Lack of Evidence for 3/4 Scaling of Metabolism in Terrestrial Plants

Hai-Tao LI[1*], Xing-Guo HAN[2] and Jian-Guo WU[3]

(1. *Institute of Geographic Sciences and Natural Resources Research*, the Chinese Academy of Sciences, Beijing 100101, China;

2. *Laboratory of Quantitative Vegetation Ecology, Institute of Botany*, the Chinese Academy of Sciences, Beijing 100093, China;

3. *Faculty of Ecology, Evolution and Environmental Science, School of Life Sciences*,

Arizona State University, Tempe, AZ 85287-4501, USA)

Abstract: Scaling, as the translation of information across spatial, temporal, and organizational scales, is essential to predictions and understanding in all sciences and has become a central issue in ecology. A large body of theoretical and empirical evidence concerning allometric scaling in terrestrial individual plants and plant communities has been constructed around the fractal volume-filling theory of West, Brown, and Enquist (the WBE model). One of the most thought-provoking findings has been that the metabolic rates of plants, like those of animals, scale with their size as a 3/4 power law. The earliest, single most-important study cited in support of the application of the WBE model to terrestrial plants claims that whole-plant resource use in terrestrial plants scales as the 3/4 power of total mass, as predicted by the WBE model. However, in the present study we show that empirical data actually do not support such a claim. More recent studies cited as evidence for 3/4 scaling also suffer from several statistical and data-related problems. Using a forest biomass dataset including 1 266 plots of 17 main forest types across China, we explored the scaling exponents between tree productivity and tree mass and found no universal value across forest stands. We conclude that there is not sufficient evidence to support the existence of a single constant scaling exponent for the metabolism-biomass relationship for terrestrial plants.

Key words: metabolism; 3/4 power; scaling; terrestrial plants; water use.

The recent resurgence of interest in biological allometry, a search for organism size-related scaling relationships, has resulted in a number of exciting generalizations (Brown *et al.* 2004), as well as skepticism and criticisms (Dodds *et al.* 2001; Agutter and Wheatley 2004; Bokma 2004; Cyr and Walker 2004; Horn 2004; Kaitaniemi 2004; Kozlowski and Konarzewsk 2004; Makarieva *et al.* 2004; Tilman *et al.* 2004). A number of recent studies on allometric scaling are based on, or stimulated by, the fractal volume-filling theory of West *et al.* (1997, 1999; hereafter referred to as the WBE model). As the earliest, single most-important empirical support for the WBE model, Enquist *et al.* (1998) asserted that field measurements supported the model prediction of whole-plant resource use in terrestrial plants scaling as the 3/4 power of total mass (i.e. $Q_0 \propto M^{3/4}$, where Q_0 is the whole-plant xylem water transport assumed to be a surrogate for metabolism and M is plant mass). This is in contrast with the traditional expectation $Q_0 \propto M^{2/3}$, derived from consideration of Euclidean geometry and related to the −3/2 thinning rule (Yoda *et al.* 1963; Harper 1977; White 1981; Weller 1989; Lonsdale 1990; Hamilton *et al.* 1995; Dodds *et al.* 2001). The 3/4 scaling result is critical for attempts to apply WBE model predictions to whole populations and communities of plants (Enquist and Niklas 2001; Enquist 2002, 2003; Enquist and Niklas 2002; Niklas *et al.* 2003; Brown *et al.* 2004) and has been used to

transform data in order to test WBE predictions for plant communities (Ernest *et al.* 2003).

In the present study, we first revisit Enquist *et al.* (1998) to assess the extent to which that paper provides evidence for 3/4 scaling of metabolism and, in particular, whether the data allow for discrimination between 3/4 and 2/3 scaling. The sources of data cited in the paper of Enquist *et al.* (1998) are re-examined and the conclusions are reinterpreted based on additional data published since 1998. We then review other data that have been reported as evidence for 3/4 scaling and end the present paper with an exploration of the empirical evidence for scaling power between tree annual growth rate and tree biomass based on a complete Chinese forest biomass database. The present study is not intended to add to published criticisms of the theoretical foundations of the WBE model (Dodds *et al.* 2001; Dreyer and Puzio 2001; Banavar *et al.* 2002a, 2002b; Makarieva *et al.* 2003; Agutter and Wheatley 2004; Cyr and Walker 2004; Kozlowski and Konarzewsk 2004; Makarieva *et al.* 2004). Neither do we attempt to examine the applicability of the WBE model to animals or aquatic plants, for which evidence for 3/4 scaling (in animals and algae) seems strong (Niklas 1994; Ernest *et al.* 2003; Savage *et al.* 2004) regardless of some objections (Dodds *et al.* 2001; White and Seymour 2003).

