

Research article

Are fine roots 'leaves underground' in terms of allometry? A test in a tropical forest successional series in southwest China

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Fine roots have been hypothesized to be 'leaves underground' in terms of vascular network, but this hypothesis has rarely been tested within the framework of metabolic scaling theory (MST). We measured average fine-root (diameter < 1 mm) mass (M), surface area (A), volume (V), diameter (D) and length (L) for 216 soil cores from 24 plots across four successional stages in tropical forests of Xishuangbanna (southwest China), and examined eight scaling relationships between these variables at the individual root scale. We tested whether fine-root allometries conformed to MST's model for leaf (MST_l) or model (MST_w) for woody organs (e.g. trunk). We also assessed the relative effects of environmental factors, tree size, species composition and diversity, and stand structural factors on allometric relationships using structural equation models (SEMs). Our results showed that: 1) fine-root scaling exponents rarely conformed to MST_l's predictions. 2) The scaling exponents between fine-root M , A , V and D all conformed to MST_w's predictions in later successional forests, but showed greater deviation towards early successional stage. 3) The scaling exponents associated with fine-root length differed markedly from MST_w's predictions. 4) Changes of some fine-root scaling exponents across successional stage were mainly affected by tree size or soil fertility, and species composition affected allometry only indirectly via tree size. Our results suggested that the allometries of individual fine roots largely conform to the scaling rules governing woody organs instead of leaves, probably because leaves are nearly two-dimensional objects while the other two are three-dimensional. We showed that MST_w can well predict some fine-root allometries in later successional forests, suggesting great potential of utilizing MST_w to better estimate fine-root biomass and productivity. However, the present MST_w still needs to be improved for predicting the scaling relationships concerning fine-root length, and also for better quantifying allometric exponents in earlier successional forests.

Keywords: fine roots, leaf, metabolic scaling theory (MST), scaling relationship, successional stage, tree size



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Introduction

Fine root (the most distal portion of root systems) is one of the most physiologically active organs of trees, but its roles in ecosystem have been less well understood compared with the aboveground organs. Fine roots grow and turnover rapidly (McCormack et al. 2015), they account for only 0.5–10% of forest biomass but may contribute to 10–60% of global forest net primary productivity (Jackson et al. 1997, Steele et al. 1997, Ruess et al. 2003, Chen et al. 2013). In contrast to woody organs (e.g. trunks, branches and coarse roots), fine roots are characterized by low construction cost and high resource utilization efficiency. This may cause fine-root allometries to be different from other woody organs (Robinson et al. 2003, Bodner et al. 2013), but more similar to leaves (Chen et al. 2019). It is well known that sampling and measuring fine roots are difficult, thus understanding the allometries of fine roots is of great significance for improving the estimation of fine-root biomass and production, as well as forest carbon storage.

The mechanisms underlying plant allometry have received wide attention in ecology, and a series of hypotheses and models have been proposed. Earlier models (e.g. geometric and elastic similarity) were based on geometric and physical constraints of plant allometry (Shinozaki et al. 1964, Rich et al. 1986). The metabolic scaling theory (MST) further incorporated assumptions of biological constraints (e.g. the self-similarity of vascular networks and maximization of metabolic rate) into the model, and provided a series of testable predictions from the organ to ecosystem scales (West et al. 1999, Brown et al. 2004, Enquist et al. 2007b, 2009). An earlier version of MST, generally known as the WBE (West, Brown and Enquist) model, has made predictions for the allometries of trunks, branches, leaves and other fractal-like architecture organs at the individual tree scale, including scaling exponents between stem or leaf petiole diameter (D), tree height or leaf length (L), mass (M), surface area (A) and volume (V) (Supporting information). The original WBE states that these predictions can be applied for allometries of individual leaf (West et al. 1999). However, Price and Enquist (2007) noted that: leaves are near two-dimensional objects, and do not meet a key assumption of WBE that plant vascular network is volume (three-dimensional) filling. Thus, WBE is suitable for woody organs but not for leaves. They also extended the WBE model to leaves and proposed a set of specific predictions for leaf allometries (Supporting information). Hereafter, we abbreviated the original WBE model for woody organs (West et al. 1999) as MST_w , while the extended model for leaves as MST_l .

