^2/M_L kg), and shape parameter (R).

** $p < 0.05$.

*** $p < 0.001$; n.s. not significant.

^aAs reported by our statistical software.

beach and oak high-scoring. PC3 identified a trade-off between reduced h and increased M_S and M_T , with maize low-scoring and pine and oak high-scoring. PC4 identified a trade-off between high A_L and low M_L (i.e., species differences in A_L/M_L), with beech, sunflower, alfalfa, and maize high-scoring and pine low-scoring. (Tables 7 and S6).

DISCUSSION

There is now a very large volume of literature on plant allometry. A search by us in the Clarivate Web of Science database on keywords “allometry” and “plant scaling” yielded 1393 items, and a search for publications authored by plant allometry specialist Karl Niklas at Cornell University identified 426 articles. The volume of publications is indicative of the immense variation among plant species and environments they colonize.

TABLE 6 Species group means for Regression Model 3 intercept and for ecological indicators; h_a denotes allometric height; A_L/M_L , specific leaf area, and R is the dimensionless plant shape parameter of Matthew et al. (1995).

Species group	n	Regression 3 intercept	h_a	A_L/M_L ($\text{m}^2 \text{kg}^{-1}$)	R
Norway spruce	280	0.445	4.00	5.1	264
Beech	145	−0.243	4.66	12.9	139
Scots Pine	50	0.247	3.60	3.4	118
Oak	68	−0.266	4.02	6.5	73
Maize	12	0 (Reference)	4.64	19.9	309
Sunflower	98	−0.706	4.02	45.1	148
Alfalfa	48	−0.576	3.67	48.7	200
Grasses	82	n.s.	2.96	24.9	210
SEM ^a		0.069	0.122	1.29	12.8

Abbreviation: SEM, standard error of mean.

^aMean of species SEMs.

Therefore, for succinctness and clarity, it is necessary to focus this discussion on what the data indicate to be the answers to our research questions, and avoid being drawn into a more general review of plant allometry research.

Do the data confirm a universal 3/4 power or equivalent −4/3 power allometric exponent?

The answer to this question that emerged from our data analysis surprised us. The 3/4 power relationship is confirmed for $M_L: M_S$ allometry, while the 2/3 power relationship is confirmed for $A_L: M_S$ allometry. Niklas and Kutschera (2009) find it convenient to refer to plant “body plans” in discussing such considerations. The non-1:1 relationship between A_L and M_L has previously been identified by Niklas and Cobb (2008) and is linked to a systematic decrease in SLA with increase in plant size referred to by these authors as a diminishing returns phenomenon, but here identified as a mechanism which allows these two different allometric exponents to co-exist in different categories of allometry within the same plant body plan. To the authors' knowledge, this finding of simultaneous 3/4-power organ mass scaling and 2/3-power LA scaling is without precedent in the allometric literature to date. Allometric relationships for other trait pairs have been found here for the most part intermediate between −4/3 and −3/2 power allometry. Further investigation is needed to explore if intermediate allometries for other trait pairs facilitate the different allometries of $M_L: M_S$ and $A_L: M_S$ or if they arise from other unrelated factors.

Is the allometric exponent invariant with plant size?

No, in our data set it is not. For smaller plants ($\log M_S < -2.0$), the allometric scaling relationship in our data was

TABLE 7 Principal component analysis (PCA) loading coefficients, eigenvalues, and cumulative proportion of variance explained on PCA for pattern detection among the traits height (h), leaf area (A_L), leaf mass (M_L), and stem mass (M_S) of the D783 plant trait data set.

Trait	Loading coefficients			
	PC1	PC2	PC3	PC4
h	-0.497	-0.691	-0.470	-0.231
A_L	-0.501	0.424	-0.407	0.635
M_L	-0.500	0.524	–	-0.683
M_S	-0.502	-0.260	0.777	0.276
Eigenvalue	3.9378	0.0503	0.0067	0.0052
Cumulative variance explained (%)	98.4	99.7	99.9	100.0
Significance of species group effect	$F_{(7, 775)} = 1157$	$F_{(7, 775)} = 74.6$	$F_{(7, 775)} = 40.3$	$F_{(7, 775)} = 71.8$

statistically indistinguishable from 1:1, and the reduction in regression sum of squares from fitting separate regression lines for plants with $\log M_S < \text{or} > -2.0$ was highly statistically significant. A corresponding indication of allometry differing between smaller and larger plants appears on visual inspection of data in Fig. 2a of Niklas (2004). Hence, it appears our present findings would be supported by reanalysis of other extant data sets, and this slope-change data feature is latent in other data sets but has not been reported because it is unexpected and visually subtle.

