

## 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)

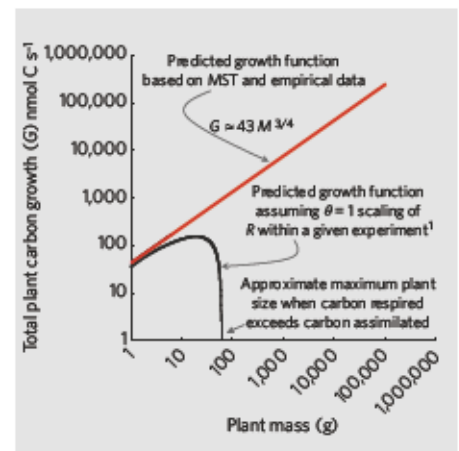
Reich *et al.*<sup>1</sup> report that the whole-plant respiration rate,  $R$ , in seedlings scales linearly with plant mass,  $M$ , so that  $R = c_R M^\theta$  when  $\theta = 1$ , in which  $c_R$  is the scaling normalization and  $\theta$  is the scaling exponent. They also state that because nitrogen concentration ( $N$ ) is correlated with  $c_R$ , variation in  $N$  is a better predictor of  $R$  than  $M$  would be. Reich *et al.* and Hedin<sup>2</sup> 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Reich *et al.* and Hedin do not cite an explicit caveat in metabolic scaling theory that  $\theta$  will deviate from  $3/4$  in plants that violate the secondary optimizing assumptions, including small plants such as seedlings and saplings<sup>3,4</sup>. The core assumption<sup>3,5</sup> 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  $\theta$  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,  $l_{k+1}/l_k \equiv n^{-b}$ )<sup>3,6</sup>; and  $n$  is the branching ratio. The  $\theta = 3/4$  rule then originates from secondary assumptions<sup>3</sup>, 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  $a = 1/2$ ,  $b = 1/2$ , and consequently,  $\theta = 3/4$ . Violations of any of these assumptions yield different values<sup>5,7</sup> of  $a$  and/or  $b$ , and hence of  $\theta$ .

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  $b > 1/2$ . 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 develops<sup>3</sup>, so metabolic scaling theory predicts a shift in  $\theta$  from  $\approx 1$  to  $\approx 3/4$  (Fig. 1b).

Independent data sets support these predictions. First, intraspecific scaling of metabolism<sup>8</sup> from saplings to trees is closer to  $3/4$  than to 1. Second, intra- and interspecific scaling of  $M_L$  all show<sup>4</sup> a transition from  $\theta = 1$  in seedlings to  $\theta = 3/4$  in larger plants (Fig. 1b). Furthermore, the data of Reich *et al.* for  $R$  show a shift from  $\theta = 1$  for seedlings to  $\theta = 3/4$  for saplings that

