



Whether respiration in trees can scale isometrically with bole surface area: A test of hypothesis



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ABSTRACT

Respiration measurements of whole tree have been reported to give evidence that the relative respiration per volume/mass unit decreases with increase in tree size. Based on published datasets, a hypothesis that the relative respiration per area unit in trees can be independent of tree surface area was tested. There is a gap in the published data when the allometric studies of tree size do not intercept with studies on tree respiration. The indirect comparison showed that the scaling exponents, volume vs. surface area and respiration vs. stem volume, are slightly larger than they should be for the hypothesis to hold. The data studied showed that the relative respiration per area unit slightly increases with increase in tree surface area. Possible explanations of the relationship include a different distribution of metabolically active parts of stem and higher nitrogen content in larger trees. Also, the published datasets might include large fast growing trees which had higher growth respiration. To close the data gap, an experiment is required in which the respiration measurements should be performed for the same data as the measurements of scaling between stem volume and surface area.

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1. Introduction

Respiration is known to be one of the most fundamental processes in living organisms. The interest in respiration in trees originates both from the endeavor to understand the basics of life and the need to estimate the global role of forests in climate change.

Theory developed by West et al. (1997, 1999) (known as WBE theory) provided the basis for understanding allometrical relationships in a wide range of organisms. Among other relationship they inferred that the metabolism B of an organism should scale to its body mass M with the power exponent $3/4$, i.e. $B \propto M^{3/4}$. For smaller plants, WBE theory predicted an isometrical scaling, i.e. $B \propto M^0$ (Niklas, 2004).

Direct measurements of respiration on a whole plant level are rather scarce because of obvious technical difficulties. Nevertheless recent studies have provided important data on whole plant respiration and the scaling of it across species and plant sizes (Reich et al., 2006; Cheng et al., 2010, 2014; Mori et al., 2010). Reich et al. (2006) reported measurements of about 500 seedlings and saplings belonging to 43 species that were both laboratory and field-grown

specimens and argued that the whole-plant respiration rate scales approximately isometrically with total plant mass, which implies that the power exponent varies about unity. The authors observed also an isometric scaling of whole-plant respiration rate to total nitrogen content, with this isometric scaling being unaffected by various growth conditions like variation in light, nitrogen availability, temperature and atmospheric CO_2 concentration.

Cheng et al. (2010) also showed that the aboveground respiration rates scaled as 0.82-power of the biomass. In another study, Cheng et al. (2014) reported of the differences in scaling exponents for conifer and angiosperm tree seedlings: the scaling exponent for angiosperms was significantly higher (1.15) and for conifers lower (0.76) than unity. A combination of all the data in one dataset produced a scaling exponent of 1. Mori et al. (2010) also conducted an extensive research of direct measuring of respiration in seedlings and large trees and established that the scaling allometric exponent varied continuously from unity for smallest plants to $3/4$ in larger saplings and trees.

Obviously, as the tree total size increases the total respiration of the tree body increases as well. However the relative respiration per unit of body size may show at least two distinct behaviors as the body grows larger. Let R stand for the total respiration, γ for the scaling exponent and V for the plant body volume. (For the sake of consistence, I will use the plant volume V as a measure of the total

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body size assuming a good relationship between body volume and body mass.) So, the scaling relationship is given by

$$R \propto V^\gamma. \quad (1)$$

If the scaling exponent γ is equal to unity then per volume unit respiration should be constant, i.e. independent of V , since $R/V \propto V^0$. However, if the scaling exponent γ is less than unity then per volume unit respiration cannot be a constant but should be a decreasing function of V :

$$\frac{R}{V} \propto V^{\gamma-1}.$$

It is widely understood that for larger trees the relative respiration per volume unit decreases with tree volume. Ground for this relationship is due to the fact while the bodies of smaller plants are metabolically active in the whole volume, low-active stem wood constitutes most of the biomass of larger trees (Mori et al., 2010; Pruyn et al., 2005).

The same logic can be applied in respect to another measure of tree size, the stem surface area. The respiration of tree stem is largely located in the thin sheath of inner bark (Pruyn et al., 2002, 2005). Unlike stem volume, an increase in bole surface area may result in increased metabolically active tissues. It can be therefore hypothesized that the relative respiration per area unit can be a constant independent of the size of the surface area.