Here we tested whether the predictions of MST for leaves were more applicable for fine roots than for woody organs. This test is based on reasons as follows: compared with other fractal-like architecture organs (e.g. woody organs), 1) only fine roots and leaves are located at the terminal parts of the plant vascular network. Further, Chen et al. (2019), based on the pipe model (Shinozaki et al. 1964) and the predictions of Niklas and Enquist (2002a, b), proposed that the fine-root

modules were analogous to leaves in terms of vascular network (for details, Chen et al. 2019); 2) fine roots and leaves are more similar in structure and functions related to resource acquisition (e.g. low proportion of secondary woody tissue, high turnover rate and physiologically more active). Taken together, it is reasonable to speculate that, fine roots can be regarded as 'leaves underground', at least in terms of allometry (Chen et al. 2019). Thus, we tested the hypothesis (H1) that MST_l 's predictions (Supporting information) for leaves may be more suitable for fine roots than MST_w 's predictions for woody organs.

MST has been controversial since it was proposed. A major reason it is criticized is because MST predicts a specific exponent for each scaling relationship, around which trees from different taxa and environments should cluster (West et al. 1999, Enquist and Niklas 2001). However, many studies found that the observed scaling exponents not only differed among taxonomic groups, but also varied regularly with climate, tree size and other factors (Muller-Landau et al. 2006, Wang et al. 2006, Lines et al. 2012, Duncanson et al. 2015, Poorter et al. 2015). As a result, many observations were not consistent with MST's predictions. However, the current MST has proposed hypotheses to explain these discrepancies. One explanation (the 'steady-state hypothesis', hereafter) argued that MST is based on some simplifying assumptions, including: 1) forests are in an approximate steady-state in terms of resources and demographics, and 2) forest is space-filling because trees grow and fill up all the available space (West et al. 1999, Enquist et al. 2007a). Clearly, these assumptions can only be met in late successional forests. Thus it is predictable that, in disturbed forests at an earlier successional stage, the 'steady-state' assumption is more seriously violated, hence it's natural that the scaling exponents should deviate more from MST's predictions. In recent years, this prediction has been supported by studies on aboveground allometries, e.g. tree diameter versus height, tree size distribution and biomass allocation (Rüger and Condit 2012, Duncanson et al. 2015, Sun et al. 2017b, 2020). If fine-root allometries also showed a similar pattern across successional stages, then it is clearly a good support to MST. Consequently, here we tested the 'steady-state hypothesis' (H2) that the fine-root scaling exponents may deviate more from MST's predictions towards early successional stage.

As for why scaling exponents change with forest succession, there are still other competing hypotheses. 1) As mentioned above, many studies have found that tree allometries change significantly with environmental gradients and species (taxa). It is well known that during forest succession, the forest habitat changes significantly from a more xeric one to a mesic one, with an increase in soil water and nutrient availability (Reich et al. 1995, Jing et al. 2015). Meanwhile, forest succession is also characterized by striking changes in species composition, as well as species diversity (Lasky et al. 2014, Miao et al. 2021). Thus, it is possible that changes of allometry across forest succession may be mainly caused by these environmental, species composition and diversity factors. 2) In contrast, MST assumes that these abiotic

and biotic factors do not affect scaling relationships directly (Enquist et al. 2000, 2007a). Current MST has extended the MST_w model and has proposed models with flexible exponent (flexible MST, hereafter) which can explain the variation of allometry with environmental gradient and species composition (Niklas and Spatz 2004, Enquist et al. 2007a). The flexible MST suggests that the allometry of vascular plants is a continuum that varies with plant size: the scaling exponents for herbs and shrubs conform to the MST's predictions for small plants (Niklas 2004, Sun et al. 2017a), but gradually changed to be closer to the predictions of MST_w with increasing tree size (Niklas and Spatz 2004, Enquist et al. 2007a, Duncanson et al. 2015). The flexible MST further suggests that plant size is the main driver of changes in allometry, and the observed significant changes of scaling exponents with species composition and climate may be simply caused by the fact that species composition and environmental gradients affect tree size, which in turn lead to changes in allometry (Niklas and Spatz 2004, Price et al. 2007). So far, the flexible MST has gained some supports. For example, a study on forest plots across the United States showed that the exponents of tree diameter–height scaling and tree size distribution conformed to MST_w 's predictions when forest height > 35 m, but revealed more deviation for shorter forests (Duncanson et al. 2015). In addition to species composition change, the difference in tree size may be the other most striking change during forest succession. Thus, forest successional series provide an idea system for testing the above hypotheses on changes in allometric relationships.

In this study, we set plots across different successional stages (early, mid, mid-late and late) in the tropical forests of Xishuangbanna, southwest China. We examined eight scaling relationships between fine-root mass (M), diameter (D), surface area (A), volume (V) and length (L) at the individual root scale to test three hypotheses as follows: (H1) the predictions of MST_l for leaves are more applicable for fine roots than the predictions of MST_w for woody organs; (H2) fine-root scaling exponents deviate more from the predictions of MST in earlier successional stage; (H3) the variations of fine-root allometries during forest succession are mainly due to changes in tree size, while species composition, diversity and environmental gradient only affect allometric exponents indirectly via tree size.