1 Allometry of Metabolism in Relation to Stem Diameter

It has been argued (Enquist *et al.* 1998; Enquist 2002, 2003) that whole-plant xylem transport is an appropriate measure of nutrient and water use, as well as metabolic rates of plants, a claim that does not seem to be backed up by recent empirical studies (Midgley 2003). Enquist *et al.* (1998) did not compare metabolism and biomass data directly. Rather, separate allometries were combined to give an implied relationship. Using ordinary least squares regression (OLS), Enquist *et al.* (1998) found that $Q_0 \propto D^{1.778}$ where D is stem diameter, close to the WBE prediction that $Q_0 \propto D^{1.778}$, and that $D \propto M^{0.412}$, close to the predicted $D \propto M^{3/8}$. Together,

these results implied $Q_0 \propto M^{0.732}$, close to the predicted $Q_0 \propto M^{3/4}$. Both empirical results are examined below.

Enquist *et al.* (1998) related whole-plant transport Q_0 (measured from heat balance or radioactive tracers) to stem diameter D (see Enquist *et al.* 1998, fig. 1). Unfortunately, the source of the data used to generate the figure was not given. The references cited (Schulze *et al.* 1985; Kozlowski and Pallardy 1997) contain no data from measurements of heat balance or radioactive tracers. Several sapflow flux figures are given in Kozlowski *et al.* (1997), but the data shown are from heat pulse measurements, different from the heat balance in theory (Baker and van Bavel 1987; Baker and Nieber 1989). Schulze *et al.* (1985) does not contain any data from radioactive tracer measurements. Therefore, we must conclude that Enquist *et al.* (1998) collected the data themselves, citing Kozlowski *et al.* (1997) and Schulze *et al.* (1985) for methodology.

From the data presented in fig. 1, Enquist *et al.* (1998) found that $Q_0 \propto D^{1.778}$. It was concluded that this supported the prediction $Q_0 \propto D^2$ from the WBE model (West *et al.* 1997). This conclusion is problematic, because the 95% confidence interval (CI) for the exponent given in Enquist *et al.* (1998) is 1.644–1.912, which does not contain the predicted value of 2. Enquist *et al.* (1998) concluded that this mismatch between the data and predictions was due to measurement error (e.g. from overestimating the diameter of large trees; see Enquist *et al.* (1998), pp. 164), stressing that the underlying relationship is $Q_0 \propto D^2$. However, in light of more recent evidence, a more parsimonious conclusion is that 1.778 is close to the correct average scaling exponent and reflects the scaling of functional xylem area (A_s) with D. Whole-plant xylem transport measurements, expressed as litres per day, rely on multiplying sapflux density or sap velocity (V_{max}) with A_s (Waring and Roberts 1979; Meinzer *et al.* 2001). So, to understand how Q_0 scales with D, we need to know how both V_{max} and A_s scale with D: $Q_0 \propto V_{max}(D) \times A_s(D)$. Meinzer *et al.* (2001), in a study of 107 individuals from 24 tree species, found that $A_s \propto D^{1.764}$. Thus, $Q_0 \propto D^{1.778}$, the empirical result given

in Enquist *et al.* (1998), is very close to what we would expect if V_{max} did not vary systematically with D.

If the result of Meinzer *et al.* (2001), namely $A_s \propto D^{1.764}$, holds in general, then, for the WBE model prediction $Q_0 \propto D^2$ to also hold, V_{max} would have to increase with increasing D. In contrast, the available information suggests that, in terrestrial plants, V_{max} decreases with D. Meinzer *et al.* (2001) found that V_{max} declined sharply with increasing D over a range of D from 20 to 120 cm ($V_{max} = -0.084 + 0.39e^{-0.010\,5D}$; $R^2 = 0.85$; $n = 48$; see also figs. 3 and 4 in Meinzer *et al.* 2001). Meinzer (2003) found a similar relationship in individuals with smaller stem diameters. This, together with the result that A_s scales with D with an exponent less than 2 (see above), implies that, in general, the scaling exponent relating Q_0 and D is likely to be not only lower than the value of 2 predicted by the WBE model, but also lower than the empirical result of Enquist *et al.* (1998) of 1.778 (see example below). Importantly, the studies quoted above (Meinzer *et al.* 2001; Meinzer 2003) were published after 1998, so the information used above was not available to Enquist *et al.* (1998) at the time of publication. However, Enquist *et al.* (1998) continues to be quoted as evidence supporting the application of the WBE model to plants (e.g. Savage *et al.* 2004) and Meinzer *et al.* (2001) has also recently been quoted as additional evidence for the applicability of the WBE model to terrestrial plants (see Enquist 2002, pp. 1052).

