

BIOLOGICAL SCALING

Does the exception prove the rule?

Arising from: P. B. Reich, M. G. Tjoelker, J.-L. Machado & J. Oleksyn *Nature* 439, 457–461 (2006)

Reich *et al.*¹ report that the whole-plant respiration rate, R , in seedlings scales linearly with plant mass, M , so that $R = c_R M^\theta$ when $\theta \approx 1$, in which c_R is the scaling normalization and θ is the scaling exponent. They also state that because nitrogen concentration (N) is correlated with c_R , variation in N is a better predictor of R than M would be. Reich *et al.* and Hedin² incorrectly claim that these “universal” findings question the central tenet of metabolic scaling theory, which they interpret as predicting $\theta = 3/4$, irrespective of the size of the plant. Here we show that these conclusions misrepresent metabolic scaling theory and that their results are actually consistent with this theory.

Reich *et al.* and Hedin do not cite an explicit caveat in metabolic scaling theory that θ will deviate from $3/4$ in plants that violate the secondary optimizing assumptions, including small plants such as seedlings and saplings^{3,4}. The core assumption^{3,5} of this theory states that carbon assimilation by the whole plant, or gross photosynthesis, P , stem fluid flow rate, Q_0 , and that the number (n_L) and mass of leaves (M_L) all co-vary and scale together, as $R \propto P \propto Q_0 \propto n_L \propto M_L \propto M^\theta$, in which θ is derived from vascular network geometry, dynamics and biomechanics. Specifically, $\theta = 1/(2a + b)$, in which a characterizes the branch radii, r , between different branching levels, k (that is, $k: r_{k+1}/r_k \equiv n^{-a}$); b characterizes the ratio of branch lengths, l , between

levels (that is, $l_{k+1}/l_k \equiv n^{-b}$)^{3,5}; and n is the branching ratio. The $\theta = 3/4$ rule then originates from secondary assumptions³, whereby the branching network is volume-filling; hydrodynamic resistance is minimized; the terminal branch (that is, M_L, R_L, P_L, Q_L) is independent of M ; and biomechanical adaptations negate the effects of gravity. Together, these assumptions lead to $a = 1/2$, $b = 1/3$, and consequently, $\theta = 3/4$. Violations of any of these assumptions yield different values⁶ of a and/or b , and hence of θ .

Isometric scaling relationships for small plants are the result of such violations. For small plants, gravity is relatively unimportant, so $r_k \approx l_k$ and $a \approx 1/2$, rather than $a = 1/2$ (Fig. 1a). Also, there are few branching levels, so space-filling is incomplete and $b > 1/3$. Thus, metabolic scaling theory predicts that $\theta \approx 1$ for the extreme case of very small plants. However, as plants grow, gravity becomes increasingly important and volume-filling architecture develops³, so metabolic scaling theory predicts a shift in θ from ≈ 1 to $\approx 3/4$ (Fig. 1b).

Independent data sets support these predictions. First, intraspecific scaling of metabolism⁷ from saplings to trees is closer to $3/4$ than to 1. Second, intra- and interspecific scaling of M_L all show⁴ a transition from $\theta \approx 1$ in seedlings to $\theta \approx 3/4$ in larger plants (Fig. 1b). Furthermore, the data of Reich *et al.* for R show a shift from $\theta \approx 1$ for seedlings to $\theta \approx 3/4$ for saplings that

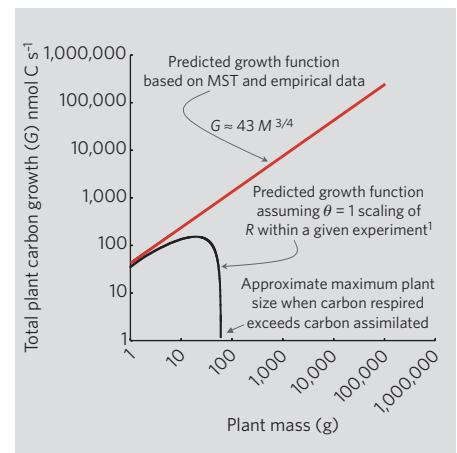


Figure 2 | Plant carbon growth. This is represented by $G = P - R$, in which $P = P_L M_L$, and P_L is the rate of assimilation. Metabolic scaling theory (MST) predicts that $M_L = c_L M^{3/4}$ for plants larger than seedlings. Given that $c_L \approx 0.7 \text{ g}^{3/4}$ (Fig. 1b) and that the geometric mean¹⁰ of P_L ($95.5 \text{ nmol C g}^{-1} \text{ s}^{-1}$) yields $P \approx 67 M^{3/4}$ ($\text{nmol C g}^{-3/4} \text{ s}^{-1}$), Reich *et al.* claim that, within treatments, $R = c_R M^\theta$, in which $\theta \approx 1$ and $c_R \approx 24 \text{ nmol C g}^{-1} \text{ s}^{-1}$. Thus, $G = P - R \approx 67 M^{3/4} - 24 M$ (nmol C s^{-1}). Growth ceases when $G \rightarrow 1$ (and $P = R$), yielding the erroneous prediction of an unrealistic maximum size (curved black line) of $\sim 1 \text{ kg}$. The red line ($G \approx 67 M^{3/4} - 24 M$), in which c_L has units of $\text{nmol C g}^{-3/4} \text{ s}^{-1}$, is for plants larger than seedlings when $\theta = 3/4$, as predicted by MST (Fig. 1b). Note that, as discussed^{13,14}, the potential variation in c_L and c_R is influenced by nutrient stoichiometry. These results show that isometric scaling within individual experiments cannot continue as plants grow larger than seedlings.

