

REVIEW

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Testing allometric scaling relationships in plant roots

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Abstract

Background: Metabolic scaling theory predicts that plant productivity and biomass are both size-dependent. However, this theory has not yet been tested in plant roots.

Methods: In this study, we tested how metabolic scaling occurs in plants using a comprehensive plant root dataset made up of 1016 observations from natural habitats. We generated metabolic scaling exponents by log-transformation of root productivity versus biomass.

Results: Results showed that the metabolic scaling exponents of fine root (< 2 mm in diameter) productivity versus biomass were close to 1.0 for all ecosystem types and functional groups. Scaling exponents decreased in coarse roots (> 2 mm in diameter).

Conclusions: We found isometric metabolic scaling in fine roots, a metabolically active organ similar to seedlings or saplings. Our findings also indicate a shift in metabolic scaling during plant development. Overall, our study supports the absence of any unified single constant scaling exponent for metabolism-biomass relationships in terrestrial plants, especially for forests with woody species.

Keywords: Allometry, Biomass, Metabolic scaling, Plant roots, Productivity

Introduction

Many theories suggest that plant and animal body sizes scale with fundamental characteristics, such as metabolic rate (West et al. 1997, 2001; Enquist et al. 2002; O'Connor and Bernhardt 2018; Burger et al. 2019; Pettersen et al. 2019). The scaling relationship is determined by the power function:

$$Y = Y_0 X^b,$$

where Y is an attribute, in this case, metabolic rate, Y_0 is a normalization constant (antilog of the intercept in a log–log plot), and b is the scaling exponent (slope in a log–log plot). The metabolic scaling exponent b was once widely

considered to be 2/3, based on studies of differently sized dogs (Rubner 1883). However, Kleiber (1932), found that b for metabolic scaling was closer to 3/4 in 1932. Kleiber's law, or the 3/4-power law, is still widely used and supported by many metabolic studies showing quarter-power scaling for many animals, plants, and single cells (Beuchat 1997; Oviedo et al. 2003; West and Brown 2005; da Silva et al. 2006; Nidziedo 2018; Yoshikawa et al. 2019). Allometric scaling relationships are not only found in metabolic rates, but also other biological, chemical, ecophysiological and physical traits in animals and plants (Enquist et al. 1998; Glazier 2006; Strauss and Reinhold 2010; Slot et al. 2014; Yuan and Chen 2015; Ballesteros et al. 2018).

According to the metabolic theory of ecology that predicts a nonlinear power law for NPP scaling based on an ideally and fractally vascular system (i.e., $NPP = a \times (\text{biomass})^b$) (Enquist et al. 1998; West et al. 1999; Niklas and Enquist 2001; Brown et al. 2004; Enquist et al. 2009; West et al. 2009), a linear model (i.e., $\log NPP = a + b \times (\log(\text{biomass}))$) can describe this relationship in log–

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log space when using $(\log\text{NPP})/(\log\text{B})$ axes that are standard in allometry. Similar to biogeographical species–area and productivity–diversity relationships, allometric scaling research based on the metabolic theory initially focused on bivariate power laws and then argued about a theoretically ideal (or canonical) power law exponent b . More recently, multiple predictor variables have been rapidly evolved to be recognized because the coefficient a and other predictors are also important to their respective response variables (Rosenzweig 1995; Lomolino 2000; Jenkins and Pierce 2017).

However, the universal application of Kleiber’s law is contested (Brown et al. 2005; da Silva and Barbosa 2009; Glazier 2010; Hamilton et al. 2011; Glazier 2014; Yates et al. 2020). For example, Kozłowski and Konarzewski (2004) argue that Kleiber’s law cannot be explained using any limiting factor because metabolic rates vary by factors of 4–5 between rest and activity. Also, Reich et al. (2006) demonstrated that the dark respiration rate in whole seedlings scales isometrically with plant mass, showing that the allometric Kleiber’s law cannot be extended to vascular plants. Li et al. (2005, 2006) asserted that there is no sufficient evidence to support the existence of a single constant scaling exponent for the metabolism–biomass relationship for terrestrial plants. However, most studies of metabolic scaling in vascular plants are based on aboveground parts, and much less is known about plant roots, which are important to the ecosystem but difficult to measure (Hanson et al. 2000; Sibly et al. 2012; Starko and Martone 2016; Jenkins and Pierce 2017; Minden et al. 2018; Ogawa 2019).

Like other plant organs, roots scale according to metabolic, chemical, and structural traits, in a manner sometimes consistent with animal scaling (Niklas 2006; Reich et al. 2006; Marba et al. 2007; Hamilton et al. 2011; Rudgers et al. 2019). Roots are metabolically active organs expected to scale according to Kleiber’s law. For example, fine root productivity may allometrically scale with biomass, because fine root productivity is dictated by metabolic rate and often serves as a surrogate measure for fine root metabolic rate (West et al. 1999; Niklas and Enquist 2001; Enquist and Niklas 2002). Importantly, due to different morphology, compared with stems and leaves plant root systems are more like “open network”, water and nutrient uptake can occur along any part of the root network (Biondini 2008). Therefore, the scaling exponent in roots is unlikely to be the same as for aboveground parts. Additionally, root productivity and plant biomass both change across soil environments at local and global scales (Vogt et al. 1998; Hertel and Leuschner 2002; Yuan and Chen 2012a; Yuan and Chen 2012b; Yuan et al. 2018). However, it is unknown whether plant root productivity allometrically scales with biomass or if the allometric scaling exponent would follow the 3/4-power law.