We used additional data to examine the relationship between Q_0 and D in trees and compared our results with those of Enquist *et al.* (1998). Wullschleger *et al.* (1998) reported a survey of 52 studies providing quantitative estimates of maximum whole-plant water use for trees growing in stands or plantations. Using only data from thermal techniques and radioisotope tracers (Table 1), as was done by OLS in the paper of Enquist *et al.* (1998), gives a scaling exponent of 1.057: $\log_{10}(Q_0) = 0.373\,6 + 1.057\log_{10}(D)$ ($r^2 = 0.55$; $n=42$; $P < 0.000\,1$; 95% CI for exponent 0.751 8–1.362 2). This implies $Q_0 \propto D^{1.057}$. The result with reduced major axis regression shows that $Q_0 \propto D^{1.425}$ ($r^2 = 0.55$; $n=42$;

Table 1 Stem diameter (cm) and water use based on maximum daily rates (kg/d) for different species of trees as measured with thermal balance or heat dissipation methods (TM) and radioactive or stable isotopes (R/SI), excerpted from Wullschleger (1998, pp. 501–502)

Species	Method	Diameter (D)	Water use (Q_0)
Pinus taeda	R/SI	8	40
Carya illinoensis	TM	8	123
Quercus pertraea	TM	9	10
Picea abies	TM	10	10
Quercus pertraea	TM	10	11
Pinus caribaea	R/SI	13	100
Populus trichocarpa $\times$ *P. deltoids*	TM	15	51
Picea abies	TM	15	66
Cassipourea guianensis	TM	17	24
Eucalypus grandis	R/SI	18	94
Picea abies	TM	19	49
Pseudotsuga menziesii	TM	20	22
Cecropia longipes	TM	20	47
Pinus contorta	R/SI	25	25
Acacia dealbata	TM	25	59
Larix gmelinii	TM	25	67
Caryocar glabrum	TM	26	48
Sloanea berteriana	R/SI	27	140
Eucalypus grandis	TM	30	141
Hirtella glandulosa	TM	32	62
Pinus pinaster	TM	34	161
P. pinaster	TM	35	125
Picea abies	TM	36	175
Luehea seemannii	TM	37	129
Eucalyptus regnans	TM	37	151
Carapa procera	TM	38	52
Lecythis idatimon	TM	39	94
Abies amabilis	TM	40	98
Pinus radiate	TM	42	349
Spondias mombin	TM	44	80
Eperua falcate	TM	45	166
Vouacapoua Americana	TM	49	29
Fagus sylvatica	TM	54	137
Ficus insipida	TM	54	164
Dacryodes excelsa	R/SI	55	372
Eperua grandifolia	TM	55	151
Dicorynia guianensis	TM	57	212
Nothofagus fusca	TM	60	110
Dryobalanops aromatica	TM	75	310
Eucalyptus regnans	TM	89	285
Anacardium excelsum	TM	102	379
Pseudotsuga menziesii	R/SI	134	530

$P<0.000\ 1$; 95% CI for exponent 1.119–1.730). Both of the results for the scaling exponent are significantly lower than the value of 2 predicted by the WBE model or the empirical result of 1.778 reported by Enquist *et al.* (1998). Midgley (2003) also reported studies showing that whole-tree daily water flux varies approximately as D^1 in Douglas firs.

2 Allometry of Biomass in Relation to Stem Diameter

Enquist *et al.* (1998) provided a second empirical result, apparently confirming a separate prediction of the WBE model, of $D\propto M^{0.412}$, which, in combination with the result $Q_0\propto D^{1.778}$ (see above), implied $Q_0\propto M^{0.732}$. Enquist *et al.* (1998) stated "… other studies report relationships between stem diameter and above ground dry mass; averaging these gives $D\propto M^{0.412}$ ($n=78$, $SD = 0.356$), so that $Q_0\propto M^{0.732}$", citing two references as data sources, namely White (1981) and Smith and Brand (1983). However, details of how the data were selected from these sources were not given.