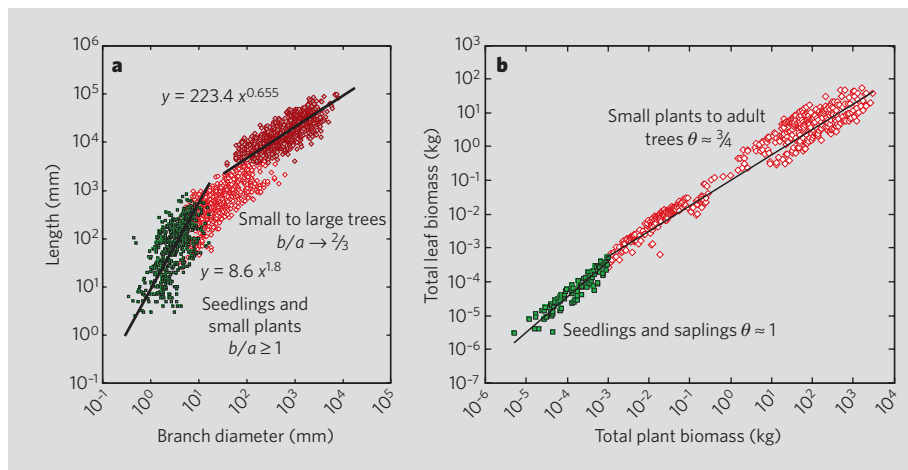


Figure 1 | Metabolic scaling theory (MST) predicts a coordinated shift in allometric exponents. a, Interspecific scaling for branch diameters ($2 \times r$) and lengths (l) from seedlings to trees¹⁵. As predicted, the scaling exponent changes from ≥ 1 for small plants and seedlings (green squares, above-ground biomass $< 1 \text{ g}$, reduced major axis (RMA) fit, $b/a = 1.8 \pm 0.12$; see text) to $b/a = 0.97 \pm 0.048$ for all the larger plants (red and brown diamonds; RMA fit not shown) to $\sim 2/3$ (RMA fit, $b/a = 0.65 \pm 0.02$) for the maximum interspecific heights achieved¹⁵ (brown diamonds). **b,** As the scaling of branch lengths and radii changes, the scaling of total leaf biomass¹², M_L , as well as R and P , are then all predicted to change. Indeed, $\theta = 1.01 \pm 0.7$ ($n = 95$, $r^2 = 0.88$) for plants with a mass of $< 1 \text{ g}$ and $\theta = 0.77 \pm 0.2$ for plants with a mass of $> 1 \text{ g}$ ($n = 563$, $r^2 = 0.959$), which is consistent with the MST-predicted shift from $\theta = 1$ to $\theta = 3/4$ and the scaling relationships in **a**.

have an above-ground biomass of more than 30 g ($\theta = 0.78 \pm 0.08$, $r^2 = 0.86$).

Reich *et al.* do not cite studies of plants larger than seedlings, which show the predicted $3/4$ -power scaling for M_L (Fig. 1b), Q_0 , carbon growth rate ($G = P - R$), and chlorophyll concentration^{6,8}. Thus, within each of their experimental treatments, extrapolation of isometric scaling of R to plants larger than seedlings will erroneously predict that the ratio of R/G should increase, as $R/G \propto M^1/M^{3/4} = M^{1/4}$, and an unrealistic maximum plant size (Fig. 2). Metabolic scaling theory resolves these inconsistencies³ by showing that $R \propto P \propto Q_0 \propto n_L$, so that R/G is invariant with size from seedlings to trees, as observed⁹.

Reich *et al.* point to the correlation between R and N as an alternative scaling mechanism. This is problematic and misleading. First, the literature¹⁰ on leaf-level physiology shows that $R \propto N$ cannot be assumed to apply to whole plants. Nitrogen is present, in varying concentrations, in all structures¹¹, so it is unclear how

N scales. As size increases, the metabolically inert pith and heartwood constitute an increasing fraction of biomass¹², but the fraction of nitrogen-rich leaves decreases as $M^{-1/4}$. Second, work extending metabolic scaling theory^{13,14} anticipated their result by showing how variation in nutrients influence R and related rates by changing the intercept of the predicted c_R , as observed¹.

For both plants and animals, metabolic scaling theory provides a general mechanistic baseline theory to predict how the scaling of metabolism is linked to the geometry and scaling of branching vascular networks, θ , temperature and nutrient stoichiometry — that is, nitrogen concentration. As a result, metabolic scaling theory can successfully resolve apparent exceptions and deviations^{3,6}, including isometric scaling in seedlings.