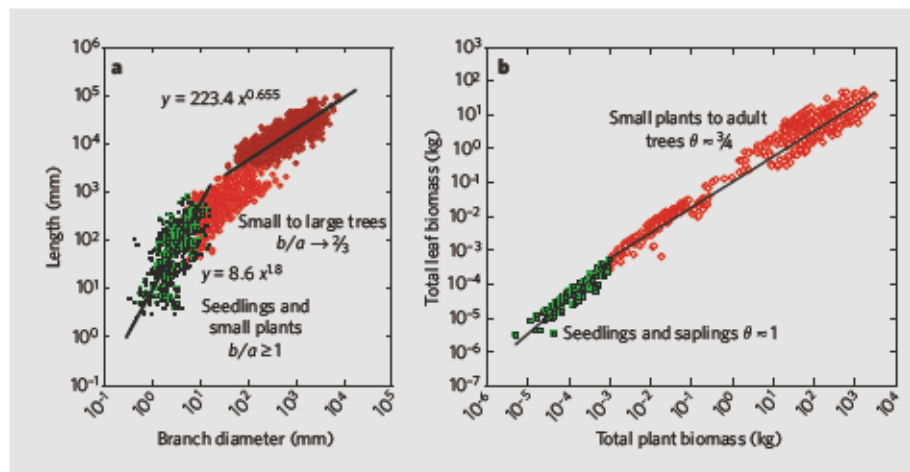


**Figure 2 | Plant carbon growth.** This is represented by  $G = P - R$ , in which  $P = P_L M_L$ , and  $P_L$  is the rate of assimilation. Metabolic scaling theory (MST) predicts that  $M_L = c_L M^{3/4}$  for plants larger than seedlings. Given that  $c_L \approx 0.7 \text{ g}^{-3/4}$  (Fig. 1b) and that the geometric mean<sup>10</sup> 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,  $G = P - R \approx 67 M^{3/4} - 24 M$  ( $\text{nmol C s}^{-1}$ ). Growth ceases when  $G \rightarrow 0$  (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<sup>13,14</sup>, 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.

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<sup>5,7</sup>. 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 inconsistencies<sup>3</sup> 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 observed<sup>9</sup>.

Reich *et al.* point to the correlation between  $R$  and  $N$  as an alternative scaling mechanism. This is problematic and misleading. First, the literature<sup>10</sup> 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 structures<sup>11</sup>, so it is unclear how



**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 trees<sup>15</sup>. As predicted, the scaling exponent changes from  $\geq 1$  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  $\sim 3/4$  (RMA fit,  $b/a = 0.65 \pm 0.02$ ) for the maximum interspecific heights achieved<sup>15</sup> (brown diamonds). b, As the scaling of branch lengths and radii changes, the scaling of total leaf biomass<sup>12</sup>,  $M_L$ , 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.

$N$  scales. As size increases, the metabolically inert pith and heartwood constitute an increasing fraction of biomass<sup>12</sup>, but the fraction of nitrogen-rich leaves decreases as  $M^{-\kappa}$ . Second, work extending metabolic scaling theory<sup>13,14</sup> anticipated their result by showing how variation in nutrients influence  $R$  and related rates by changing the intercept of the predicted  $c_R$ , as observed<sup>1</sup>.

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,  $\theta$ , temperature and nutrient stoichiometry — that is, nitrogen concentration. As a result, metabolic scaling theory can successfully resolve apparent exceptions and deviations<sup>3,6</sup>, including isometric scaling in seedlings.

Brian J. Enquist<sup>†</sup>, Andrew P. Allen<sup>‡</sup>,  
James H. Brown<sup>†§</sup>, James F. Gillooly<sup>||</sup>,

Andrew J. Kerkhoff<sup>¶</sup>, Karl J. Niklas<sup>#</sup>,  
Charles A. Price<sup>\*</sup>, Geoffrey B. West<sup>†</sup>

<sup>\*</sup>Department of Ecology and Evolutionary Biology,  
University of Arizona, Tucson, Arizona 85721, USA  
e-mail: benquist@email.arizona.edu

<sup>†</sup>The Santa Fe Institute, Santa Fe, New Mexico  
87501, USA

<sup>‡</sup>National Center for Ecological Analysis and  
Synthesis, University of California, Santa Barbara,  
California 93101, USA

<sup>§</sup>Department of Biology, University of New  
Mexico, Albuquerque, New Mexico 87131, USA

<sup>||</sup>Department of Zoology, University of Florida,  
Gainesville, Florida 32611, USA

<sup>¶</sup>Department of Biology and Department of  
Mathematics, Kenyon College, Gambier, Ohio  
43022, USA

<sup>#</sup>Department of Plant Biology, Cornell University,  
Ithaca, New York 14853, USA