White (1981) gave the allometric relationship between stem dry weight, $M(stem)$, and diameter at breast height, D, as $M(stem)\propto D^a$, listing 51 values of a (Table 2). Smith and Brand (1983) compared total aboveground biomass $M(above)$ to D for herbs, shrubs, and small trees as $M(above)\propto D^a$ and presented 27 values of a (Table 2). Taken together, the 78 values of a given in White (1981) and Smith and Brand (1983) give an average value for a of 2.43 ($n=78$, $SD = 0.356$). This implies $D\propto M^{0.412}$, the result given in Enquist *et al.* (1998). Presumably, this was the calculation as

performed originally. However, this calculation ignored the difference between $M(stem)$, given in White (1981), and $M(above)$, given in Smith and Brand (1983) (Table 2). Smith and Brand (1983) also gave 49 values of a for the relationship between total woody aboveground biomass $M(above,woody)$ and D (Table 2). There is a statistically significant difference between the a values given for $M(above)$ and those for $M(above,woody)$ in Smith and Brand (1983) ($P=0.000\ 3$, t-test). Therefore, the choice of which set of a values from Smith and Brand (1983) to group with the a values in White (1981) would be expected to have a significant effect on the calculated average scaling exponent.

The species in White (1981) are all trees, so the a values for $M(above,woody)$ in Smith and Brand (1983) are likely to be the closest to the a values given in White (1981). In addition, Smith and Brand (1983) gave more values for $M(above,woody)$ than for $M(above)$, namely 49 compared with 27 (Table 2). Both these facts suggest that the most logical choice is the $M(above,woody)$ from Smith and Brand (1983). At the very least, the choice of the $M(above,woody)$ values is as valid as the choice of the $M(above)$ values or the choice to combine all data together. Grouping the a values for $M(above,woody)$ from Smith and Brand (1983) with the a values for $M(stem)$ from White (1981) gives $M\propto D^{2.695}$ ($n=100$; SD on exponent$=0.622$), implying $D\propto M^{0.371}$. Interestingly, this exponent is much closer to the prediction of the WBE model ($3/8=0.375$) than the result given by the grouping used in Enquist *et al.* (1998) of 0.412. However, if 0.371 is combined with the earlier result $Q_0\propto D^{1.778}$, as Enquist *et al.* (1998) did with

Table 2   Data available in the data sources cited by Enquist *et al.* (1998), where sets A and B were grouped together to give an allometry for mass versus stem diameter. The WBE model (West *et al.* 1997) predicts that the average value of a is 8/3 (=2.67). Grouping data sets A and C support this prediction

Dataset	Source	In the function $M\propto D^a$, M refers to	No. a values	Minimum, median, and maximum a values	Mean ($\pm SE$) a value
A	White (1981)	$M(stem)$: aboveground stem biomass	51	2.00, 2.45, 3.26	2.46±0.23
B	Smith and Brand (1983)	$M(above)$: aboveground total biomass	27	1.22, 2.38, 3.81	2.371±0.518
C	Smith and Brand (1983)	$M(above,woody)$: aboveground woody biomass	49	1.58, 2. 70, 5.26	2.939±0.788

0.412, the result implies $Q_0 \propto M^{0.660}$. This is remarkably close to the traditional expectation 2/3, but it is substantially lower than the WBE model prediction of 3/4. Thus, had the calculations in Enquist *et al.* (1998) used the other set of values for $M(above,woody)$ from Smith and Brand (1983), the result would have produced a scaling exponent of 2/3, instead of 3/4, for the metabolism and biomass relationship in terrestrial plants.

Niklas (1994), West *et al.* (1999), Enquist and Niklas (2001, 2002), and Niklas and Enquist (2002) contain no data for productivity or metabolism for terrestrial plants, whereas the results of others are equivocal. For example, Enquist *et al.* (1999) tested 3/4 scaling indirectly, because they used diameter growth rates only, and used an indirect test to compare these with the predictions of combining 3/4 scaling of metabolism with the $D \propto M^{3/8}$ prediction from the WBE model (see Enquist *et al.* 1999, box 1). Savage *et al.* (2004) reanalysed the metabolism versus diameter data in Enquist *et al.* (1998) by converting the D values into biomass ($M \propto D^{2.53}$) and regressing Q_0 against (predicted) biomass, resulting in $Q_0 \propto M^{0.736}$. However, the reported CI on the exponent was not able to exclude 2/3 (Savage *et al.* 2004).

Different studies often use different values for the scaling exponent in $D \propto M^a$. For example, Enquist *et al.* (1998) used 0.412, Enquist *et al.* (1999) used 3/8, and Savage *et al.* (2004) used 0.395. Different scaling exponents for the relationship between mass and diameter lead to different scaling exponents for the metabolism-biomass relationship. This makes it difficult to compare and interpret the calculated exponents for the metabolism-mass relationship among different studies. Thus, the results close to 3/4 reported by these studies rely on the particular choices for the mass-diameter allometry used in each case. It is of note that the average exponent of M versus D calculated from 279 compiled studies was significantly different from the theoretical one of 2.67 (Zianis and Mencuccini 2004).