It also appears from visual inspection of Figure 1 that there may be a second change in $M_L:M_S$ allometry, with a slope less than 3/4 for larger plants with $\log M_S > 2.0$. Accordingly, we used the same methodology as that used to confirm the change in allometric exponent between small and large plants at 10^{-2} kg M_T in Table 3. Here, we tested for allometric exponent change in $M_L:M_S$ at $M_T > 10^3$ kg. We found in this analysis an allometric exponent adjustment for the larger trees in our data set of -0.499 ($p = 0.043$), indicating approximately 1/4-power scaling of $M_L:M_S$ in large trees. This may well reflect the mechanical need of large trees to have increased stem mass to avoid buckling (McMahon & Kronauer, 1976), and would be an interesting point for future study.

Functional interpretation

The functional significance of 3/4 power allometry of mass of plant parts, such as the $M_L:M_T$ relationship observed in our data, is well explained by Enquist et al. (1998) as a fundamental property of vascular distribution networks. In contrast, the 2/3-power allometry we observed for $A_L:M_S$ is consistent with light capture considerations determined by Euclidean geometry of area:volume relationships governing resource allocation to and formation of leaf area as plants grow. From the considerations theoretically underpinning $-4/3$ or $-3/2$ power allometry outlined in our introduction above, these findings from our data of a simultaneous 0.75-power $M_L:M_T$ allometry and 0.66 $A_L:M_T$ allometry predict a $-3/2$ -power $M_T:d$ allometry as reported in the self-thinning literature, rather than a $-4/3$ -power $M_T:d$ allometry as claimed by Enquist et al. (1998), but

confirm the WBE model prediction of 3/4-power allometry of $M_L:M_S$. This prediction that our data are indicative of $-3/2$ -power $M_T:d$ allometry, of course, needs empirical validation, though the extant self-thinning literature cited here goes a long way toward providing that. Meanwhile, the mechanism whereby these different allometries can occur simultaneously for different plant traits is revealed as a systematic decline in A_L/M_L with increasing plant size, as already noted above.

While Enquist et al. (1998) in developing the theory of 3/4-power allometry and Brown et al. (2005) in subsequent defense focus almost exclusively on the properties of vascular nutrient resource distribution networks as the underpinning theory for plant allometry, the present findings indicate that integration of vascular distribution and light capture considerations is necessary for a full understanding. More recently, it has become apparent that there are numerous potential theoretical derivations for a $-3/2$ self-thinning rule (and by inference for allometries of size), with Mrad et al. (2020) outlining eight different approaches to deriving the relationship, including “dynamical systems theories,” “size distribution arguments,” and “neighborhood interaction arguments” in addition to the more traditional dimensional analysis, or allometric, structural, or biomechanical constraint theories.

The allometric slope change at plant size $< \log M_S = -2.0$ is likely related to the fact that this is about the point in a scale of increasing plant size where woody stem tissue forms that primarily elevates leaves above ground for light capture, as distinct from the primary stem function of providing vascular connection between roots and leaves in smaller plants. Hence, a change in allometry above and below this point is intuitively reasonable, and a 1:1 allometry between leaf mass and mass of “stems,” which do not provide structural support to hold leaves to light, but merely connect leaves to roots for exchange of water, nutrients, and photosynthates, is logical. A search of the literature will undoubtedly reveal many exceptions to this general idea, however. For example, in many small species but also young individuals of trees or trees in harsh environments, supporting tissue may considerably contribute to photosynthesis (Natale et al., 2023).