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

- Hedin, L. O. *Nature* **439**, 399–400 (2006).
- West, G. B., Brown, J. H. & Enquist, B. J. *Nature* **400**, 664–667 (1999).
- Sack, L., Marafón, T., Grubb, P. J., Enquist, B. J. & Niklas, K. J. *Science* **296**, 1923 (2002).
- Niklas, K. J. & Enquist, B. J. *Proc. Natl Acad. Sci. USA* **98**, 2922–2927 (2001).
- Price, C. A. & Enquist, B. J. *Ecology* (in the press).
- Enquist, B. J. *Tree Physiol.* **22**, 1045–1064 (2002).
- Hemmingsen, A. M. *Rep. Steno Memorial Hosp. Nord Insulinlab.* **4**, 7–51 (1950).
- Gifford, R. M. *Funct. Plant Biol.* **30**, 171–186 (2003).
- Wright, I. J. et al. *Nature* **428**, 821–827 (2004).
- Kerkhoff, A. J., Fagan, W. F., Elser, J. J. & Enquist, B. J. *Am. Nat.* **168**, E103–E122 (2006).
- Enquist, B. J. & Niklas, K. J. *Science* **295**, 1517–1520 (2002).
- Kerkhoff, A. J., Enquist, B. J., Elser, J. J. & Fagan, W. F. *Glob. Ecol. Biogeogr.* **14**, 585–598 (2005).
- Gillooly, J. F., Charnov, E. L., West, G. B., Savage, V. M. & Brown, J. H. *Nature* **417**, 70–73 (2002).
- Niklas, K. J. & Spatz, H. C. *Proc. Natl Acad. Sci. USA* **101**, 15661–15663 (2004).

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# Reich et al. reply

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

Enquist et al.<sup>1</sup> raise several points that they claim cast doubt on our findings and interpretation<sup>2</sup> 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 opposite<sup>2</sup>, 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 data<sup>2</sup>.

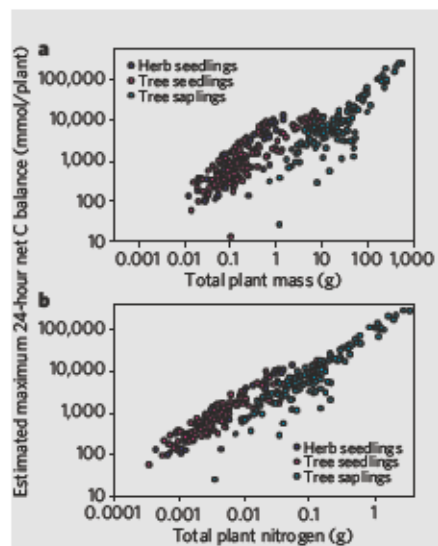
Enquist et al.<sup>1</sup> also claim that isometric scaling is evident only for very small seedlings that have a dry mass of less than 3 g (for example, see their Fig. 1b), but that leaf mass in larger plants is proportional to  $M^\kappa$  and  $R \propto M^\kappa$ . By contrast, our results show that  $R \propto M^{1.0}$  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 relationships<sup>2</sup>. 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 differences<sup>2</sup>. Enquist et al.<sup>1</sup> also criticize us for not noting their earlier suggestion<sup>3</sup> that  $\theta$  might deviate from  $\theta = \frac{3}{4}$  for small plants, although they themselves predicted  $\frac{3}{4}$  metabolic scaling in plants of all sizes<sup>3–5</sup>.

The allometry presented in Fig. 1 of Enquist et al.<sup>1</sup> does not address our findings, which

directly test their prediction<sup>3–5</sup> that  $R \propto M^\kappa$ . 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  $M^\theta$  show isometric scaling for seedlings of less than 1 g and  $\theta \approx \frac{3}{4}$  for larger plants, although their Fig. 1 shows a  $\theta$  that changes continuously across the entire gradient of size. As noted previously in a critique<sup>6</sup> of the works of West, Brown and Enquist, arbitrary data parsing such as in Fig. 1 of Enquist et al.<sup>1</sup> can lead to widely varying  $\theta$  values: for instance, in their Fig. 1b, leaf  $M \propto$  total  $M^\theta$  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 study<sup>7</sup> of leaf to whole-tree allometry for large trees showed that  $\theta$  could vary from much lower than  $\frac{3}{4}$  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  $\frac{3}{4}$  scaling rules.

