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Allometric scaling of plant energetics and population density

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Scaling relationships that describe variation in population density with body size in ecological communities, such as the thinning law in plant ecology[1–3], can be explained in terms of how individuals use resources as a function of their size. Data for rates of xylem transport as a function of stem diameter show that rates of resource use in individual plants scale as approximately the 3/4 power of body mass, which is the same as metabolic rates of animals[4–7]. Here we use this relationship to develop a mechanistic model for relationships between density and mass in resource-limited plants. It predicts that average plant size should scale as the −4/3 power of maximum population density, in agreement with empirical evidence and comparable relationships in animals[5,6,8], but significantly less than the −3/2 power predicted by geometric models[1]. Our model implies that fundamental constraints on metabolic rate are reflected in the scaling of population density and other ecological and evolutionary phenomena, including the finding that resource allocation among species in ecosystems is independent of body size[5,6,8].

Many characteristics of organisms vary with body size, as described by allometric equations of the form

$$Y = Y_0 M^b \qquad (1)$$

where Y is the dependent variable, M is body mass, b is a power exponent and Y_0 is a normalization constant that varies with the nature of Y and with the kind of organism. Studies of animals suggest that many variables scale with quarter-powers of mass, for example $b \approx 3/4$ for metabolic rate, $-3/4$ for population density and $1/4$ for lifespan[4–9]. There is now a general model to explain why

many anatomical and physiological scaling exponents of both plants and animals scale as quarter-powers[7]. However, the mechanistic connections between these organismal processes and their ecological consequences remain poorly understood. Allometric studies have traditionally not been an important theme in plant biology[9]. One exception is the relationship between population density and plant size. When the dry mass of the average plant ($\bar{M}$) in mature populations is plotted against the maximum plant density (N_{max}) there is a distinct upper boundary that has traditionally been characterized by a power-law with an exponent of −3/2 (refs 1–3). This pattern, known as the thinning law, has been shown to hold for plants in both single- and mixed-species stands and over a size range spanning 23 orders of magnitude from unicellular algae to the tallest trees[1–3,10]. The fact that a plant fills a volume and covers an area has suggested a simple geometric explanation for the '−3/2 thinning law'[1].

However, the theoretical and empirical bases for the density–mass boundary have been called into question[11–18]. The −3/2 exponent, derived from purely geometric considerations, is difficult to reconcile with known mechanisms of plant growth, resource uptake and competition. Furthermore, increasingly precise data suggest that the boundary is closer to −4/3 (refs 14, 17), indicating that population density scales as $M^{-3/4}$, the same as in animals[5,6,8]. Because the metabolic rates of animals scale as $M^{3/4}$, similar relationships in plants suggest that both share a common scaling law that reflects how resource requirements of individual organisms affect competition and spacing among individuals within ecological communities. Here we apply our general model[7] for the design of biological resource distribution networks to provide mechanistic connections between resource requirements and population density for plants. The model predicts a fractal-like branching architecture and numerous allometric scaling relationships, for example total leaf mass scales as $M^{3/4}$, trunk diameter as $M^{3/8}$ and resource use, metabolic rate and gross photosynthetic rate as $M^{3/4}$. Although most of these predictions are well supported by data, there have been few allometric studies of total resource use or metabolism of plants.

Our analysis of data in the literature shows that whole-plant resource use scales as $M^{3/4}$. Several studies report the total rate of
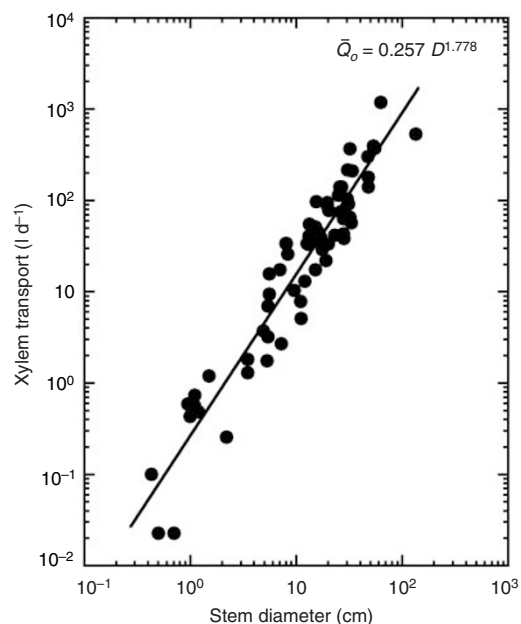
Figure 1 Relationship between the rate of whole-plant xylem transport and basal stem diameter. Data are from 69 individuals and 37 species, including herbaceous plants, shrubs, tree seedlings and mature evergreen and deciduous trees ($r^2 = 0.913$, $n = 69$, $P < 0.0001$; 95% confidence interval: 1.644 to 1.912).