Plant roots show both similarity and difference in comparison to aboveground parts. Terrestrial productivity is greatest in lowland tropical forests near the equator and declines toward the temperate regions to the north or south (Huston and Wolverton 2009; Yuan et al. 2011). Given that plant roots, particularly fine roots < 2 mm in diameter, are a significant proportion of total plant productivity (Nadelhoffer and Raich 1992; Vogt et al. 1996; Clark et al. 2001; Yuan and Chen 2010), root productivity is expected to vary similarly to aboveground productivity. However, global patterns of root productivity are unclear. For instance, fine root biomass is high in grasslands but low in forests (Jackson et al. 1997; Schenk and Jackson 2002; Cleland et al. 2019). Furthermore, fine root productivity and biomass differ between life forms (Bauhus and Messier 1999; Pavon 2005). The differences between biomes and life forms suggest that plant root productivity and biomass depend on organism size. However, no studies have tested whether scaling between plant root productivity and biomass changes across ecosystems and life forms. Here, we examined how plant root productivity scales with biomass by compiling 327 published reports with 826 estimates of root productivity and biomass that cover the global terrestrial ecosystem.

Materials and methods

To examine the relationship between root biomass and production in natural habitats, we searched the keywords “plant roots, biomass, production/productivity” in the Web of Science database (1965–2020) to retrieve relevant data for our meta-analysis using the following inclusion criteria: (1) reported at least one parameter including plant roots or belowground biomass, production; (2) included the mean, standard deviation or error, and sample size of reported parameters; and (3) reported the measurements of roots biomass and production, and defined/described the ecosystem types, life forms, leaf phenology and phylogeny of the experimental site. We used Image-Pro Plus (Media Cybernetics, Rockville, Maryland, USA) to extract numerical data from graphs. Data of root biomass ($\text{Mg}\cdot\text{ha}^{-1}$) were derived from direct measurement via soil coring. Data for estimating root production ($\text{Mg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$) were derived from eleven methods: ingrowth, minirhizotrons, max-min, decision matrix, sum of all positive changes, sum of significant positive changes, compartment-flow model, N budget, C budget, isotopic and correlation methods. To avoid those using root biomass as a proxy for root production, we excluded the data of estimating root production by correlation methods. Thus the variables of root biomass and production in our dataset were independent from each other.

Our dataset included 1016 observations compiled from 327 published studies of plant root productivity and biomass in natural habits. The dataset excluded agricultural, fertilized, and greenhouse studies (a list of the data

Table 1 Fine root biomass, productivity (Mean ± 1 S.E. with range in parentheses), and number of samples (*n*) for plant groups by ecosystem types, life forms, leaf phenology, and phylogeny. Differences between ecosystem types are tested using a one-way ANOVA with a Tukey’s post hoc test for significance. Significant differences ($\alpha = 0.05$) are indicated by different letters

Plant groups	Biomass (Mg·ha ⁻¹)	Productivity (Mg·ha ⁻¹ ·yr ⁻¹)	<i>n</i>
Ecosystem types			
Boreal forests	2.23 ^B ± 0.14 (0.04–10.70)	2.72 ^C ± 0.17 (0.12–14.19)	184
Temperate forests	3.19 ^B ± 0.21 (0.02–30.00)	2.81 ^C ± 0.22 (0.07–35.09)	254
Subtropical forests	2.84 ^B ± 0.27 (0.08–14.48)	2.61 ^C ± 0.24 (0.05–10.40)	101
Tropical forests	3.54 ^B ± 0.29 (0.19–20.58)	2.98 ^C ± 0.27 (0.06–20.84)	118
Temperate grasslands	10.10 ^A ± 1.64 (0.32–65.70)	4.87 ^{BC} ± 0.83 (0.21–29.31)	50
Tropical grasslands	8.71 ^A ± 1.83 (1.22–24.00)	6.97 ^{AB} ± 1.33 (3.06–15.92)	12
Tundra	9.75 ^A ± 2.85 (0.23–28.25)	6.66 ^{AB} ± 1.77 (0.36–19.70)	16
Wetlands	8.97 ^A ± 1.19 (0.04–49.01)	8.03 ^A ± 1.24 (0.10–54.45)	91
Life forms			
Forbs	14.35 ^A ± 8.31 (0.70–40.60)	10.55 ^A ± 5.58 (1.00–29.17)	5
Graminoids	11.62 ^A ± 1.17 (0.04–65.70)	8.76 ^A ± 1.09 (0.10–54.45)	103
Shrubs	10.61 ^A ± 2.52 (0.36–28.25)	7.58 ^A ± 1.67 (1.02–19.70)	16
Trees	2.95 ^B ± 0.11 (0.02–30.00)	2.74 ^B ± 0.11 (0.05–35.09)	702
Leaf phenology			
Deciduous	6.35 ^A ± 0.48 (0.04–65.71)	4.81 ^A ± 0.41 (0.05–54.45)	333
Evergreen	3.85 ^B ± 0.25 (0.02–54.92)	2.84 ^B ± 0.14 (0.04–35.09)	493
Phylogeny			
Angiosperm	5.34 ^A ± 0.34 (0.04–65.71)	4.18 ^A ± 0.27 (0.05–54.45)	497
Gymnosperm	2.59 ^B ± 0.14 (0.02–15.00)	2.79 ^B ± 0.16 (0.11–35.09)	329
All	4.24 ± 0.22 (0.02–65.71)	3.63 ± 0.19 (0.04–54.45)	826