Material and methods

Study site and data collection

The study site was located in the Tropical Botanical Garden of Xishuangbanna, Yunnan Province, southwest China (21°54'N, 101°46'E). The zonal vegetations here are tropical rainforest and monsoon rainforests, which are the north-most tropical forests in Southeast Asia. Xishuangbanna is one of the global biodiversity hotspots, harboring more than 5000 species of vascular plants (Cao et al. 2006), which account for 16% of vascular plant species in China. The climate in

this region is controlled by the southwest monsoon, with an average annual temperature of 21.5°C, and average temperature in June and January of 25.5°C and 14.8°C, respectively. The mean annual precipitation is 1557 mm, with 87% (1335 mm) rainfall in the wet season (May–October) and only 13% in the dry season (November–April). The average relative humidity is about 80% and there is no frost in the winter.

In 2018, we set 24 plots (20 × 30 m) across four successional stages (six replicated plots in each stage), including early, middle, mid-late and late stages. We selected the four successional stages based on species composition, stand basal area and previous studies on forest types in this region (Bai et al. 2019). The dominant species in the early successional stage were *Engelhardtia spicata*, *Ficus vasculosa* and *Machilus melanophylla*. The middle successional stage was dominated by *Barringtonia pendula*, *Litsea panamanja* and *Polyalthia simiarum* (Table 1). Meanwhile, the mid-late successional stage was mainly composed of *Barringtonia pendula*, *Polyalthia simiarum* and *Ficus callosa*, and the dominant species in the late stage included *Cleistanthus macrophyllus*, *Lasiococca comberi* and *Terminalia bellirica*.

In each plot, we recorded geographic coordinates (latitude, longitude and elevation) and local topography (aspect and slope). All trees with DBH (diameter at breast height) ≥ 3 cm were tagged, and recorded for their species name, DBH, height and within-plot coordinates, following the standard protocol for plot inventory in China (Fang et al. 2009).

Fine-root sampling and measurements

In August 2019, we evenly distributed nine points for fine roots sampling in each plot (Supporting information). A target tree was selected near each sampling point, and fine roots were sampled within a distance of 50–120 cm from the target tree stem, so as to avoid collecting coarse roots and facilitate extracting more distal portion of root system (Jourdan et al. 2008, Levillain et al. 2011). At each point we extracted a soil core of 30 cm depth, using a soil auger with an internal diameter of 50 mm, and a total of 216 soil cores (24 plots × 9 cores) were sampled from the 24 plots. The soil cores were transported in an ice-filled cooler from the field to the laboratory, and stored at 4°C before they were processed (Levillain et al. 2011).

For the fine-root measurements, each soil core was passed through a 0.50 mm sieve and carefully washed with running water, and any soil adhering to the root surface was gently brushed away. Roots < 1 mm in diameter (determined using calipers) were selected as fine roots, live versus dead roots were distinguished by observing the color of the epidermis and the degree of separation of root cortex from the stele (Brassard et al. 2011). The average live fine root diameter across all our samples was 0.46 mm, with a range of variations among the 24 plots from 0.25 mm to 0.87 mm (Supporting information). More recently, many studies have assigned increasingly smaller diameter cutoffs (e.g. 1.0 mm) in an effort to explicitly emphasize more absorptive fine roots (McCormack et al. 2015,

Table 1. Site and community characteristics for four successional stages of tropical forests in Xishuangbanna, southwest China. For each forest type, the mean value (\pm SE) of six replicate plots were reported for each stand parameter. Different letters denote significant difference among successional stages ($p < 0.05$). H_{\max} , maximum tree height in a plot; TBA, total basal area; SOC, soil organic carbon.