Nonetheless, the work by Enquist and colleagues has stimulated the field by providing testable predictions<sup>3</sup>, such as a universal  $R \propto M^\kappa$  relationship<sup>4</sup>. The plant data of Gillooly et al.<sup>4</sup> ( $n = 20$ ) 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<sup>5,8</sup>, we tested it using a comprehensive data set<sup>2</sup> that included coupled whole-plant mass and respiration measures. Those data do not support predictions of a universal  $R \propto M^\kappa$  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 relationships<sup>11</sup>, and scaling carbon gain and respiratory carbon loss to the whole plant based on tissue nitrogen and biomass distribution.

Enquist *et al.* largely sidestep our main findings, namely the whole-plant scaling of  $R \propto N^{1.0}$ . This finding is supported across five orders of magnitude in plant size and, unlike  $R \propto M^k$  or  $R \propto M^{1.0}$ , is consistent within as well as across all data sets. They claim<sup>1</sup> that the idea of general scaling of  $R$  in relation to  $N$  is problematic and misleading, which ignores abundant evidence of globally convergent mass-specific scaling relations in terms of both photosynthesis and respiration being proportional to tissue nitrogen concentration<sup>9–11</sup>.

Our findings<sup>2</sup> are misrepresented by Enquist *et al.*<sup>1</sup> when they suggest that these are incompatible with the existence of plants over 60 g, because such plants will respire more carbon than they can acquire (although we did in fact present data for  $R$  in much larger plants<sup>2</sup>). Their simulation creates a problem that does not exist by using assumptions we both agree are incorrect, including universal  $R \propto M^{1.0}$  scaling, which the data do not support<sup>2</sup>, and by arbitrary selection of photosynthesis and respiration rates without regard to whether these are appropriately scaled to each other or to plant nitrogen concentrations. Thus, the “erroneous prediction of an unrealistic maximum plant size”, incorrectly attributed to our findings<sup>2</sup>, is solely a result

of their model assumptions<sup>1</sup>, is unsupported by published data and cannot be reconciled with data in Fig. 1a. By contrast, net photosynthetic rates generally scale with tissue nitrogen<sup>11</sup> and are about ten times higher than respiration rates at any given leaf nitrogen concentration<sup>11</sup>. Modelling net photosynthesis for plants in ref. 2 from these relationships<sup>11</sup>, and scaling carbon gain and respiratory carbon loss to the whole plant based on tissue nitrogen and biomass distribution, we find positive maximum 24-hour whole-plant net carbon gain across plants of all sizes (Fig. 1a). In addition, the maximum whole-plant carbon gain is positively related to total plant nitrogen (Fig. 1b), indicating that a nitrogen-based scaling approach is consistent with observations on plants that maintain a positive carbon balance.

A debate aimed at reconciling models that focus on generality in scaling relationships<sup>3,4</sup>, mechanistic understanding of the underlying biology<sup>5,12–14</sup>, and uncertainties regarding statistical approaches<sup>6,14</sup> is sorely needed to advance this field.

Peter B. Reich\*, Mark G. Tjoelker†, Jose-Luis Machado‡, Jacek Oleksyn§

\*Department of Forest Resources, University of Minnesota, St Paul, Minnesota 55108, USA

e-mail: preich@umn.edu

†Department of Forest Science, Texas A&M University, College Station, Texas 77843, USA