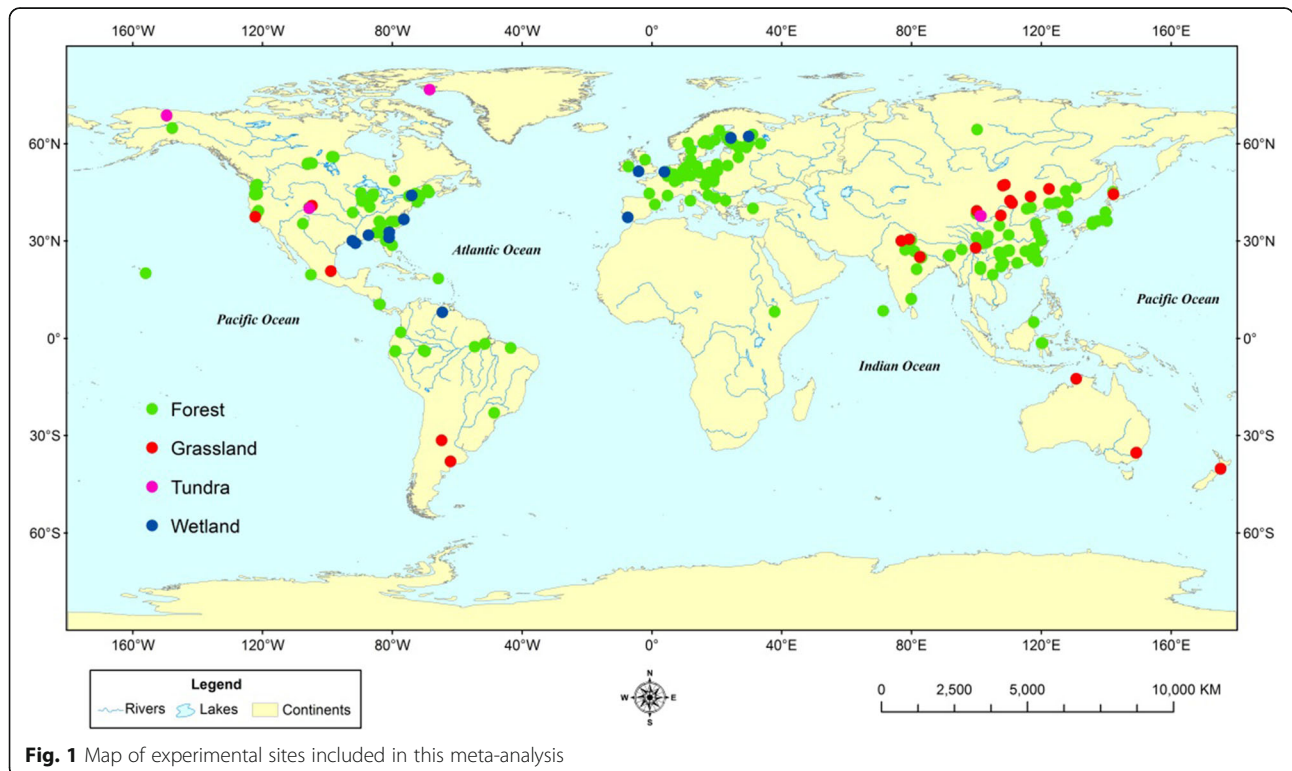
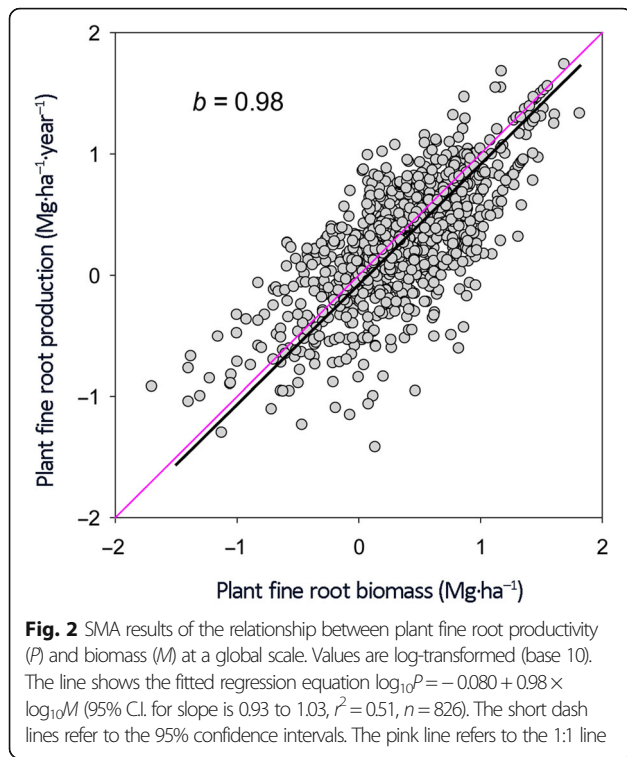


Fig. 1 Map of experimental sites included in this meta-analysis



sources is found in the Electronic [Supplementary Material](#)). The combined data represented 257 sites and covered a wide range of ecosystems, including arctic tundra, forest, grassland, and wetland (Fig. 1). We further classified forests into four types: boreal, temperate, subtropical, and tropical. Site elevation ranged from 5 to 3600 m above sea level and latitude ranged from -40°S to 76°N . Mean annual temperature ranged from -11°C to 27°C and mean annual rainfall ranged from 120 to 10,370 mm per year, covering most areas with a natural distribution of plants (Table 1 and supporting information (SI)). The broad coverage of the dataset allowed us to quantify scaling relationships between root productivity and plant biomass. Plant roots were classified into fine roots (< 2 mm in diameter) and coarse roots (> 2 mm in diameter).

