

NEWS & VIEWS

PHYSIOLOGY

Plants on a different scale

Lars O. Hedin

Is there a unified theory that relates size and metabolic rate across all organisms? Maybe not, according to the results of experiments that measured respiration in plants of widely varying mass.

It is not every day that a 'law of nature' is challenged by empirical data, but on page 457 of this issue¹ we find just that. Peter Reich and colleagues¹ offer convincing evidence that refutes the idea that Kleiber's law — the all-encompassing prediction that metabolic rate should scale as the $3/4$ power of size across animals — can be extended to vascular plants (Fig. 1). Their findings question our understanding of how plant metabolism is organized. More broadly, they raise serious doubts about the notion^{2–4} that there exists a unified metabolic theory of scaling based on mechanisms that apply equally across plants and animals.

Here is the basic plot. In 1932, Max Kleiber showed that metabolic rates of mammals and birds scale as the $3/4$ power of body mass⁵. Kleiber's law has since become a standard of biology textbooks, demonstrating that mammals as different as mice, men and elephants obey the same quantitative metabolic relationship: a single line with a $3/4$ slope on a logarithmic plot of respiration versus body mass (Fig. 2a, overleaf). In 1960, Axel Hemmingsen⁶ showed that this $3/4$ slope applies even across a variation of six orders of magnitude in body size of mammals, fish, reptiles, insects and selected unicellular organisms. This extraordinarily broad metabolic pattern has all the makings of a universal biological principle⁷.

It has proven more difficult to identify the biophysical mechanisms responsible for the observed $3/4$ scaling slope. But Geoffrey West, James Brown and Brian Enquist have proposed a daring theoretical model^{2–4} to explain the $3/4$ metabolic exponent specifically, and the apparent ubiquity of quarter-power scaling relationships in biology generally. At its heart, this "metabolic theory of ecology"⁴ assumes that metabolism is constrained by resource delivery through internal branching networks in organisms. In the case of mammals, this means a circulatory system that supplies oxygen and nutrients to tissues. In the case of vascular plants, it means a system that delivers water and nutrients throughout the plant. If one assumes that natural selection acts to minimize transport costs through such networks, and given a set of rules for fractal branching,



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Figure 1 | Little and large in the plant world. Reich *et al.*¹ find that Kleiber's law relating metabolic rate and mass does not apply to vascular plants across the six orders of magnitude in mass that they tested. One outstanding question, however, is whether their results extend to mature trees.

the model predicts that $3/4$ metabolic scaling ought to apply universally to all organisms that depend on such transport networks.

But here the plot thickens. Questions have emerged about whether the model is mathematically and conceptually consistent^{8,9}, and whether the best-fit regression slope is $3/4$, or $2/3$, or even variable across taxonomic groups¹⁰. (The idea¹¹ of $2/3$ metabolic scaling based on surface-to-volume considerations is an old one, predating Kleiber's monograph⁵ by five decades.) This current debate is largely focused on animals, for which there is an extensive data set of metabolism across species of varying sizes.

In contrast, direct measures of whole-plant respiration have been surprisingly rare. This means that early confirmations of the $3/4$ scaling prediction for plants were based either on indirect evidence³, which assumed that whole-plant transport of xylem water could substitute for metabolism (an assumption that has been questioned elsewhere^{12,13}), or on few samples, few species and few individuals¹⁴.

This is where Reich and colleagues¹ enter the picture. They report direct measurements

of whole-plant respiration, measured as carbon dioxide efflux in the dark (so ruling out the confounding factor of light-driven photosynthesis). Their results cover some 500 individual plants, across 43 species, from varying environments, and across six orders of magnitude variation in plant mass. The extent and quality of this new data set is refreshing, as statistical estimates of scaling slopes are notoriously sensitive to small sample sizes, or to heterogeneity in sampling techniques.

Reich and colleagues' results are astounding. Whole-plant respiration failed to fit the $3/4$ slope predicted by metabolic scaling theory. Rather, respiration scaled isometrically (that is, with a slope of 1.0 on a logarithmic plot) against plant mass. Mathematically, this means that, on a linear scale, respiration changes in direct proportion to variations in plant mass, as opposed to the more complex logarithmic relationship defined by the $3/4$ power function of Kleiber's law (Fig. 2b). Such a proportionate response in respiration against mass is perhaps intellectually less interesting, as it does not demand the kind of physiological complexity implied by $3/4$ scaling and metabolic scaling theory^{2–4}. Reich

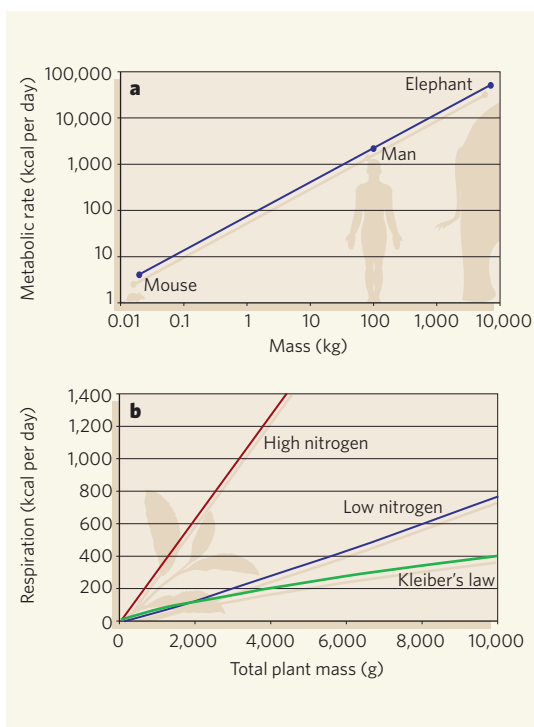


Figure 2 | Metabolism and mass.