3   Other Issues with Allometry of Metabolism for Terrestrial Plants

Brown (2004) and Savage *et al.* (2004) also reported

a value of close to 3/4 for biomass production (*B*; assumed as the surrogate of metabolic rate) versus mass in plants, based on data from (Ernest *et al.* 2003; exponent 0.759, 95% CI 0.75–0.76; see Savage *et al.* 2004, table 1). The exponent in this case did exclude 2/3 but, importantly, the biomass production data used in Ernest *et al.* (2003) were corrected for growing season temperature (*T*), multiplying by a factor of $e^{E/kT}$, where *e*, *E*, and *k*, but not *T*, are all constants (Gillooly *et al.* 2001); that is, $B(corrected)=Be^{E/kT}$. This correction of Ernest *et al.* (2003) implies that the original biomass production (*B*) is actually the function of *T* and could not be scaled as 0.759 to biomass. In other words, according to Gillooly *et al.* (2001), $B=constant\ f(T,M)=constant\ f_1(T)f_2(M)=constant\ e^{-E/kT}M^{3/4}$, which contradicts $B=constant'\ f_2(M)=constant'\ M^{3/4}$ and, hence, $B \propto f_2(M) \propto M^{3/4}$, which is consistent with the prediction of the WBE model. This seems to call into question all previous studies that claimed to support the 3/4 scaling but that did not consider temperature correction.

The most direct test of 3/4 scaling in terrestrial plants is that of Niklas and Enquist (2001), which used the stand-level data of Cannell (1982) for the average productivity and average mass of individuals per stand, reporting an exponent of 0.791 ± 0.030 by RMA. This value is closer to 3/4 than 2/3, but the interval contains neither value. Furthermore, the data appear to have been selected for this calculation: there were 600 appropriate stands claimed by the authors for computing productivity and mass for terrestrial metaphytes, but the later regressions were based on many fewer data points (n=178 for trees and 334 for all terrestrial and aquatic plants grouped together). The details of how this data selection was performed in this context were not given. Coincidentally, also using the data of Cannell (1982), Niklas *et al.* (2003) showed that n=178 was for log$M$ (*root*) versus log(tree density) for angiosperm-dominated communities, n=343 was for log$M$(*root*) versus log(tree density) for conifer-dominated communities, and n=347 was for log M(*root*) versus log (*tree density*) across all communities (see Niklas *et al.* 2003, pp. 462).

Unfortunately, no justification for the selection of data was given.

Also based on the data of Cannell (1982), Enquist (2003) broke the whole dataset into angiosperms and gymnosperms subsets, took leaf mass ($M(leaf)$) as the surrogate of annual biomass production (G), and separately presented two empirical exponents for annual biomass production and $M(total)$: 0.739 with a 95% CI of 0.646–0.831 for angiosperms, and 0.756 with a 95% CI of 0.664–0.846 for gymnosperms. Both the CIs could not discriminate 2/3 and 3/4 (see Enquist 2003, pp. 328). Furthermore, using $M(leaf)$ to replace G here may be problematic. According to Enquist and Niklas (2002), $M(leaf)=constant\ M(total)^{3/4}$, $M(leaf) =constant'\ M(stem)^{3/4}=constant''\ M(root)^{3/4}$, then we have $M(stem)=constant'''\ M(leaf)^{4/3}$, $M(root)=constant''''\ M(leaf)^{4/3}$, and $M(leaf)=constant\ M(total)^{3/4} =constant(M(leaf)+constant'''\ M(leaf)^{4/3}+constant''''\ M(leaf)^{4/3})^{3/4}$. Only if $M(leaf)$ is forced to be $M(leaf)^{4/3}$ is the latter equation tenable. Therefore, $M(leaf)=constant\ M(total)^{3/4}$ cannot hold true in this case. If $G \propto M(total)^{3/4}$ is true, then $M(leaf) \propto G$ is false.

4   Using Chinese Forest Biomass Dataset to Test

3/4 Scaling

We have used a Chinese forest biomass dataset for standing community biomass and productivity from 1 266 plots originally reported in Luo (1996) to test the scaling relationship between productivity, aboveground biomass ($M(above)$), and total biomass for trees ($M(total)$). The data covered 17 forest types (Tables 3–6) representative of the entire forest vegetation of China ranging from 18 to 53° N latitude and between elevations of 10 and 4 240 m above sea level. Most of these data came from inventories of the Forestry Ministry of China between 1989 and 1993. Additional data were sorted from published forest reports, as well as over 60 Chinese journals (*Acta Botanica Sinica*, *Acta Phytoecologica Sinica*, *Acta Ecologica Sinica*, *Chinese Journal of Ecology*, *Forestry Science of China* etc.), and some unpublished literature in the past 20 yr over China. The dataset includes site name, latitude, longitude, elevation, total stand biomass (Luo 1996), density for trees, total biomass for trees, total aboveground biomass for trees, and estimated annual production rate for trees (Luo 1996; Ni 2001), as well as all the available, information including the components of biomass and