We log₁₀-transformed the data for root productivity and biomass. Normality tests were performed on the transformed data. When neither root productivity or biomass could be clearly separated into independent or dependent categories, we used reduced major axis regression (RMA), a Model II regression method (Rohlf and Sokal 1981), to characterize scaling relationships. We performed Model II regression analysis in R using the LMODEL2 package (Legendre 2008). Two-tailed t -tests determined whether slopes were significantly

Table 2 Summary of model II (reduced major axis) regressions of log₁₀- fine-root productivity (y) and -biomass (x) by ecosystem types, life forms, leaf phenology, and phylogeny. n is the number of samplings

Biome	Intercept	95% CI intercept	Slope	95% CI slope	r^2	n
Ecosystem types						
Boreal forests	0.082	0.108 ~ 0.053	1.003	0.833 ~ 1.139	0.238	184
Temperate forests	-0.036	-0.057 ~ -0.015	0.930	0.853 ~ 1.015	0.511	254
Subtropical forests	-0.125	-0.177 ~ -0.080	1.112	0.958 ~ 1.292	0.433	101
Tropical forests	-0.131	-0.203 ~ -0.068	1.078	0.923 ~ 1.258	0.286	118
Temperate grasslands	-0.279	-0.417 ~ -0.166	0.938	0.780 ~ 1.128	0.594	50
Tropical grasslands	0.166	-0.287 ~ 0.423	0.731	0.415 ~ 1.284	0.287	12
Tundra	-0.085	-0.212 ~ 0.020	0.944	0.774 ~ 1.151	0.878	16
Wetlands	-0.149	-0.197 ~ -0.105	1.026	0.944 ~ 1.115	0.843	91
Life forms						
Forbs	0.238	-0.350 ~ 0.496	0.738	0.323 ~ 1.685	0.747	5
Graminoids	-0.036	-0.140 ~ 0.082	0.928	0.814 ~ 1.057	0.850	38
Shrubs	0.043	-0.125 ~ 0.176	0.828	0.655 ~ 1.047	0.829	16
Trees	-0.050	-0.068 ~ -0.035	1.026	0.969 ~ 1.087	0.400	702
Leaf phenology						
Deciduous	-0.135	-0.165 ~ -0.105	0.983	0.920 ~ 1.050	0.626	333
Evergreen	-0.011	-0.031 ~ 0.008	1.010	0.942 ~ 1.082	0.387	493
Phylogeny						
Angiosperm	-0.136	-0.162 ~ -0.111	1.016	0.959 ~ 1.077	0.564	497
Gymnosperm	0.046	0.028 ~ 0.063	0.967	0.890 ~ 1.050	0.418	329
All	-0.080	-0.121 ~ -0.039	0.980	0.934 ~ 1.029	0.508	826