Re-evaluation of the WBE data

A question that needs to be addressed here is the finding by Enquist et al. (1998) of a $-4/3$ allometry in their $M_T:d$ data. We noted that visual inspection of the data of Enquist et al. (1998) in their Fig. 2 also suggests a change in allometric slope for smaller plants corresponding to that seen in our data: these authors' data points in the mid-range of size tend to fall below the universal trend line while the points at either end tend to fall above it. Finally, their data set contains two outliers with average mass $<10^{-4}$ g which undoubtedly have a disproportionate influence on the slope calculation in regression analysis. Hence, we obtained those data from one of the authors and reanalyzed them using the two-line model reported in Table 4 and omitting the two outlying data just mentioned. In these $M_T:d$ data of Enquist et al. (1998), we found a slope near -1.5 for larger plants and a slope near -1 for smaller plants, with the SD term for larger and smaller plants statistically significant. Thus, in our opinion, the data used by Enquist et al. (1998) for the empirical confirmation of a $-4/3$ -power $M_T:d$ slope better support a split-slope model with $-3/2$ $M_T:d$ allometry for larger plants and -1 allometry for smaller plants. If this is correct, the finding by those authors of a $-4/3$ $M_T:d$ allometry arises fortuitously from fitting a single slope across a two-phase relationship. Moreover, the two-phase relationship is not unexpected since our own analysis of internal $A_L:M_S$ internal plant allometries shows a two-phase relationship predictive of such a pattern in $M_T:d$ allometry.

Additionally, Enquist et al. (1998) used ordinary least squares (OLS) regression (which does not allow for the effect on slope estimate of variability in X , instead of major axis regression, which is more appropriate to their data and always gives a steeper slope than OLS regression (Sackville Hamilton et al., 1995). However, in their case the regression r^2 is high (>0.96), meaning that the major axis slope would have been only about 0.02 units steeper than that presented, so use of OLS regression is not a major issue in their analysis seeking to confirm an allometric exponent of -1.34 rather than -1.50 .

What follows from allometric scaling for plant species ecological strategy?

Our data confirm what many other authors have also asserted—the WBE model is overly simplistic. Müller et al. (2000) eloquently established the concept of “allometric strategy” in the adaptation of plants to differences in nutrient supply. They elucidated three distinct patterns: (a) different exponents for root:shoot allometry with increasing plant size (increased allocation to roots at low nutrient status, seen in one species among 27 studied); (b) parallel trajectories for $\log(\text{root}):\log(\text{leaf})$ biomass with different intercepts (in some species increased, and in other species, decreased allocation to roots early in the development of the plants was seen in five species among 27 species studied), and (c) increased plant size at high nutrient status along a common allometric trajectory for root:shoot allocation (seen in 21 species among

27 species studied). These might be regarded as different mechanisms to achieve alternative body plan configurations and trajectories over time.

In our study, the indices h_a , A_L/M_L , and R seek to identify competitive strategies, respectively, of prioritization of height attainment, formation of greater leaf area from a given leaf mass (which gives no indication of difference in allocation to stem), and formation of leaf area from a given total plant mass (where difference in allocation to stem tissue may be involved). It is interesting to note that the reciprocal of A_L/M_L , leaf mass area (LMA), is a key trait in the worldwide LES where high LMA (i.e., low A_L/M_L) is linked to slower turnover and lower productivity. This raises interesting questions as to what solutions nature will arrive at in situations where A_L/M_L requirements for allometry are not aligned with A_L/M_L requirements for environmental adaptation under the LES.

In our data, we were able to statistically demonstrate variation between plant species in body plan characteristics by fitting unique species-group intercepts, by the introduction to the regression of the three derived parameters, h_a , A_L/M_L , and R , and by performing a PCA on the data. In the regression analyses, leaf area effects captured in the indices R and A_L/M_L were found to be much more important for explaining data scatter around the universal scaling line than differences in body mass allocation to height attainment captured in h_a . In turn, between-species leaf-area effects were more strongly expressed in A_L/M_L than in the shape parameter R , which is logical, considering that A_L/M_L reduction in larger plants can be seen as the mechanism that allows supporting three-quarter power allometry of plant mass allocation and two-thirds allometry of A_L with plant size simultaneously. These ecological indices do not substitute for more detailed modeling of plant shape factors, such as that presented by Müller et al. (2000), Pretzsch (2019), or Pretzsch et al. (2012), but they do show unequivocally that such strategy differences exist both between and within the nine species groups for which we collected data, and they provide a tool to quantify the extent to which leaf-area-related body plan adjustments coexist with overarching 3/4-power-driven body mass allocation to organs, such as leaves and stems, across a spectrum of plant size.