Table 3   Ordinary least squares regression statistics for the relationship of log$G$ versus log$M(above)$, where G is annual biomass production and $M(above)$ is aboveground total biomass

Forest type	Sampling size	Intercept	Slope	Confidence interval	r^2
Boreal/temperate *Larix* forest	48	−1.378	0.745	0.693–0.796	0.948
Boreal/alpine *Picea-Abies* forest	168	−1.652	0.6155	0.579–0.652	0.868
Boreal *Pinus sylvestris* var. *mongolica* forest	10	−1.789	0.379	0.258–0.499	0.868
Temperate *Pinus tabulaeformis* forest	154	−1.330	0.743	0.714–0.772	0.944
Temperate mixed coniferous-broadleaved forest	22	−1.518	0.590	0.516–0.664	0.932
Temperate typical deciduous broadleaved forest	165	−1.147	0.783	0.740–0.826	0.887
Temperate/subtropical montane *Populus-Betula* deciduous forest	127	−1.09	0.849	0.802–0.895	0.913
Desert riverside woodland	9	−1.172	0.834	0.677–0.990	0.958
Subtropical mixed evergreen-deciduous broadleaved forest	22	−1.409	0.582	0.398–0.766	0.686
Subtropical evergreen broadleaved forest	238	−1.211	0.763	0.725–0.802	0.867
Sclerophyllous evergreen *Quercus* forest	9	−1.196	1.100	0.825–1.375	0.927
Tropical rainforest and monsoon forest	13	−1.187	0.711	0.500–0.922	0.833
Subtropical montane *Pinus yunnanensis* and *P. khasya* forest	46	−1.308	0.761	0.710–0.813	0.953
Subtropical *Pinus massoniana* forest	66	−1.185	0.713	0.648–0.778	0.882
Subtropical montane *Pinus armandii*, *P. taiwanensis*, and *P. densada* forest	55	−1.311	0.676	0.613–0.740	0.895
Subtropical *Cunninghamia lanceolata* forest	98	−1.333	0.644	0.562–0.726	0.717
Subtropical montane *Cupressus* and *Sabina* forest	16	−1.722	0.397	0.167–0.628	0.494
All data	1 266	−1.421	0.617	0.598–0.635	0.771

Table 4 RMA regression statistics for the relationship of log*G* versus log*M*(*above*), where *G* is annual biomass production and *M*(*above*) is aboveground total biomass

Forest type	Sampling size	Intercept	Slope	Confidence interval	r^2
Boreal/temperate *Larix* forest	48	−1.355	0.765	0.713–0.817	0.948
Boreal/alpine *Picea-Abies* forest	168	−1.628	0.661	0.624–0.698	0.868
Boreal *Pinus sylvestris* var. *mongolica* forest	10	−1.766	0.407	0.286–0.527	0.868
Temperate *Pinus tabulaeformis* forest	154	−1.302	0.765	0.736–0.794	0.944
Temperate mixed coniferous-broadleaved forest	22	−1.500	0.611	0.537–0.685	0.932
Temperate typical deciduous broadleaved forest	165	−1.090	0.831	0.788–0.874	0.887
Temperate/subtropical montane *Populus-Betula* deciduous forest	127	−1.047	0.888	0.842–0.934	0.913
Desert riverside woodland	9	−1.156	0.852	0.695–1.008	0.958
Subtropical mixed evergreen-deciduous broadleaved forest	22	−1.288	0.703	0.519–0.887	0.686
Subtropical evergreen broadleaved forest	238	−1.155	0.820	0.782–0.859	0.866
Sclerophyllous evergreen *Quercus* forest	9	−1.179	1.142	0.867–1.417	0.927
Tropical rainforest and monsoon forest	13	−1.119	0.779	0.568–0.989	0.833
Subtropical montane *Pinus yunnanensis* and *P. khasya* forest	46	−1.296	0.780	0.729–0.831	0.953
Subtropical *Pinus massoniana* forest	66	−1.138	0.759	0.694–0.824	0.882
Subtropical montane *Pinus armandii*, *P. taiwanensis*, and *P. densada* forest	55	−1.268	0.715	0.651–0.779	0.895
Subtropical *Cunninghamia lanceolata* forest	98	−1.178	0.7603	0.678–0.842	0.717
Subtropical montane *Cupressus* and *Sabina* forest	16	−1.548	0.565	0.335–0.795	0.494
All data	1 266	−1.334	0.703	0.684–0.721	0.771