Successional stage	Early	Middle	Mid-late	Late
Dominant species	<i>Engelhardtia spicata</i> , <i>Ficus vasculosa</i> , <i>Machilus melanophylla</i>	<i>Barringtonia pendula</i> , <i>Litsea panamanja</i> , <i>Polyalthia simiarum</i>	<i>Barringtonia pendula</i> , <i>Polyalthia simiarum</i> , <i>Ficus callosa</i>	<i>Cleistanthus macrophyllus</i> , <i>Lasiococca comberi</i> , <i>Terminalia bellirica</i>
Stand factors				
Stand density (ha^{-1})	581 \pm 27a	675 \pm 52a	611 \pm 91a	564 \pm 77a
H_{\max} (m)	37.2 \pm 1.70a	29.5 \pm 2.14b	32.9 \pm 1.80a	38.7 \pm 1.01a
TBA ($\text{m}^2 \text{ha}^{-1}$)	11.1 \pm 0.75c	15.8 \pm 1.06bc	20.9 \pm 1.79a	20.7 \pm 0.83ab
Diversity				
Species richness	29 \pm 1a	34 \pm 2a	38 \pm 4a	15 \pm 3b
Shannon index	2.9 \pm 0.02a	3.0 \pm 0.06a	3.1 \pm 0.08a	1.9 \pm 0.30b
Pielou's evenness	0.9 \pm 0.00a	0.9 \pm 0.01a	0.9 \pm 0.01a	0.7 \pm 0.07b
Tree size				
Leaf biomass (kg)	259.6 \pm 14.48a	318.3 \pm 25.57a	351.1 \pm 36.82a	319.4 \pm 27.08a
Above-ground biomass (kg)	5814 \pm 349.6b	7924 \pm 678.8b	14069 \pm 1640.3a	16018 \pm 462.0a
Coarse-root biomass (kg)	934 \pm 68.4b	1545 \pm 125.2b	2995 \pm 477.9a	3881 \pm 105.3a
Total biomass (kg)	6749 \pm 416.3b	9946 \pm 802.6b	17064 \pm 2112.7a	19898 \pm 565.3a
Environmental factors				
Soil water content (g g^{-1})	0.36 \pm 0.012a	0.38 \pm 0.008a	0.36 \pm 0.016a	0.35 \pm 0.015a
Bulk density (g cm^{-3})	0.98 \pm 0.019a	0.92 \pm 0.020a	0.97 \pm 0.045a	0.99 \pm 0.013a
SOC (g kg^{-1})	1.40 \pm 0.057a	1.53 \pm 0.015a	1.41 \pm 0.144a	1.43 \pm 0.144a
Soil N (g kg^{-1})	2.20 \pm 0.400a	1.86 \pm 0.124a	1.74 \pm 0.104a	2.50 \pm 0.154a
Soil P (g kg^{-1})	0.31 \pm 0.006b	0.34 \pm 0.037b	0.46 \pm 0.022b	0.90 \pm 0.164a
Soil pH	3.87 \pm 0.014b	3.79 \pm 0.055b	4.22 \pm 0.220b	6.40 \pm 0.166a

Valverde-Barrantes et al. 2015, Kramer-Walter et al. 2016).

Absorptive roots are generally suggested as organs lacking secondary growth and associated with nutrient and water acquisition (McCormack et al. 2015). Therefore, in this study, we focused on roots < 1 mm in diameter to emphasize that the vast majority of our root samples consisted of absorptive fine roots. Further, using this classification of fine roots allowed us to better analogize the functional similarity between fine roots and leaves in resource acquisition so as to test H1 more reasonably.

The number of live fine root was recorded for each soil core, and then the roots were spread out in a tray and scanned (300 DPI). The scanned image was then analyzed with the software of WinRhizo Pro V2009C to obtain the total root length, root surface area, root volume and average diameter for each core. After root scanning, the roots were dried in an oven at 65°C to a constant weight, and weighed on a precision balance (0.1 mg) to obtain the total root mass of each soil core. In order to investigate allometric relationships at the individual root scale, total root length, total surface area, total volume and total dry weight of each core were divided by the number of roots to obtain averaged root length (L), root surface area (A), root volume (V) and root mass (M), respectively. Average root diameter was determined directly by the WinRhizo software. These averaged traits for live fine roots were used for subsequent analyses of scaling relationships. In this study, we used the average individual root data to test the predictions of MST for the individual leaf or woody organ, which is a commonly used approach in many studies on above-ground allometries (Enquist 2002).

Environmental factors

The environmental changes during forest succession generally include changes in soil moisture, nutrients and light availability (Jing et al. 2015, Matsuo et al. 2021). Since our plots were all canopy-closed stands, the variation of light availability was not considered in our study. To measure soil moisture and fertility, we extracted two soil samples at the 0–10, 10–20, 20–30 cm depths from a soil profile in each plot. One sample was used to determine soil bulk density, water content and pH, and another sample was used for soil chemistry analyses. Soil organic carbon (SOC) was assessed by the potassium dichromate oxidation method (Shamrikova et al. 2022), soil total nitrogen (N) was determined by the Kjeldahl method (Li et al. 2022), and soil total phosphorus (P) was determined by the alkali fusion-molybdenum antimony spectrophotometry method (Li et al. 2022). Finally, to be consistent with the depth of fine root sampling, we used the mean values of the 0–10, 10–20 and 20–30 cm layers for each soil metric in statistical analyses.