fluid transport in the xylem ($\dot{Q}_0$) as a function of stem diameter (D); this can be described as $\dot{Q}_0 \propto D^{1.778}$ (Fig. 1). Other studies report relationships between stem diameter and above-ground dry mass[11,19]; averaging these gives $D \propto M^{0.412}$ ($n = 78$, s.d. $= 0.356$), so that $\dot{Q}_0 \propto M^{0.732}$.

The above relationships are nearly indistinguishable from those predicted from our model: $\dot{Q} \propto D^2$, $D \propto M^{3/8}$ and

$$\dot{Q}_0 \propto M^{3/4}. \qquad (2)$$

Small deviations from the predicted exponents can have many sources, including measuring techniques that slightly overestimate the diameter of large trees[15].

Whole-plant xylem transport provides a measure not only of nutrient and water use[20,21], but also of gross photosynthesis and therefore of metabolic rate. Because of stoichiometric and physiological constraints, the allometric scaling exponents for water, nutrient and photosynthate fluxes must be equivalent. Thus, rates of transpiration or xylem transport are appropriate, although generally overlooked, indices of plant metabolism. Both the theoretical model and the empirical evidence indicate that whole-plant metabolic rates scale as $M^{3/4}$, so that mass- or tissue-specific rates scale as $M^{-1/4}$. This agrees with the qualitative observation that size-specific growth rates are generally highest in annuals and small herbs and lowest in large trees[21–24]. More quantitatively, whole-plant rates of twig and leaf production (P_L) and wood and bark production (P_B), in six species of temperate trees, scale as $P_L \propto D^{1.653}$ and $P_B \propto D^{1.807}$ (ref. 25). Using the scaling of diameter in these species ($D \propto M^{0.438}$), the rate of new tissue production is $P_L \propto M^{0.724}$ and $P_B \propto M^{0.791}$, which brackets the predicted value of $M^{3/4}$.

Having established that whole-plant resource uses scales as $M^{3/4}$, we now model the relationship between maximal population density (N_{max}) and average plant mass ($\bar{M}$) in ecological communities. We assume that: (1) sessile plants compete for spatially limited resources; (2) their rate of resource use scales as $M^{3/4}$; and (3) plants grow until they are limited by resources[21,23,26]. The maximum number of individuals that can be supported per unit area (N_{max}) is related to the rate of resource supply (R) per unit area and the average rate of resource use per individual ($\bar{Q}$) by $R = N_{max}\bar{Q} \propto N_{max}\bar{M}^{3/4}$. At equilibrium in any given environment,

R is constant, giving

$$N_{max} \propto \bar{M}^{-3/4}. \qquad (3)$$

This is the form of the allometric equation traditionally used by animal ecologists, who often find a similar $-3/4$ scaling exponent for population density[5,6,8]. Plant ecologists have traditionally treated mass as the dependent variable, giving $\bar{M} \propto N_{max}^{-4/3}$.