a, Kleiber's law. Logarithmically, the basal metabolic rate of mammals varies with body mass as a straight line with a slope of 0.74. **b**, When expressed on a linear scale, the $3/4$ scaling relationship of Kleiber's law (green line) shows total respiration rate decreasing proportionately as a function of body mass. In contrast, the isometric (slope 1.0) logarithmic scaling relationships described by Reich *et al.*¹ for vascular plants are consistent with a strictly proportional (linear) relationship between whole-plant respiration and mass. The authors also report that the intercept of the log-log scaling relationship depends on plant nitrogen. On the linear scale shown here, this translates to steep proportionality for plants in nutrient-rich greenhouse soils (red line) and less-steep proportionality for plants in nutrient-poor natural soils (blue line). Note that it is difficult to distinguish visually between isometric and $3/4$ scaling lines on a linear scale, as this projection draws attention to only a limited part of the dynamic range.

et al. also report that the intercept of the scaling line differed between plants grown in the greenhouse and in the field, showing that respiration per unit mass differed systematically between these two environments.

The next observation is even more intriguing. When Reich *et al.* expressed plant respiration against the whole-plant content of nitrogen (instead of plant mass), the dissimilarity in intercept between environments entirely disappeared, but the overall scaling slope remained isometric. This suggests that the systematic difference in respiration per unit mass was caused by higher supplies of nitrogen in greenhouse compared with field environments. More importantly, across the different environments plant respiration was consistently more closely linked to variations in nitrogen than in mass. This result challenges not only the idea of a universal $3/4$ scaling law, but also the notion that size alone is the dominant determinant of differences in metabolism across species. In hindsight, this need to explicitly consider nutrients might not be so surprising given that nitrogen is an essential component of enzymes such as Rubisco (responsible for carbon fixation in plants), and of proteins, chlorophyll and other biomolecules involved in plant photosynthesis and respiration.

Do the results simply imply that it is the business ends of plants — leaves and roots — in which most respiration occurs, and therefore most nitrogen is stored? In such a case, the metabolism versus nitrogen relationship might largely reflect rather pedestrian proportionate variations in crown and root volumes across individuals and species. A key issue is whether Reich and colleagues' findings extend beyond the size of tree saplings, the largest individuals sampled. Nitrogen allocation may

very well change as trees mature within natural forests and become increasingly subject to constraints of self-thinning¹⁵ and competition for nutrients¹⁶. A second question is why nitrogen emerges as such a strong correlate of metabolism, when phosphorus is generally considered the better predictor¹⁷.

Nonetheless, we find ourselves with a theory challenged. There is no question of the value

of ideas such as those of West and colleagues^{2–4}, as they dare to invoke first-principle universal mechanisms. But these new findings question a central tenet of the metabolic scaling theory — that size-dependent distribution networks exert the primary constraint on metabolic rates in vascular plants. Reich and colleagues' results¹ will spark considerable debate among ecologists and physiologists: at stake is the issue of whether there is a truly unified theory of metabolism that encompasses all organisms. ■ Lars O. Hedin is in the Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey 08540, USA. e-mail: lhedin@princeton.edu

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EXTRASOLAR PLANETS

Light through a gravitational lens

Didier Queloz

A planet with a mass lower than that of Neptune has been detected as its gravity bent the light from a remote star. This lensing technique adds to our arsenal for spotting small planets outside the Solar System.

Ten years ago, Michel Mayor and I discovered the first planet outside the Solar System orbiting a Sun-like star¹. This 'exoplanet' orbits the star 51 Pegasi in 4 days and has about the same mass as Jupiter (more than 300 times that of Earth). Its existence was revealed through highly accurate measurements of a tiny 'Doppler' variation in 51 Pegasi's radial velocity — the speed at which its position changes relative to an observer. This variation is caused by the gravitational pull of an orbiting planet with a mass 1,000 times less than that of 51 Pegasi. The discovery triggered many more Doppler surveys to search for planets around nearby stars. As a result, more than 160 planets with masses ranging from ten times that of Jupiter down to that of Neptune (which

is around 17 times Earth's mass) have been found (Fig. 1).

The range of planet masses and orbital parameters that can be identified by the Doppler technique is limited both by the detection sensitivity of the technique and by the time needed to survey at least one orbital period of each planet. The largest Doppler variation is caused by planets of high mass and those on short orbits. Therefore, low-mass planets can be detected only if they are on short orbits.

On page 437 of this issue, Beaulieu *et al.*² report the use of a different technique, known as gravitational microlensing, to detect a planet with a mass less than that of Neptune. Its orbital distance is about 2 AU (1 AU, or astronomical unit, is the Earth–Sun distance),