‡Department of Biology, Swarthmore College, Swarthmore, Pennsylvania 19081, USA

§Polish Academy of Sciences, Institute of Dendrology, 62-035 Kornik, Poland

1. Enquist, B. J. *et al.* *Nature* **445**, doi:10.1038/nature05548 (2007).
2. Reich, P. B., Tjoelker, M. G., Machado, J.-L. & Oleksyn, J. *Nature* **439**, 457–461 (2006).
3. West, G. B., Brown, J. H. & Enquist, B. J. *Nature* **400**, 664–667 (1999).
4. Gilliooly, J. F., Brown, J. H., West, G. B., Savage, V. M. & Charnov, E. L. *Science* **293**, 2248–2251 (2001).
5. Brown, J. H., Gilliooly, J. F., Allen, A. P., Savage, V. M. & West, G. B. *Ecology* **85**, 1771–1789 (2004).
6. Kozłowski, J. & Konarzewski, M. *Funct. Ecol.* **19**, 739–743 (2005).
7. Mäkelä, A. & Valentine, H. T. *Ecology* **87**, 2967–2972 (2006).
8. Enquist, B. J. *et al.* *Nature* **423**, 639–642 (2003).
9. Field, C. & Mooney, H. A. in *On the Economy of Plant Form and Function* (ed. Givnish, T. J.) 25–55 (Cambridge University Press, Cambridge, 1986).
10. Ryan, M. G. *Ecol. Appl.* **1**, 157–167 (1991).
11. Wright, I. J. *et al.* *Nature* **428**, 821–827 (2004).
12. Mencuccini, M. *Plant Cell Environ.* **26**, 163–182 (2003).
13. Meinzer, F. C., Bond, B. J., Warren, J. M. & Woodruff, D. R. *Funct. Ecol.* **19**, 558–565 (2005).
14. Glazier, D. S. *BioScience* **56**, 325–332 (2006).

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# Hedin replies

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

In my News & Views article<sup>1</sup>, I argued for the need to include factors other than body size to create a truly universal theory of plant scaling. I based my expectations for the metabolic scaling theory on Enquist’s own conclusion that “unlike animal clades...all plants comply with a single allometric formula that spans 20 orders of magnitude in body mass”<sup>2</sup>. Because in this recent analysis the authors applied a ¾ scaling slope across plants ranging in size from unicellular algae (< 10<sup>-7</sup> g body mass), to duckweed (10<sup>-5</sup> to 10<sup>-2</sup> g), to forest herbs and trees including giant *Sequoia* (10<sup>-1</sup> to 10<sup>5</sup> g), I found the comparison to the data of Reich *et al.*<sup>3</sup> entirely reasonable. Nevertheless, I explicitly discussed my concern about whether and how the findings of Reich *et al.* could extend to mature trees<sup>4</sup>.

I am glad to see the more nuanced state-

ment of metabolic scaling theory by Enquist *et al.*<sup>4</sup>, which now explicitly introduces the idea of scale dependence in scaling slope between smaller and larger plants. This seems to be an important improvement, especially as many of Earth’s plant species are smaller than adult trees, and within the size range considered by Reich *et al.* (< 10<sup>4</sup> g). What is less clear, however, is whether the proposed change in slope is abrupt or gradual, and across what size range it takes place. However, this revision by Enquist *et al.* does not address the effect of nitrogen on plant respiration<sup>5</sup> shown by Reich *et al.*, an effect that is well documented theoretically and experimentally at the scale of individual leaves as well as of whole plants<sup>5,6</sup>. It is interesting that there is even recent evidence that plant hydraulic architecture varies as a function of nitrogen supply<sup>7</sup>. Future investigations should seek to

resolve this vexing interaction of body size, nutrient status and metabolic scaling slopes.

Lars O. Hedin

Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey 08540, USA

e-mail: lhedin@princeton.edu

1. Hedin, L. O. *Nature* **439**, 399–400 (2006).
2. Niklas, K. J. & Enquist, B. J. *Proc. Natl Acad. Sci. USA* **98**, 2922–2927 (2001).
3. Reich, P. B., Tjoelker, M. G., Machado, J.-L. & Oleksyn, J. *Nature* **439**, 457–461 (2006).
4. Enquist, B. J. *et al.* *Nature* **445**, doi: 10.1038/nature05548 (2007).
5. Cannell, M. G. R. & Thornley, J. H. M. *Ann. Bot.* **85**, 45–54 (2000).
6. Ryan, M. G., Hubbard, R. M., Pongracic, S., Raison, R. J. & McMurtrie, R. E. *Tree Physiol.* **16**, 333–343 (1996).
7. Bucci, S. J. *et al.* *Plant Cell Environ.* **29**, 2153–2167 (2006).

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