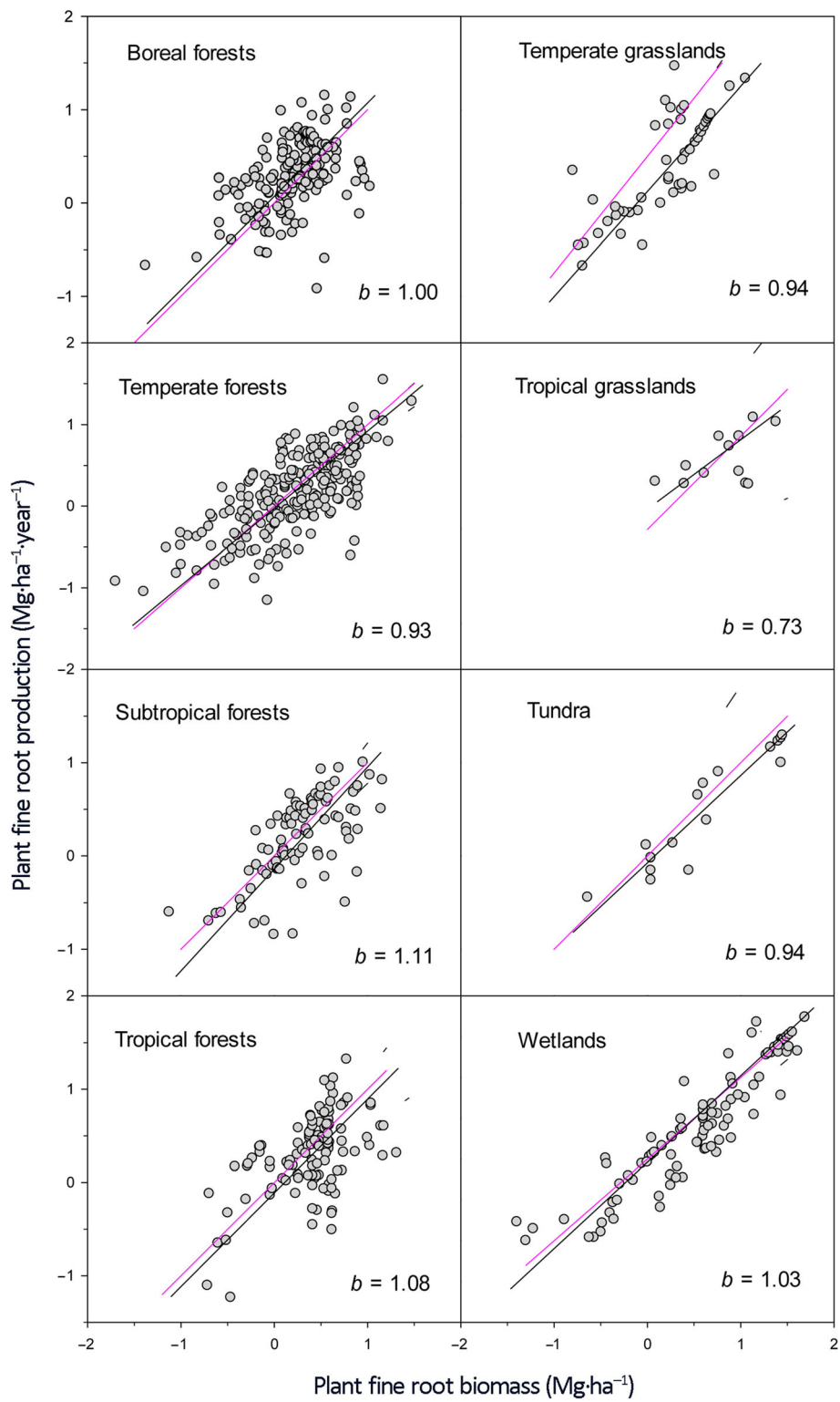


Fig. 3 (See legend on next page.)

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Fig. 3 SMA results of the relationship between plant fine root productivity (P) and biomass (M) among ecosystems. Values are log-transformed (base 10). The lines show the fitted regression equations for boreal forests: $\log_{10}P = 0.082 + 1.00 \times \log_{10}M$ (95% C.I. for slope is 0.83 to 1.14, $r^2 = 0.24$, $n = 184$); temperate forests: $\log_{10}P = -0.036 + 0.93 \times \log_{10}M$ (95% C.I. for slope is 0.85 to 1.02, $r^2 = 0.51$, $n = 254$); subtropical forests: $\log_{10}P = -0.125 + 1.11 \times \log_{10}M$ (95% C.I. for slope is 0.96 to 1.29, $r^2 = 0.43$, $n = 101$); tropical forests: $\log_{10}P = -0.131 + 1.08 \times \log_{10}M$ (95% C.I. for slope is 0.92 to 1.26, $r^2 = 0.29$, $n = 118$); temperate grasslands: $\log_{10}P = -0.279 + 0.94 \times \log_{10}M$ (95% C.I. for slope is 0.78 to 1.13, $r^2 = 0.59$, $n = 50$); tropical grasslands: $\log_{10}P = 0.166 + 0.73 \times \log_{10}M$ (95% C.I. for slope is 0.42 to 1.28, $r^2 = 0.29$, $n = 12$); tundra: $\log_{10}P = -0.085 + 0.94 \times \log_{10}M$ (95% C.I. for slope is 0.77 to 1.15, $r^2 = 0.88$, $n = 16$); wetlands: $\log_{10}P = -0.149 + 1.03 \times \log_{10}M$ (95% C.I. for slope is 0.94 to 1.12, $r^2 = 0.84$, $n = 91$). The short dash lines refer to the 95% confidence intervals. The pink line refers to the 1:1 line

different from the number 1. All statistical analyses were performed in R version 3.62 for Windows.

Results

When we pooled all data ($n = 826$), we found that fine root productivity ($\text{Mg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$) positively ($r^2 = 0.508$, $p < 0.001$) correlated with biomass ($\text{Mg}\cdot\text{ha}^{-1}$), with $b = 0.980$ (95% CI of $b = 0.934\text{--}1.027$, $\log_{10}Y_0 = -0.055$). The analysis was based on a reduced major axis (RMA) regression of log transformed Eq. 1 (Fig. 2). The value of b was not significantly different from 1.0. Slope estimates generated by ordinary least squares (OLS) or standard major axis

(SMA) did not differ from estimates generated by RMA. We further analyzed the scaling relationships of fine root productivity versus biomass across ecosystem types and plant functional groups. We found that the scaling slope was consistent across most ecosystem types (except for tropical grasslands), with b close to 1.0 with 95% CIs (Table 2, Fig. 3), and among major functional groups, the scaling exponents of b were again close to 1.0 with 95% CIs for graminoids and trees (Fig. 4).