Our model, based on resource use by individual plants, predicts a mass–density scaling exponent of $-4/3$, rather than $-3/2$ predicted by the geometric model[1]. Various studies also suggest that the thinning exponent is close to $-4/3$ (refs 14, 17, 18). Our analysis of data from the literature relating $\bar{M}$ and N_{max} (Fig. 2) shows that the exponent, -1.341, has statistical confidence intervals that include $-4/3$ but not $-3/2$. Other sources in the literature express total above-ground plant biomass per unit area (M_{tot}) as a function of maximum population density[12]. Using equation (3), our model predicts the scaling of total plant mass

$$M_{tot} = N_{max}\bar{M} \propto N_{max}N_{max}^{-4/3} \propto \bar{N}_{max}^{-1/3}. \qquad (4)$$

The geometric model[1] predicts an exponent of $-1/2$. A previous analysis of data on interspecific populations found an exponent of -0.379, (ref. 17), which is closer to $-1/3$ than to $-1/2$. Using a different data set, we performed a similar analysis (Fig. 3) and found that biomass per unit area scales as $N_{max}^{-0.325}$, which is statistically indistinguishable from the $-1/3$ predicted by our model, but significantly different from the $-1/2$ predicted by the geometric model.

Because the rate of resource use per unit area is the product of population density and the rate of resource use per individual, from equations (2) and (3) we have

$$Q_{tot} = N_{max}\bar{Q} \propto \bar{M}^{-3/4}\bar{M}^{3/4} \propto \bar{M}^0. \qquad (5)$$

Therefore, total energy use or productivity of plants in ecosystems is predicted to be invariant with respect to body size. We calculated Q_{tot} from the data used to compile Figs 1 and 2. As shown in Fig. 4, the rate of resource use per surface area scales as $\bar{M}^{0.014}$. This empirical value does not differ statistically from the size invariance ($\bar{M}^0$) predicted by the model. The relationship holds across variation of 12 orders of magnitude in plant size. The variation around
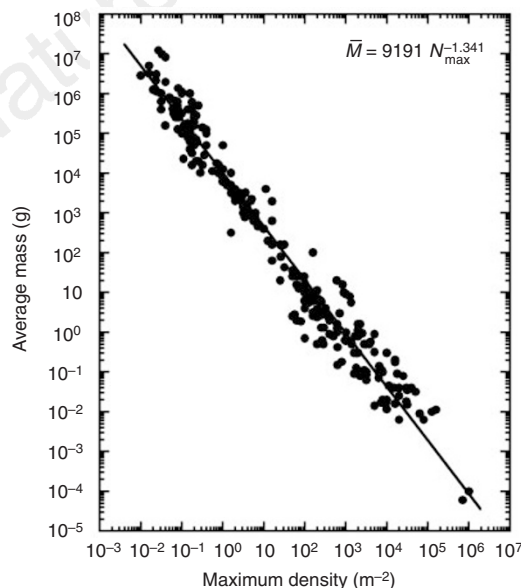
Figure 2 Relationship between average plant mass and maximum population density. Plant sizes range from *Sequoia* to *Lemma*. Data are from 251 populations ($r^2 = 0.963$, $n = 251$, $P < 0.0001$; 95% confidence interval: -1.374 to -1.309). The exponent is statistically indistinguishable from $-4/3$, indicating that maximum population density scales as $M^{-3/4}$.
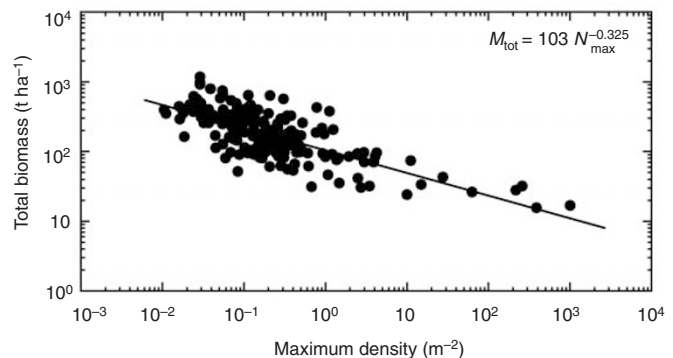
Figure 3 Relationship between total plant biomass (roots, shoots and leaves) and maximal population density[30]. ($r^2 = 0.9534$, $n = 189$, $P < 0.0001$; 95% confidence interval: -0.281 to -0.368). The fitted equation has an exponent statistically indistinguishable from $N_{max}^{-1/3}$ predicted from our model.
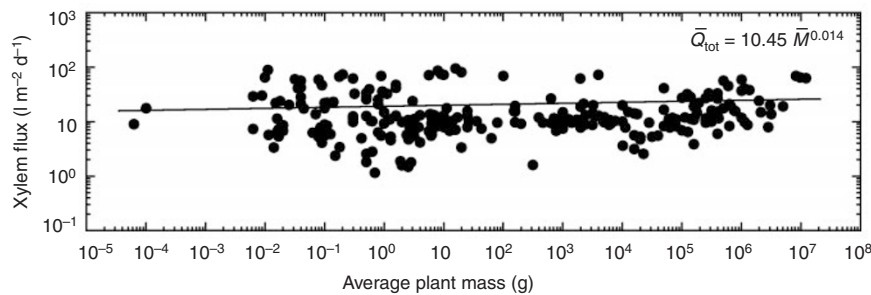
Figure 4 Relationship between total xylem flux and average size of the dominant plants in diverse ecosystems. ($r^2 = 0.009$, $n = 251$, $P < 0.127$; 95% confidence interval: −0.004 to 0.031). The stoichiometric equivalence of rates of water, nutrient and photosynthate flux within individual plants (see text) explains why evapo-transpiration can be used to estimate productivity[27]. Because the allometric equation has an exponent that is statistically indistinguishable from zero, ecosystem productivity is independent of plant size.

