Reich et al. 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 Hedlin incorrectly claim that these “universal” findings question the central tenet of metabolic scaling theory, which they interpret as predicting \( \theta = \frac{3}{4} \), irrespective of the size of the plant. Here we show that these conclusions misrepresented metabolic scaling theory and that their results are actually consistent with this theory.

Reich et al. and Hedlin do not cite an explicit caveat in metabolic scaling theory that \( \theta \) will deviate from \( \frac{3}{4} \) in plants that violate the secondary optimizing assumptions, including small plants such as seedlings and saplings. The core assumption of this theory states that carbon assimilation by the whole plant, or gross photosynthesis, \( P \), stem fluid flow rate, \( Q_o \), and that the number (\( n_L \)) and mass of leaves (\( M_L \)) all co-vary and scale together, as \( R \propto P \propto Q_o \propto n_L \propto M_L \propto M^\theta \), 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, \( k; r_{k+1}/r_k \equiv n^k \)); \( b \) characterizes the ratio of branch lengths, \( l \), between levels (that is, \( l_{k+1}/l_k \equiv n^{-b} \)^{k+1}/2; and \( n \) is the branching ratio. The \( \theta = \frac{3}{4} \) rule then originates from secondary assumptions, 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 \( a = \frac{1}{2}, b = \frac{3}{2} \), and consequently, \( \theta = \frac{3}{4} \). Violations of any of these assumptions yield different values 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 \( r_{k+1} \approx l_k \) and \( a \approx \frac{1}{2} \), rather than \( a \approx \frac{1}{2} \) (Fig. 1a). Also, there are few branching levels, so space-filling is incomplete and \( b > \frac{3}{2} \). Thus, metabolic scaling theory predicts that \( \theta = 1 \) for the extreme case of very small plants. However, as plants grow, gravity becomes increasingly important and volume-filling architecture develops, so metabolic scaling theory predicts a shift in \( \theta \) from \( \approx 1 \) to \( \approx \frac{3}{4} \) (Fig. 1b).

Independent data sets support these predictions. First, intraspecific scaling of metabolism from saplings to trees is closer to \( \frac{3}{4} \) than to 1. Second, intra- and interspecific scaling of \( M_L \) all show a transition from \( \theta = 1 \) in seedlings to \( \theta = \frac{3}{4} \) in larger plants (Fig. 1b). Furthermore, the data of Reich et al. for \( R \) show a shift from \( \theta = 1 \) for seedlings to \( \theta = \frac{3}{4} \) for saplings that 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 \( M_L \), so that \( c_R M^\theta \) (Fig. 1b), \( Q_o \), carbon growth rate (\( G = P - R \)), and chlorophyll concentration. 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 \( R/G \propto M^\theta \propto M^\frac{3}{4} \), and an unrealistic maximum plant size (Fig. 2). Metabolic scaling theory resolves these inconsistencies by showing that \( R \propto P \propto Q_o \propto n_L \) so that \( R/G \) is invariant with size from seedlings to trees, as observed.

Reich et al. point to the correlation between \( R \) and \( N \) as an alternative scaling mechanism. This is problematic and misleading. First, the literature 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, so it is unclear how
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\textsuperscript{2,4}, including isometric scaling in seedlings.

\textbf{Reich et al. reply}

Enquist \textit{et al.}\textsuperscript{1} raise several points that they claim cast doubt on our findings and interpretation\textsuperscript{2} regarding whole-plant relations of respiration, \(R\), with plant mass, \(M\), and total plant nitrogen content, \(N\). We agree with Enquist \textit{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\textsuperscript{2}, 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\textsuperscript{2}.

Enquist \textit{et al.}\textsuperscript{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 \(M^\theta\) and \(R \propto M^\theta\). By contrast, our results show that \(R \propto M^{0.6}\) 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\textsuperscript{2}.

Thus, \(\theta < 1\) for all plants pooled and differs in individual studies, such that no single \(R \propto M\) scaling model can apply, whereas \(R \propto N^{\theta}\) reconciles all these differences\textsuperscript{2}. Enquist \textit{et al.}\textsuperscript{1} also criticize us for not noting their earlier suggestion\textsuperscript{2} 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\textsuperscript{2-5}.

The allometry presented in Fig. 1 of Enquist \textit{et al.}\textsuperscript{1} does not address our findings, which directly test their prediction\textsuperscript{1-5} that \(R \propto M^\theta\). 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 \textit{et al.} claim that allometric relations (their Fig. 1) for leaf \(M \propto M^\theta\) show isometric scaling for seedlings of less than 1 g and \(\theta = \frac{3}{4}\) 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\textsuperscript{2} of the works of West, Brown and Enquist, arbitrary data parsing such as in Fig. 1 of Enquist \textit{et al.}\textsuperscript{1} can lead to widely varying \(\theta\) values: for instance, in their Fig. 1b, leaf \(M \propto M^\theta\) 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 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 \(M\) following \(\frac{3}{4}\) scaling rules.

Nonetheless, the work by Enquist and colleagues has stimulated the field by providing testable predictions\textsuperscript{2}, such as a universal \(R \propto M^\theta\) relationship\textsuperscript{2}. The plant data of Gillooly \textit{et al.}\textsuperscript{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\textsuperscript{3,8}, we tested it using a comprehensive data set\textsuperscript{1} that included coupled whole-plant mass and respiration measures. Those data do not support predictions of a universal \(R \propto M^\theta\) 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\textsuperscript{1,2}, and scaling carbon gain and respiratory carbon loss to the whole plant based on tissue nitrogen and biomass distribution.