Because large samples from forests were obtained, we also compared scaling slopes between leaf phenology and phylogeny in forest ecosystems (Fig. 5). We again

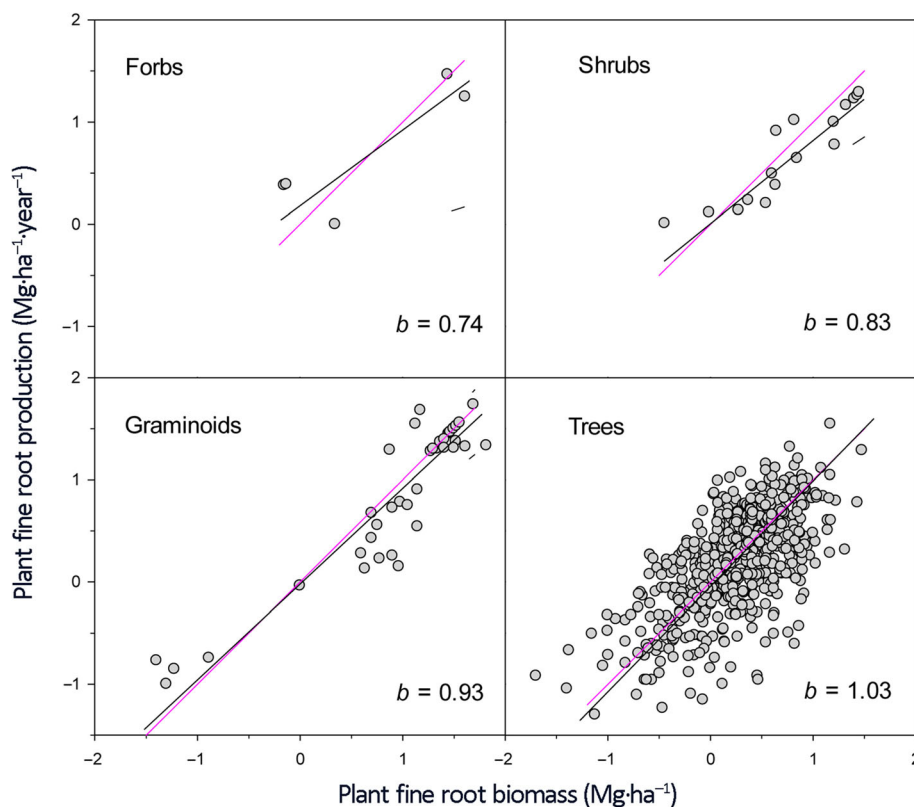


Fig. 4 SMA results of the relationship between plant fine root productivity (P) and biomass (M) among life forms. Values are log-transformed (base 10). The lines show the fitted regression equations for forbs: $\log_{10}P = 0.238 + 0.74 \times \log_{10}M$ (95% C.I. for slope is 0.32 to 1.69, $r^2 = 0.75$, $n = 5$); graminoids: $\log_{10}P = -0.036 + 0.93 \times \log_{10}M$ (95% C.I. for slope is 0.81 to 1.06, $r^2 = 0.85$, $n = 38$); shrubs: $\log_{10}P = 0.043 + 0.83 \times \log_{10}M$ (95% C.I. for slope is 0.66 to 1.05, $r^2 = 0.83$, $n = 16$); trees: $\log_{10}P = -0.050 + 1.03 \times \log_{10}M$ (95% C.I. for slope is 0.97 to 1.09, $r^2 = 0.40$, $n = 702$). The short dash lines refer to the 95% confidence intervals. The pink line refers to the 1:1 line