Table 5 Ordinary least squares regression statistics for the relationship of log*G* versus log*M*(*total*), where *G* is annual biomass production and *M*(*total*) is the total biomass for trees

Forest type	Sampling size	Intercept	Slope	Confidence interval	r^2
Boreal/temperate *Larix* forest	48	−1.423	0.788	0.727–0.850	0.936
Boreal/alpine *Picea-Abies* forest	168	−1.701	0.622	0.584–0.660	0.863
Boreal *Pinus sylvestris* var. *mongolica* forest	10	−1.807	0.402	0.277–0.527	0.873
Temperate *Pinus tabulaeformis* forest	154	−1.388	0.756	0.725–0.787	0.939
Temperate mixed coniferous-broadleaved forest	22	−1.620	0.554	0.476–0.631	0.918
Temperate typical deciduous broadleaved forest	165	−1.175	0.834	0.783–0.884	0.868
Temperate/subtropical montane *Populus-Betula* deciduous forest	127	−1.200	0.851	0.807–0.896	0.920
Desert riverside woodland	9	−1.191	0.890	0.695–1.086	0.943
Subtropical mixed evergreen-deciduous broadleaved forest	22	−1.463	0.598	0.426–0.770	0.724
Subtropical evergreen broadleaved forest	238	−1.295	0.748	0.709–0.787	0.860
Sclerophyllous evergreen *Quercus* forest	9	−1.349	1.062	0.793–1.331	0.926
Tropical rainforest and monsoon forest	13	−1.253	0.740	0.513–0.968	0.824
Subtropical montane *Pinus yunnanensis* and *P. khasya* forest	46	−1.333	0.781	0.729–0.833	0.954
Subtropical *Pinus massoniana* forest	66	−1.238	0.709	0.642–0.776	0.874
Subtropical montane *Pinus armandii*, *P. taiwanensis*, and *P. densada* forest	55	−1.367	0.671	0.608–0.735	0.896
Subtropical *Cunninghamia lanceolata* forest	98	−1.367	0.663	0.582–0.744	0.735
Subtropical montane *Cupressus* and *Sabina* forest	16	−1.735	0.414	0.182–0.645	0.512
All data	1 266	−1.472	0.625	0.606–0.644	0.766

productivity (Luo 1996). A more detailed English description on the methodology of biomass measurement and annual production estimate for the dataset can be found in Ni (2001).

Ordinary least squares regression assumes there is no measurement error on independent variables and,

Table 6   RMA regression statistics for the relationship of log$G$ versus log$M(total)$, where G is annual biomass production and $M(total)$ is the total biomass for trees

Forest type	Sampling size	Intercept	Slope	Confidence interval	r^2
Boreal/temperate *Larix* forest	48	−1.396	0.815	0.754–0.877	0.935
Boreal/alpine *Picea-Abies* forest	168	−1.681	0.669	0.631–0.707	0.863
Boreal *Pinus sylvestris* var. *mongolica* forest	10	−1.786	0.430	0.305–0.556	0.873
Temperate *Pinus tabulaeformis* forest	154	−1.36	0.780	0.749–0.811	0.939
Temperate mixed coniferous-broadleaved forest	22	−1.601	0.578	0.501– 0.656	0.918
Temperate typical deciduous broadleaved forest	165	−1.108	0.895	0.844–0.945	0.868
Temperate/subtropical montane *Populus-Betula* deciduous forest	127	−1.164	0.888	0.843–0.932	0.92
Desert riverside woodland	9	−1.169	0.917	0.721–1.112	0.943
Subtropical mixed evergreen-deciduous broadleaved forest	22	−1.37	0.703	0.531–0.875	0.724
Subtropical evergreen broadleaved forest	238	−1.242	0.806	0.768–0.845	0.860
Sclerophyllous evergreen *Quercus* forest	9	−1.337	1.104	0.835–1.373	0.926
Tropical rainforest and monsoon forest	13	−1.187	0.816	0.588–1.043	0.823
Subtropical montane *Pinus yunnanensis* and *P. khasya* forest	46	−1.322	0.800	0.748–0.852	0.954
Subtropical *Pinus massoniana* forest	66	−1.192	0.758	0.691–0.825	0.874
Subtropical montane *Pinus armandii*, *P. taiwanensis*, and *P. densada* forest	55	−1.328	0.709	0.646–0.773	0.896
Subtropical *Cunninghamia lanceolata* forest	98	−1.23	0.774	0.693–0.854	0.735
Subtropical montane *Cupressus* and *Sabina* forest	16	−1.576	0.578	0.347–0.810	0.511
All data	1 266	−1.39	0.715	0.696–0.734	0.766

