Scaling relationship between tree respiration rates and biomass

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The WBE theory proposed by West, Brown and Enquist predicts that larger plant respiration rate, R , scales to the three-quarters power of body size, M . However, studies on the R versus M relationship for larger plants (i.e. trees larger than saplings) have not been reported. Published respiration rates of field-grown trees (saplings and larger trees) were examined to test this relationship. Our results showed that for larger trees, aboveground respiration rates R_A scaled as the 0.82-power of aboveground biomass M_A , and that total respiration rates R_T scaled as the 0.85-power of total biomass M_T , both of which significantly deviated from the three-quarters scaling law predicted by the WBE theory, and which agreed with 0.81–0.84-power scaling of biomass to respiration across the full range of measured tree sizes for an independent dataset reported by Reich *et al.* (Reich *et al.* 2006 *Nature* 439, 457–461). By contrast, R scaled nearly isometrically with M in saplings. We contend that the scaling exponent of plant metabolism is close to unity for saplings and decreases (but is significantly larger than three-quarters) as trees grow, implying that there is no universal metabolic scaling in plants.

Keywords: allometry; respiration rates; tree biomass; WBE theory

1. INTRODUCTION

Many biological relationships can be expressed as a ‘power law’, mathematically taking the form: $Y = \beta Y_0^\alpha$, where Y and Y_0 are the variables of biological traits, β is the normalization constant and α is the scaling exponent (Calder 1984; Niklas 1994). Based on a model of fractal structure (and now denoted as the WBE (West, Brown, Enquist) theory), West *et al.* (1997, 1999) predict that plant metabolism scales as the three-quarters power of body size just as the model predicts for animals (but see Makarieva *et al.* 2008 for conflicting evidence). This theory has stimulated a vigorous debate concerning its validity and

predictive value over the past decade (e.g. Dodds *et al.* 2001; Muller-Landau *et al.* 2006).

A multitude of datasets used for confirmations of the WBE theory in plants is mostly derived from indirect surrogates of metabolic rates, e.g. diameter growth rates (Enquist *et al.* 1999), biomass production rates (Niklas & Enquist 2001) and leaf biomass (Enquist *et al.* 2007). However, substantial deviations have been found for such scaling relationships, especially (but not exclusively) when applied to particular taxonomic groups or ecosystems. The scaling exponent of biomass production and biomass can range between 0.407 and 1.14 depending on how the data is sorted into different vegetation types (Li *et al.* 2005); the relationship between diameter growth rate and body size in tropical forests does not categorically follow the WBE theory (Muller-Landau *et al.* 2006). Furthermore, Mäkelä & Valentine (2006) found that the scaling exponent for leaf to the whole plant biomass of large trees can vary from much lower than three-quarters to much more than 1.0, depending on the nature of the dataset. We suggest that such inconsistencies with the WBE theory may stem not only from the violation of secondary assumptions of this theory, but also from the difference between metabolism and its surrogates, which at best, are only indirectly relevant to metabolism. Therefore, a test of the WBE theory through direct measurement of respiration rate is sorely needed.

Reich *et al.* (2006) report that the whole-plant respiration, R , of seedlings and saplings scales nearly isometrically with plant mass, M , in individual studies, but without any coherent central tendency across all data pooled, because normalization constants vary among individual studies. Nonetheless, their results show respiration scaling with approximately 0.81–0.84 power of body size across all tree sizes. By contrast, respiration scales isometrically with nitrogen across all plant sizes (i.e. $\alpha \approx 1.0$), reconciling intercept differences among studies observed for the R versus M relationship (Reich *et al.* 2006). Furthermore, Enquist *et al.* (2007) propose that scaling exponents for plant R versus M shift from near 1.0 for small plants (especially for seedlings and saplings) to three-quarters for larger plants (see also Mori *et al.* 2010). However, exceedingly few studies on the whole-plant respiratory rates versus plant mass relations for plants larger than saplings have been reported. Here, we re-analysed published datasets assembled from field-grown trees to examine the scaling relationship between respiration and body size.

2. MATERIAL AND METHODS

(a) Data collection and quality

Data for larger tree respiration rates and biomass (R and M , respectively) were gathered from compendia published by Fang (1999), Zeng *et al.* (2000) and Yang *et al.* (2001). The sampled species and main geographical and climatic conditions of three studies are shown in the electronic supplementary material. The respiration rates were measured in the field using infrared gas CO₂ analysers. The total respiration rate of an individual tree was estimated as the sum of the respiration rates of leaf, stem, branch and root. The respiration rates were adjusted to 24°C using the temperature model proposed by Atkin & Tjoelker (2003) (see the electronic supplementary material for details). The biomass was converted from directly measured fresh weight using the dry/fresh weight ratio or biomass allometric equations developed by the original authors. To test whether the metabolic scaling exponent shifts with increasing plant size, we included the datasets of field-grown US tree saplings and Japanese trees used by Reich *et al.* (2006). Here, the US saplings

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Figure 1. Log–log bivariate plots for respiration rates versus biomass for small and larger trees. (a) Aboveground respiration rates versus aboveground biomass, (b) total respiration rates versus total biomass at 24°C. The US saplings ($n = 119$; data from Reich *et al.* 2006) were grouped as small trees, whereas Japanese ($n = 10$; data from Reich *et al.* 2006) and Chinese trees ($n = 36$) were grouped as larger trees. Open circles, US saplings; crosses, Japanese trees; filled circles, Chinese trees; dotted and dashed lines, regression for small trees; continuous lines, regression for larger trees.

were grouped as small trees (less than 4.5×10^2 g for aboveground biomass), while Chinese and Japanese trees were grouped as larger trees (4.5×10^2 g to 1.2×10^7 g for aboveground biomass). The data from greenhouse and growth chamber plants were excluded from the present study because they were not strictly comparable to those from field-grown plants, just as Reich *et al.* (2006) and Glazier (2010) analysed these data separately.