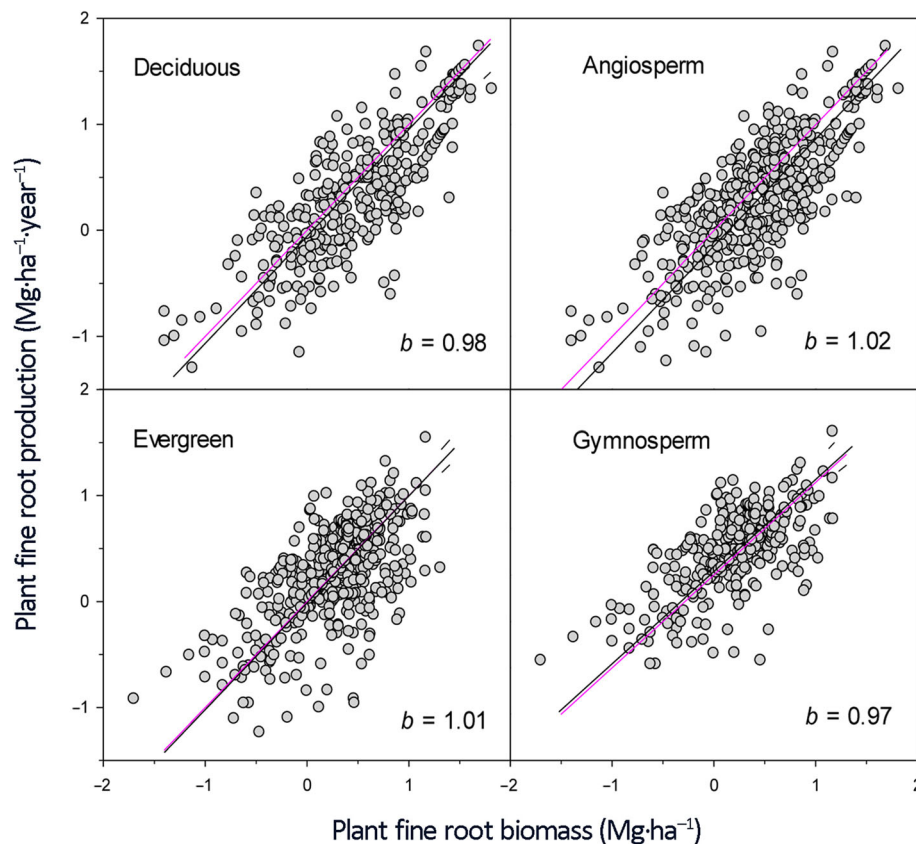


Fig. 5 SMA results of the relationship between plant fine root productivity (P) and biomass (M) for plants with different leaf phenology and phylogeny. Values are log-transformed (base 10). The lines show the fitted regression equations for deciduous species: $\log_{10}P = -0.135 + 0.98 \times \log_{10}M$ (95% C.I. for slope is 0.92 to 1.05, $r^2 = 0.63$, $n = 333$); evergreen species: $\log_{10}P = -0.011 + 1.01 \times \log_{10}M$ (95% C.I. for slope is 0.94 to 1.08, $r^2 = 0.38$, $n = 493$); angiosperm species: $\log_{10}P = -0.136 + 1.02 \times \log_{10}M$ (95% C.I. for slope is 0.96 to 1.08, $r^2 = 0.56$, $n = 497$); gymnosperm species: $\log_{10}P = 0.046 + 0.97 \times \log_{10}M$ (95% C.I. for slope is 0.89 to 1.05, $r^2 = 0.42$, $n = 329$). The short dash lines refer to the 95% confidence intervals. The pink line refers to the 1:1 line

found that results for RMA regression for fine root productivity-biomass scaling (Table 2) had a scaling exponent b near 1.0. However, the scaling relationships in coarse roots (> 2 mm in diameter) differed from fine roots (< 2 mm in diameter), such that the scaling exponent b decreased from ≈ 1.0 in fine roots to 0.86 in coarse roots (Table 3, Fig. 6).

Discussion

We found that the power law scaling exponent for plant fine root productivity versus biomass is close to 1.0 in many ecosystems (except for tropical grasslands with

small data size), functional groups (except for forbs and shrubs with small data size), and two leaf phenology and phylogeny groups in forest ecosystems. The metabolic theory represents ideal systems and has been debated (Isaac and Carbone 2010; Glazier 2014, 2015). Lomolino (2000) first pointed out that it was problematic to use power law model to investigate all qualitative patterns in the nature, and the constant Y_0 was often neglected with respect to the exponent b . Nevertheless, Y_0 varied by orders of magnitudes for biogeographical species-area and productivity-diversity relationships. Our dataset were compiled with 1016 observations from various

Table 3 Summary of model II (reduced major axis) regressions of \log_{10} - root productivity (y) and root biomass (x) by root sizes. n is the number of samplings. Slopes statistically greater or smaller than 1 ($p < 0.05$) are indicated by boldface font

Root sizes	Intercept	95% CI intercept	Slope	95% CI slope	r^2	n
< 1 mm	0.123	0.106 ~ 0.139	0.914	0.803 ~ 1.041	0.539	109
1–2 mm	−0.227	−0.298 ~ −0.164	1.009	0.901 ~ 1.129	0.745	81
> 2 mm	−0.178	−0.241 ~ −0.123	0.878	0.784 ~ 0.986	0.361	190
All	−0.075	−0.103 ~ −0.047	0.856	0.796 ~ 0.920	0.486	380