thus, can be used if the purpose is only to predict one variable based on the other. However, RMA regression, treating the two variables in the same way, is more appropriate than OLS when the independent variable is measured with error (Sokal and Rohlf 1981; McArdle 2003). We have noted that the scaling relationship of productivity with mass at the stand level is not rigorously equal to that at the individual level; however, the omission of this difference has been embodied in all previous empirical evidence supporting 3/4 scaling. With these caveats in mind, for a well-put comparison with the studies reviewed above, we used two regression methods, namely OLS and RMA, to explore the scaling exponents of G versus $M(above)$ and G versus $M(total)$.

The scaling exponents derived from OLS varied over a wide range from 0.379 to 1.100 among 17 forest types (Table 3). There are only six slope estimates for which the CI could embrace 3/4, two values included 2/3, and three values contained both 2/3 and 3/4. The remaining six values fell outside, between 2/3 and 3/4. The RMA results also show a wide range of scaling

exponents from 0.407 to 1.142 (Table 4). Among 17 forest types, six show exponents with a CI that contains 3/4, two contain 2/3, four accommodate both 3/4 and 2/3, and five drop outside between 2/3 and 3/4. Importantly, for all 1 266 plots pooled together, results of both OLS and RMA regression show that scaling exponents of G versus $M(above)$ are significantly different from 3/4 and 2/3. The scaling exponents obtained by OLS changed from 0.402 to 1.062 over 17 forest types (Table 5). Confidence intervals for five slope estimates could embrace 3/4, two included 2/3, and three contained both 2/3 and 3/4. The other seven values differed significantly from 2/3 and 3/4. The RMA results presented in Table 6 also demonstrate a wide range for scaling exponents from 0.430 to 1.104. Among 17 forest types, there are six presenting slopes with a CI that contains 3/4, two with a CI containing 2/3, four accommodating both 3/4 and 2/3, and five dropping outside between 2/3 and 3/4. For all data, results of both OLS and RMA show that scaling exponents of G versus $M(total)$ are significantly different from both 3/4 and 2/3.

Table 7　Correlation coefficients between slope estimates and sample size and significance tests

Type of regression equation		r^2	$r^2_{0.05}$ (based on *t*-test)	n
log$G$ *vs* log$M$(*above*)	OLS	0.028 2	0.456	17
	RMA	0.023 9	0.456	17
log$G$ *vs* log$M$(*total*)	OLS	0.026 1	0.456	17
	RMA	0.023 1	0.456	17

Table 8　Dependence of intercept on slope in regression equations for the 17 independent subsets

Type of regression equation		Intercept *vs* slope	r^2	P	n
log$G$ *vs* log$M$(*above*)	OLS	Intercept = −2.061+1.018slope	0.671	5.82×10^{-5}	17
	RMA	Intercept = −2.074+1.034slope	0.607	2.3×10^{-4}	17
log$G$ *vs* log$M$(*total*)	OLS	Intercept = −2.076+0.943slope	0.625	1.59×10^{-4}	17
	RMA	Intercept = −2.097+0.968slope	0.569	4.72×10^{-4}	17

Considering that different sample sizes may bias the slope estimates, we conducted correlation analysis and found no significant correlation between them (Table 7). Generally, our results showed that the exponents vary widely among the forest types investigated and the general exponent could not validate either theoretical prediction from a fractal volume-filling perspective or traditional Euclidean geometric considerations, so caution must be taken in interpreting and applying these empirical scaling relationships. In Tables 3–6, we further used 17 independent datasets of forest types to explore the dependence of intercept on slope estimates and found that the intercept could be determined by slope because there was a strong correlation between them (Table 8).

5　Conclusions

The results of the present study do not support the existence of a unique scaling exponent of 3/4 or 2/3 for the metabolism and biomass of terrestrial plants. We have shown that existing data have considerable uncertainty in terms of what the average value of the scaling exponent may be. For example, published scaling exponents for mass-diameter allometry cover a wide range for terrestrial plants (at least 1.2–5.3; Table 2), and population-level productivity for a given average biomass varies by a factor of 100 (see Niklas and Enquist 2001, fig.1a). Our analysis of a Chinese forest

biomass dataset further confirmed that the slope estimate may differ among different tree-dominated communities and populations. Thus, the validity of the WBE model and its predictions for terrestrial plants is unwarranted. Because the relationships among biomass, stem diameter, and primary production change significantly across different plant species and communities, the scaling exponent for the metabolism-biomass relationship does not seem to converge to a single constant value.

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