In our analysis, we tested a model to fit different allometric exponents for each species group. As in the study of Deng et al. (2008), species group allometric exponent differences were significant, but we do not present this information here as fitting separate intercepts for species groups made it difficult to identify the “global” allometric exponents, which was our primary research question. This could be an aspect for further investigation in future. Hence, we view this part of our data analysis as more indicative of areas for future more detailed study, similar to that carried out by Müller et al. (2000), rather than definitive of the detail of plant species difference in ecological strategy.

More generally, adaptations of particular species to specific environmental conditions and physical constraints such as hydraulic limitations to plant height will give rise to exceptions to and deviations from the model (Kozłowski &

Konarzewski, 2005; Petit & Anfodillo, 2009). The above discussion does not invalidate the WBE model, nor reduce its applicability, but merely clarifies that, while the model is applicable across the whole spectrum of plant size, the constraints of vascular distribution that the WBE model focuses on are subject to interaction with and modification by other considerations in a multitude of specific instances.

It should be noted that R is not an arbitrarily derived plant descriptive parameter, but was a necessary mathematical component of equations for conceptualizing the $-3/2$ self-thinning line (Wade, 2018) as a constant-leaf-area line representing the leaf area “carrying capacity” of a given environment (Sackville Hamilton et al., 1995; Matthew et al., 1995). Arguably, R is a property of plants that is underutilized as an explanatory index in many ecology studies. We experimented with a “smallness index” based on $1/M_T$, since under isometric scaling at constant R , a small plant has a higher A_L/M_T ratio than a larger plant, such that staying small might be thought of as a defense, rather than as a defeat, in plant competition studies. However, we did not succeed in deriving a smallness index formulation that exhibited suitable mathematical behavior.

In contrast to R , which is a measure of body shaping for leaf area attainment, SLA defines the extent to which leaf thickness is reduced to develop greater leaf area from the same leaf tissue mass.

The PCA results are highly atypical of those normally obtained from PCA, but on reflection, the PCA features seen here are to be expected based on the mathematical properties of the data. Given that the 783 data points for M_T span eight orders of magnitude, it is entirely to be expected that PC1 would be a “size PC” that overwhelmingly dominates the eigenmatrix structure (98.7% of data variation explained). The fact that this size PC has near-identical loading coefficients for all investigated plant measures is extremely informative, showing that a single allometric progression links all plant body parts across the entire size range. This holds even if its precise formulation does change with plant size and differ between plant body parts dedicated to within-plant resource distribution (i.e., M_S) and those for light capture (i.e., M_L). The remaining PCs will then describe the basis for scatter of data for individual plants around the global allometric line, and since regression r^2 is extremely high, the proportion of total variation explained by lower-order PCs will necessarily be extremely small, yet still carrying information on species differences in ecological strategy. This is analogous to the sums of squares for ecological indicators in Regression Model 4 being small in relation to the total sum of squares, yet still highly significant (Table 5).

It is expected that each PC's loadings would identify associations between h , A_L , M_L , and M_S , reflecting particular ecological indices important to describing the body-plan variation between the plants represented in the data set, or the plants' ecological strategy. To understand the structure of the PC loadings, inspection of the correlations between PC scores and h_a , A_L/M_L , and R (Table S7) is revealing. R and h_a have a low but

highly statistically significant negative correlation, whereas the PC scores, by definition, have zero correlation with each other. The patterns of trait association identified by the PCA to achieve independence of PC scores are unexpected and interesting. The “size” PC (PC1) is highly correlated with A_L/M_L , reflecting the thicker leaves of larger plants needed for reconciliation of three-quarter-power body mass allometry and two-third-power LA allometry for light capture optimization, while “tactical” species variation in A_L/M_L from the allometric rule of SLA reduction with increasing plant size is captured in PC4. Meanwhile, h_a and R are represented in the PCA by two PCs; PC2 describing a trade-off between increased h_a and decreased R , and PC3 indicating cases where a four-trait association causes h_a and R to be positively correlated in some individuals across the data set. Notably, grasses have a low score for this PC. This might be seen as the cost of a radically different body architecture (Robin et al., 2021) adapted to defoliation. Nor are allometric ratios and species differences in ecological strategy the full story—it is also clear in detailed recent research that plant leaf traits such as leaf size and A_L/M_L respond strongly to edaphic conditions such as moisture deficit (Weithmann et al., 2022), adding another layer of complexity to the overall picture.