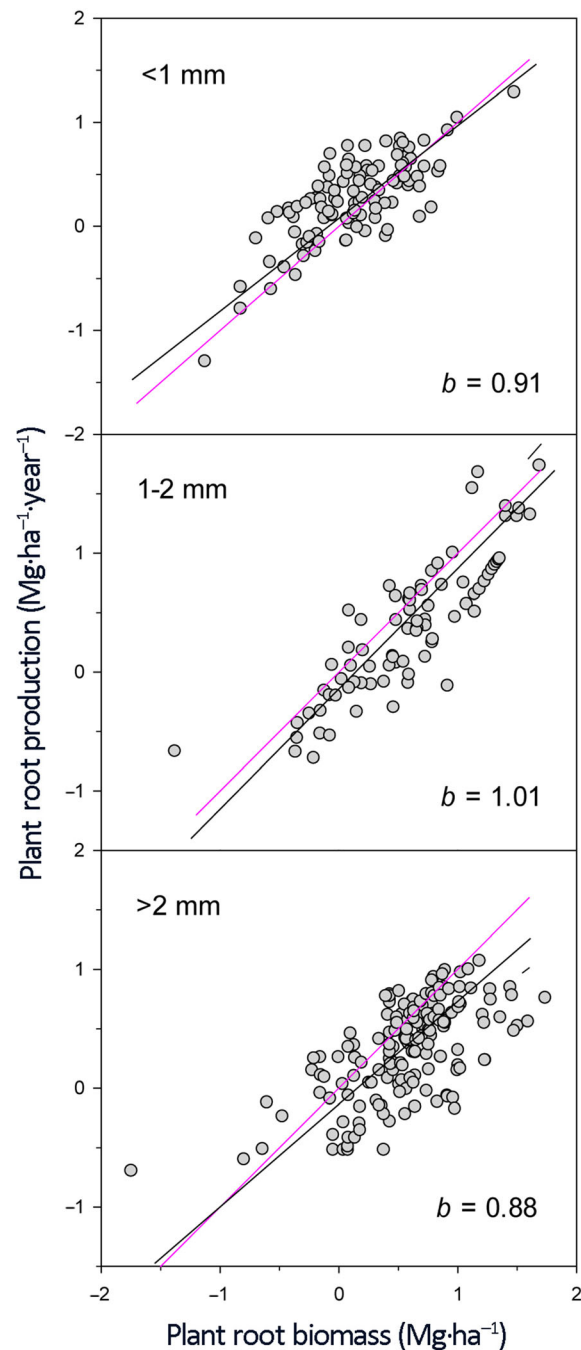


Fig. 6 SMA results of the relationship between plant fine root productivity (P) and biomass (M) for roots with different diameters. Values are log-transformed (base 10). The lines show fitted regression equations for fine roots of < 1 mm in diameter: $\log_{10}P = 0.123 + 0.91 \times \log_{10}M$ (95% C.I. for slope is 0.80 to 1.04, $r^2 = 0.54$, $n = 109$); fine roots of 1–2 mm in diameter: $\log_{10}P = -0.227 + 1.01 \times \log_{10}M$ (95% C.I. for slope is 0.90 to 1.13, $r^2 = 0.75$, $n = 81$); coarse roots of > 2 mm in diameter: $\log_{10}P = -0.178 + 0.88 \times \log_{10}M$ (95% C.I. for slope is 0.78 to 0.99, $r^2 = 0.36$, $n = 190$). The short dash lines refer to the 95% confidence intervals. The pink line refers to the 1:1 line

ecosystems all over the world, and all data analyses were conducted under the same order of magnitude. Therefore, we have continued to use only the power law model and focused on discussing exponent b . Our dataset included studies using various methods to measure

production except using biomass as a proxy for production, which could cause error and the power law scaling exponent close to 1.0 (Jenkins 2015; Jenkins et al. 2020). Fine roots are metabolically active organs (Kerkhoff et al. 2006; Peng et al. 2010) with higher respiration rates than

coarse roots (Pregitzer et al. 1998; Desrochers et al. 2002; Marsden et al. 2008). The higher respiration rate may contribute to the isometric scaling of plant fine root productivity with biomass. Additionally, gravity is relatively unimportant and space-filling is incomplete for fine roots with few branch levels (Enquist et al. 2007), resulting in the exponent $b \approx 1.0$. Our findings suggest that scaling relationships for fine roots may be similar to those in aboveground leaves, although no reports have yet studied the productivity-biomass scaling relationship in plant leaves. Although fine root productivity and biomass differed between biomes and life forms, our results revealed that there was no significant difference of the power law scaling exponent (except for tropical grasslands, forbs and shrubs with small data size), suggesting that a constant rule might exist.

We also found differences between fine roots and coarse roots. Animals transitioning from larval to adult stages undergo an ontogenetic scaling shift (Glazier 2005). For plants, metabolic scaling theory suggests an ontogenetic shift in scaling of plant respiration with body size from isometric ($b = 1.0$) to negatively allometric ($b < 1.0$) (Enquist et al. 2007; Reich et al. 2007; Savage et al. 2008; Lin et al. 2013; McCarthy et al. 2019). Measurements of whole plant respiration rates show that allometric exponents for the scaling of respiration rate with body size continuously vary from 1.0 in the smallest plants to 3/4 in larger saplings and trees (Mori et al. 2010). Ontogenetic transition of plant characteristics occurs when young seedlings grow into mature trees (Bond 2000; Ryan et al. 2004; Ishida et al. 2005). Coarse roots are metabolically more inactive and have more massive structural components than fine roots (Kerkhoff et al. 2006). As roots grow, gravity becomes increasingly important and volume-filling architecture develops (West et al. 1999; Enquist et al. 2007). For these reasons, the $b = 1.0$ allometric exponent for the productivity-biomass relationship in fine roots decreases in coarse roots, as we found in this analysis. Notably, we found the scaling exponent in coarse roots was close to 0.86, and not 3/4 as metabolic theory predicts.

In our dataset, coarse roots with diameters of 2–5 mm were about 95% of all coarse roots, suggesting that the observed scaling relationship in coarse roots is determined by these smaller roots. An ontogenetic transition in metabolic scaling would mean that the power-law scaling exponent for bigger coarse roots (> 5 mm diameter) would be near 3/4. Therefore, the metabolic scaling relationships in fine and coarse roots are similar to those in their aboveground counterparts, i.e., leaves and stems, respectively. The scaling of dark respiration rate in roots (pooled for fine and coarse roots) in relation to tissue N concentration is similar to stems, but different than leaves (Reich et al. 2008; Fan et al. 2017). However, there is no data directly comparing productivity-biomass scaling between fine roots and green leaves.

Conclusions

Our analysis of the scaling of root productivity with biomass indicates that productivity in plant fine roots (< 2 mm in diameter) scales isometrically with biomass. A gradual ontogenetic transition occurs when fine roots grow into coarse roots (> 2 mm in diameter). This transition is also seen in the scaling of respiration with body size for young seedling growing into larger mature trees (Enquist et al. 2007; Mori et al. 2010; Starko and Martone 2016; Ogawa 2019; Collalti et al. 2020). Our findings support the idea that there is not a unified and single constant scaling exponent for metabolism-biomass relationships in terrestrial plants, consistent with the hypothesis by White (2010), which argues that no universal scaling exponent can be applied to animals and plants.

Supplementary information

Supplementary information accompanies this paper at <https://doi.org/10.1186/s40663-020-00269-6>.

Additional file 1.

Additional file 2.

Authors' contributions

ZY planned the project. QD undertook most of the literature review and analyzed the data. ZY and QD wrote the manuscript. XS contributed additional literature and contributed substantially to modifying the manuscript. TRL and RLK edited the language of this manuscript. All authors read and approved the final manuscript.

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Availability of data and materials

Not applicable.

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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