Mathematically, the hypothesis is expressed as follows. Because the relationship between stem volume V and stem surface area S may be expressed through a scaling exponent β as

$$V \propto S^\beta \quad (2)$$

then substituting Eq. (2) in (1) one gets the expression for the total respiration as

$$R \propto S^{\gamma\beta}.$$

Respectively, the relative respiration per area unit can be given as

$$\frac{R}{S} \propto S^{\gamma\beta-1}. \quad (3)$$

It is obvious that the scaling exponent $\gamma\beta-1$ in relation (3) may be equal to zero, and for this the relation between the scaling exponents β and γ should be as follows

$$\gamma = \frac{1}{\beta}. \quad (4)$$

Thus it can be hypothesized that respiration per unit area in larger trees can be a constant, i.e. independent of the amount of bole surface area. Formally, the hypothesis is presented in Eq. (4). Furthermore, one can note that the relation like $R/S \propto S^0$ implies isometrical relationship of respiration R with bole surface S because increase of surface by a unit would always add a constant value to the total amount of R . Thus the relation (4) could be read as a hypothesis of isometrical respiration scaling with bole surface. The aim of the study was to test the hypothesis on the basis of available public data.

2. Materials and methods

For the study, two kinds of data were used: (i) values for γ , i.e. for exponent scaling respiration to volume and (ii) values for β , i.e. exponent scaling volume to bole surface.

The values for γ were taken from the following sources (Reich et al., 2006; Cheng et al., 2010, 2014; Mori et al., 2010). Additionally, the dataset published by Cheng et al. (2010) was partly recalculated. The dataset contained DBHs, heights, log-transformed respiration and log-transformed mass parameters for a number of

species; among them are two conifers, *Pinus tabulaeformis* Carr. and *Pinus massoniana* Lamb. For these two conifers, a two-way volume equation was applied to get bole volumes (Inoue and Kurokawa, 2001). The bole surface areas were estimated through a cone surface formula. The data for the two Pine species were then fitted by a power function to get the scaling exponent β . Independently, the log-transformed respiration and mass measures were fitted by a linear function to get the exponent γ for the same combined Pine data.

The values for β were taken from a study by Inoue and Nishizono (2015) on relationship between stem volume and stem surface area in Japanese cedar and Japanese cypress forest stands. The values for β were also estimated from the datasets of levels-of-growing-stock studies in Douglas-fir (Marshall and Curtis, 2001; Curtis and Marshall, 2009). For control plots in the Douglas-fir datasets, mean bole volumes were calculated by dividing of stand volume by the number of living trees for every age available. From the same tables, stand diameters and heights were taken to estimate the mean bole surface areas using the cone formula. The mean volume was fitted against mean bole surface area by a power function to estimate the β power exponent.

All the fittings were performed by means of STATISTICA 6 software using an ordinary least squares approach.

3. Results

The values of γ and β scaling exponents, found in the literature and estimated, are summarized in Table 1. In most of the cases, if one of the two exponents was available the other was not. Due to limited data the unknown exponent was calculated with Eq. (4) and given in Table 1 in parentheses.

According to Eq. (4) if the relative respiration per area unit were independent of the surface area then the scaling exponents γ and β should compensate each other so that their product is equal to unity. An examination of the data in the Table 1 shows that the measured values of the scaling exponent β tend to be slightly bigger than those expected through Eq. (4). For example, the multi-species study by Mori et al. (2010) gives the minimal value of γ as 0.75 which through Eq. (4) corresponds to the maximal value of β of ≈ 1.33 . The study by Cheng et al. (2010) gave a value 0.82 for γ which gives ≈ 1.22 for β . Cheng et al. (2014) established that the scaling exponent γ for seedlings of two conifers was 0.76 which gives $\beta \approx 1.32$. The results for angiosperms suggest even larger γ values and therefore smaller β values (see Table 1). The actual measurements by Inoue and Nishizono (2015) however gave the values of β from 1.35 and larger.

The values for γ tend to be slightly larger than those expected through Eq. (4). For example, the maximum γ values estimated through Eq. (4) for data by Inoue and Nishizono (2015) and Hoskins and Iron Creek amount 0.74. The minimal γ value measured by Reich et al. (2006), Cheng et al. (2010, 2014) and Mori et al. (2010) was 0.75. All the comparisons mean that the product of γ and β appears to be slightly bigger than unity.

In the only case, data by Cheng et al. (2010), it was possible to estimate the scaling exponents γ and β for the same dataset (see recalculated in Table 1). Multiplication of γ and β for the recalculated data gives $1.568 \times 0.7429 \approx 1.16$. Thus the relation in Eq. (3) is given as follows: $R/S = S^{0.16}$.

4. Discussion

The estimations for γ and β values mean that the relative respiration per area unit should slightly increase with increase in the total bole surface area.

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