the regression line reflects variation in resource supply, and therefore in productivity among ecosystems ranging from arid grasslands and tundra to temperate and tropical forests[27].

Most of the dissatisfaction with the original geometric formulation of the thinning law stems from its lack of a means of predicting empirically measured thinning trajectories, and the resulting variation in sizes and densities of plants in different environments[3,11–18]. For example, as plant populations thin, individuals attain a certain maximum size that is characteristic of local environmental conditions. Not only are individuals larger in forests than in grasslands, but also each community typically contains multiple codominant species of nearly identical size[23]. Our model does not predict thinning trajectories, but it does predict that the rate of resource use per unit area varies among plant communities with differences in resource supply but not with plant size. Thus, ecosystems composed of plants of contrasting sizes and life forms, such as certain forests, grasslands and agricultural fields, can have identical productivity[27].

We have shown that metabolic rates of plants scale indistinguishably from the predicted $M^{3/4}$, and that a model incorporating this scaling can account for the maximum sizes and densities of plants observed in different communities. Traditionally, plant ecologists have implicitly treated the sizes of individuals as if they were determined by population density, by plotting mass as the dependent variable in depicting thinning relationships. Animal physiologists and ecologists have done just the opposite, plotting density and other variables as functions of body mass. The theoretical and empirical advantage of the latter approach is that variables are expressed in terms of standard allometric equations, such as equation (1), which highlight the universality of the 3/4-power scaling of resource use and the related 1/4-power scaling of other structural, functional and ecological attributes[4–8]. It has long been known that life-history variables, such as growth rate, lifespan and age to first reproduction, scale with body size[21–24,28]. Despite this variation, rates of resource use per unit area are independent of body size. This is observed empirically in animals[8] and demonstrated here, both empirically and theoretically, for vascular plants. A common body of allometric theory promises to provide a general framework for explaining many features of biological diversity. □

Methods

Data from the literature were compiled, plotted and analysed to define the allometric relationships shown in Figs 1–4. Data and their sources are available from B.J.E. The allometric equations were fitted to log-transformed data by least-squared regression. For simplicity, scaling relationships are presented in the text with normalization constants omitted. Data of maximum whole-plant xylem transport (Fig. 1) came from measurements using heat balance[20] or radioactive tracers[29]. Data for maximum values of average plant mass and plant density (Fig. 2) were obtained from refs 1, 2, 13, 14, 17 and additional studies. Data for total plant biomass (Fig. 3) were taken from ref. 30. Values were

obtained from diverse ecosystems with woody vegetation from around the world but excluded forests with heavy epiphyte loads. Values for total ecosystem xylem flux (Fig. 4) were calculated by taking the values of plant population density and average plant mass used in Fig. 2, and multiplying by the estimated rate of xylem transport using the equation in Fig. 1. Normalization constants were incorporated[19] to express values as rates of material transported from the soil and moved vertically through plant stems (in units of $l\,m^{-2}\,d^{-1}$).

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