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BIOLOGICAL SCALING

Reich et al. reply

Replying to: B. J. Enquist *et al. Nature* **445**, doi: 10.1038/nature05548 (2007)

Enquist *et al.*¹ raise several points that they claim cast doubt on our findings and interpretation² regarding whole-plant relations of respiration, R , with plant mass, M , and total plant nitrogen content, N . We agree with Enquist *et al.* that R does not scale isometrically with M across all plants. However, their assertion that we claim that isometric scaling ($R \propto M^\theta$, with $\theta = 1$) is universal in plants of all sizes is incorrect — in fact, we conclude the opposite², noting that there is isometric scaling within individual experiments, non-isometric scaling of respiration versus mass across all data pooled, and no common relation across all data².

Enquist *et al.*¹ also claim that isometric scaling is evident only for very small seedlings that have a dry mass of less than 3 g (for example, see their Fig. 1b), but that leaf mass in larger plants is proportional to $M^{3/4}$ and $R \propto M^{3/4}$. By contrast, our results show that $R \propto M^{1.0}$ for plants ranging from 0.01 to 50 g, and from 1 to 1,000 g, within individual studies (Fig. 1a in ref. 2) and that there are significant differences in the intercepts of these relationships². Thus, $\theta < 1$ for all plants pooled and differs in individual studies, such that no single $R \propto M$ scaling model can apply, whereas $R \propto N^{1.0}$ reconciles all such differences². Enquist *et al.*¹ also criticize us for not noting their earlier suggestion³ that θ might deviate from $\theta = 3/4$ for small plants, although they themselves predicted $3/4$ metabolic scaling in plants of all sizes^{3–5}.

The allometry presented in Fig. 1 of Enquist *et al.*¹ does not address our findings, which

directly test their prediction^{3–5} that $R \propto M^{3/4}$. These allometric relations are not equivalent to measures of plant metabolism and are, at best, only indirectly relevant. Irrespective of its relevance to scaling, Enquist *et al.* claim that allometric relations (their Fig. 1) for leaf $M \propto$ total M^θ show isometric scaling for seedlings of less than 1 g and $\theta \approx 3/4$ for larger plants, although their Fig. 1 shows a θ that changes continuously across the entire gradient of size. As noted previously in a critique⁶ of the works of West, Brown and Enquist, arbitrary data parsing such as in Fig. 1 of Enquist *et al.*¹ can lead to widely varying θ values: for instance, in their Fig. 1b, leaf $M \propto$ total M^θ has $\theta \approx 0.70$ for plants of less than 1,000 g ($n = 334$), 1.10 for plants from 50,000 to 500,000 g ($n = 158$), and 2.20 for plants of more than 1,000,000 g ($n = 25$). Furthermore, an empirical study⁷ of leaf to whole-tree allometry for large trees showed that θ could vary from much lower than $3/4$ to much more than 1.0 depending on the nature of the data set, further refuting any notion of a constant allometry of leaf M to total plant M following $3/4$ scaling rules.

Nonetheless, the work by Enquist and colleagues has stimulated the field by providing testable predictions³, such as a universal $R \propto M^{3/4}$ relationship⁴. The plant data of Gillooly *et al.*⁴ ($n = 20$) were mostly for fruits or tubers (not plants) such as bananas, lemons, strawberries and carrots, with data on R and M obtained from unrelated sources. Given the general importance of this predicted relationship, including in subsequent synthesis and

modelling by this group^{5,8}, we tested it using a comprehensive data set² that included coupled whole-plant mass and respiration measures. Those data do not support predictions of a universal $R \propto M^{3/4}$ scaling in plants.

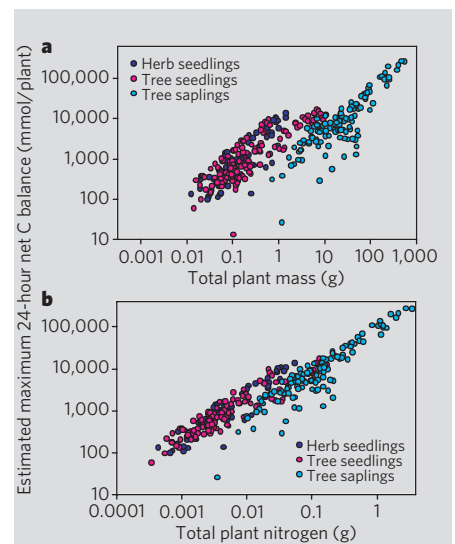


Figure 1 | Evidence for positive carbon balance across all plant sizes. **a, b**, Estimated maximum 24-hour net carbon balance in relation to total plant mass (**a**) and total plant nitrogen (**b**) for the plants in ref. 2. The 24-hour net carbon balance is based on predicting light-saturated rates of net photosynthesis from photosynthesis–nitrogen relationships¹¹, and scaling carbon gain and respiratory carbon loss to the whole plant based on tissue nitrogen and biomass distribution.