Wider considerations

In closing, it is relevant to reflect on the original reason for embarking on this study and consider what related questions remain for further examination. The original impetus was to understand tiller size-density compensation in pastures grazed at different heights; this led to a wider analysis of self-thinning (Matthew et al., 1995), and eventually to the present paper.

Our findings strongly support the challenges to the WBE theory brought forward by Kozłowski and Konarzewski (2004, 2005), who argued that the expected pattern in plant allometry would not be a single universal solution, but a range of specific adaptations to particular biotic and abiotic stresses. The thinking pattern established in our analysis of our data set enables us to see variation in plant body plan as akin to engineering solutions in building or other structure design, which can be expressed both mathematically and intuitively. Fig. 1c of Matthew (2025) illustrates this principle by conceptualizing the clover niche within a grass sward as a wedge-shaped space between allometric plant size/density compensation lines of differing slope, in the presence or absence of grazing. Specifically, more horizontally oriented clover leaves can provide light capture when LAI is reduced in a grass sward by grazing pressure, but clover tends to be outcompeted by the more upright leaves of companion grasses in longer swards. In ecology, consideration of complementarity between tactically different body plans of different plant species could contribute to the development of theory and understanding of plant community assembly processes and species succession. Such investigation could be progressed by building a

model or models to describe multispecies stands with species differing in ecological indices like A_L/M_L , h_a , and R , and is implicit in some recent papers such as the study of Hu et al. (2026).

In forestry, allometric theory has obvious implications for planning space allocation to trees of different ages in both monospecific and mixed-species stands and for development of models able to accommodate the influence of climate (Grote et al., 2020).

Two cases that may provide particularly interesting questions for future research are the growth form of tropical bamboos and the clumping of grass plants in tropical pastures. For bamboos, the tactic of forming multiple hollow stems rather than a single solid stem to hold the leaf canopy to the light is a major body plan variation, the implications of which are not intuitively obvious and would be interesting to research. In tropical pastures, where LAI accumulation between defoliation can be as high as 10, single plants tend to form spaced tussocks with size-density compensation evident both within and between tussocks. This contrasts with a typical LAI accumulation between defoliation events of 3–5 typical for temperate pastures, where the sward tends to be more spatially homogeneous. Again, further investigation would be interesting.

CONCLUSIONS

Our analysis of internal plant allometries confirms WBE prediction of four-thirds allometry of plant mass distribution between leaves and stems, as predicted from considerations of resource distribution constraints in branching vascular networks. Our data offer additional insights not captured in the WBE analysis: (1) A_L -related plant attributes exhibit $-3/2$ -power allometry with M_T , supporting a conclusion that light capture rather than vascular distribution considerations drive $M_T:d$ relationships. (2) Previously reported non-one-to-one scaling of $A_L:M_L$ can be viewed as a mechanism whereby four-thirds allometry of organ mass is reconciled with three-halves allometry of leaf area with organ mass, so simultaneously fulfilling vascular distribution and light capture considerations. (3) While our analysis supports the existence of a global allometric relationship, this relationship is not invariant with plant size. It tends toward a 1:1 allometry of plant body parts in smaller plants, is flatter in large trees, and is subject to modifications representing tactical ecological strategies of particular species or species groups.

AUTHOR CONTRIBUTIONS

Cory Matthew: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; visualization; writing—original draft; writing—review and editing. **Hans Pretzsch:** Conceptualization; data curation; investigation; methodology; project administration; visualization; writing—original draft; writing—review and editing. **Rüdiger Grote:** Conceptualization; data curation; investigation; visualization; writing—original draft; writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The primary data for this study are included in the supporting information online.

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SUPPORTING INFORMATION

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