

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 $R \propto M^{3/4}$ or $R \propto M^{1.0}$, is consistent within as well as across all data sets. They claim¹ 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^{9–11}.

Our findings² are misrepresented by Enquist *et al.*¹ 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 plants²). 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 support², 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 findings², is solely a result

of their model assumptions¹, is unsupported by published data and cannot be reconciled with data in Fig. 1a. By contrast, net photosynthetic rates generally scale with tissue nitrogen¹¹ and are about ten times higher than respiration rates at any given leaf nitrogen concentration¹¹. Modelling net photosynthesis for plants in ref. 2 from these relationships¹¹, 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^{3,4}, mechanistic understanding of the underlying biology^{5,12–14}, and uncertainties regarding statistical approaches^{6,14} is sorely needed to advance this field.

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BIOLOGICAL SCALING

Hedin replies

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

In my News & Views article¹, 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”². Because in this recent analysis the authors applied a $3/4$ scaling slope across plants ranging in size from unicellular algae ($< 10^{-7}$ g body mass), to duckweed (10^{-5} to 10^{-2} g), to forest herbs and trees including giant *Sequoia* (10^{-1} to 10^7 g), I found the comparison to the data of Reich *et al.*³ entirely reasonable. Nevertheless, I explicitly discussed my concern about whether and how the findings of Reich *et al.* could extend to mature trees¹.

I am glad to see the more nuanced state-

ment of metabolic scaling theory by Enquist *et al.*⁴, 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.* ($< 10^{-4}$ 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 respiration⁵ 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^{5,6}. It is interesting that there is even recent evidence that plant hydraulic architecture varies as a function of nitrogen supply⁷. Future investigations should seek to

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

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