(b) Statistical protocols

Data for total biomass M_T , aboveground biomass M_A (g), total respiration R_T , and aboveground respiration R_A (nanomoles of CO₂ s⁻¹) were log-transformed. Model Type II (reduced major axis, RMA) regression was used to determine the slope (scaling exponent) and Y-intercept (allometric constant) of log–log linear functions, i.e. α_{RMA} and $\log \beta_{RMA}$, respectively.

3. RESULTS

Scaling exponents of larger trees were 0.82 (95% CI = 0.77–0.87, $n = 46$, $r^2 = 0.957$, $p < 0.0001$) and 0.85 (95% CI = 0.78–0.92, $n = 35$, $r^2 = 0.939$) for R_A versus M_A and R_T versus M_T relations, respectively (figure 1). By contrast, the scaling exponent of field-grown saplings was statistically different from that of larger trees. Specifically, R_A scaled as the

1.09-power of M_A (95% CI = 1.01–1.18, $r^2 = 0.887$, $p < 0.0001$), and R_T scaled as the 1.12-power of M_T (95% CI = 1.05–1.19, $r^2 = 0.904$, $p < 0.0001$) in field-grown saplings. When all data were pooled together, scaling exponents were 0.81 (95% CI = 0.79–0.84, $n = 165$, $r^2 = 0.962$) and 0.82 (95% CI = 0.80–0.84, $n = 154$, $r^2 = 0.965$) for the aboveground and whole-plant respiration rates, respectively.

4. DISCUSSION

Enquist *et al.* (2007) make some modifications to their original WBE model and restate that scaling exponents are close to 1.0 for seedlings owing to the violation of WBE assumptions in seedlings and shift to three-quarters in larger plants. However, our results indicate that scaling exponents of R_A versus M_A and R_T versus M_T relationships for larger trees (figure 1) differ significantly from three-quarters ($p = 0.0075$ and 0.0074 , respectively). Exponents (0.82–0.85) and confidence intervals for respiration–mass scaling using data for larger trees from the current study closely agree with the values reported by Reich *et al.* (2006) (i.e. 0.81–0.84) and Mori *et al.* (2010) (i.e. 0.838–0.844) across all observations in their studies, although the latter study uses fresh biomass. Furthermore, across all data-sets, scaling exponents of these relationships remain significantly different from three-quarters ($p < 0.0001$ for both). Thus, our results cast doubt on the validity of the $R \propto M^{3/4}$ scaling for larger plants. In addition, there is evidence that field-grown tree saplings have a metabolic scaling slope of nearly 1.0 (Reich *et al.* 2006), and that the metabolic scaling exponents of seedlings can vary during a short-term developmental period (Peng *et al.* in press). Together, we conclude that no ‘canonical metabolic scaling’ exists in plants and that the scaling exponent is nearly 1.0 for saplings, and smaller than 1.0 (but still significantly larger than three-quarters) as trees age. This is consistent with the previous findings (Niklas 2004; Cheng *et al.* 2009) that the scaling exponents between tree production rates and biomass vary from 1.0 to less than 1.0 with increasing biomass and stand age.

We argue that shifting of plant scaling exponents may partially result from the increasing accumulation of necromass as plants grow. That is, metabolic rates scale isometrically with the biomass of metabolic tissue (e.g. sapwood, leaf) and accumulation of non-metabolic tissue (e.g. heartwood) would therefore lead to a decline in the mass-specific metabolic rate and the scaling slope. Such an argument is reasonably supported by the previous findings that: (i) respiration allometry shifts over ontogeny (Mori *et al.* 2010; Peng *et al.* in press); (ii) scaling exponent for leaf mass and total mass shifts from 1.0 to approximately three-quarters as plants grow (Enquist *et al.* 2007); (iii) metabolism scales more closely with nitrogen content (expected to be more related to live tissue mass) than total mass (Reich *et al.* 2006). Our data do not enable us to directly quantify the scaling relationship between plant metabolism and nitrogen content. However, some insight is gained from the scaling of forest nitrogen content and biomass. Nitrogen content

scales isometrically with biomass in plants of similar age, but scales as the 0.85 power of biomass (95% CIs = 0.82–0.87) across the entire data (D. L. Cheng & K. J. Niklas 2009, unpublished data). This, combined with the result that R_T scaled as 0.85 power with M_T , yields a nearly isometrical relationship between R and N (i.e. $R_T \propto N^{0.85/0.85} = 1.00$). Therefore, our results provide some support for the notion (e.g. Ryan 1991; Reich *et al.* 2006) that plant metabolism is more restricted by nitrogen content.

Respiration rates are important to plant performance and the ecosystem carbon cycle. Progress into understanding the scaling of plant respiration rates requires additional data to explore the relationships among plant respiration rate, nitrogen content, metabolic, and non-metabolic biomass allocation patterns. It also needs theoretical interpretation of how and when plant metabolic patterns shift from isometry to allometry.

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