Species composition and diversity

Species composition (and thus diversity) changes significantly during forest succession, and it was also found that the allometry of shade-intolerant species at early successional stage differed significantly from that of shade-tolerant species at late successional stage (Lines et al. 2012, Duncanson et al. 2015). To investigate the potential effect of species composition and diversity, we calculated the plot-species matrix based on relative basal area (RBA) for each species by each plot.

Then we used the R package *vegan* to obtain three diversity metrics: species richness, Shannon index and Pielou's evenness (Dixon 2003). To quantify difference in species composition among plots, we used NMDS (non-metric multidimensional scaling) to conduct ordination analyses with the RBA plot-species matrix. We extracted plot scores on the first two axes (MDS1 and MDS2) as metrics of species composition, which is a commonly used method in ecology (Fotis et al. 2018). The NMDS analysis was performed using the *metaMDS* function in the R package of *vegan*.

Stand factors

Studies have found that stand factors change regularly with forest succession and may be important in affecting tree allometries (Sun et al. 2017b, Matsuo et al. 2021). In this study, we selected maximum tree height (H_{\max}), stand density and total basal area (TBA) of each plot to investigate the effects of stand factors on fine-root allometry. H_{\max} is a commonly-used proxy for forest height, and Duncanson et al. (2015) showed that forest height may be an important driver for changes in above-ground allometries. Stand density and TBA are generally suggested to be related to competition for light, water and nutrients among individuals (Matsuo et al. 2021), and previous studies have also reported that competition may be a critical modulator of tree allometry across successional stages (Sun et al. 2017b, 2020).

Tree size

To test the MST's hypothesis that changes in allometry may be mainly caused by variation in tree size instead of species composition and environment (Niklas and Spatz 2004, Enquist et al. 2007a), we estimated plot biomass with DBH and height data for each tree, using the species and forest-type specific biomass equations. The biomass equations were provided by the Xishuangbanna National Forest Scientific Observation and Research Station (www.cnern.org.cn/). We calculated the leaf biomass, above-ground biomass, coarse root biomass and total biomass (the sum of the above-ground and coarse root biomass) for each plot. We used these metrics to reflect the overall size of trees within a plot, to examine whether and how tree size affects fine-root allometry, and which biomass component is more important.

Statistical analysis

In summary, we used the average individual fine-root data to examine eight scaling relationships (M–D, A–D, V–M, A–M, A–V, L–D, M–L and A–L), so as to test three hypotheses as follows: 1) we first fitted scaling exponents with all root data pooled together (24 plots \times 9 cores) to test whether the predictions of MST_l for leaves are more applicable for fine roots than the predictions of MST_w for woody organs (H1); 2) we then fitted data from each successional stage separately (6 plots \times 9 cores) to test whether fine-root scaling exponents deviate more from the predictions of MST in

earlier successional stage (H2); 3) the scaling exponents were also fitted for each plot to test whether the variations of fine-root allometries are mainly due to changes in tree size, while other abiotic and biotic factors affect allometric exponents only indirectly via tree size (H3). All scaling relationships were fitted with the standardized major axis (SMA) analysis to obtain the exponents, i.e. the slope of the log–log linear relationship. SMA analysis is superior to least square regression (which may underestimate regression slope), and thus is commonly used in allometric analyses (Warton et al. 2006).

To investigate the main drivers of changes in fine-root allometries, we explained the scaling exponents of the 24 plots with six categories of variables: 1) successional stages, i.e. the early, middle, mid-late and late successional stages; 2) environmental factors, including soil bulk density, pH, water content, SOC, N and P; 3) stand factors, including stand density, H_{\max} and TBA; 4) species composition, including MDS1 and MDS2; 5) diversity metrics, including species richness, Shannon index and Pielou's evenness; 6) tree size, including leaf biomass, above-ground biomass, coarse root biomass and total biomass of each plot.

First, we used one-way ANOVA and LSD (least significant difference method) multiple comparisons to explore the difference in the above-mentioned variables among successional stages. Second, we used bivariate and multivariate analyses to explore the major modulators of the eight fine-root scaling exponents. Finally, we used structural equation modeling (SEM) to test H3. SEM is a stable and efficient multivariate method that allows us to test the causal relationships involved in our hypothesis (Malaeb et al. 2000), and here we conducted SEM with the R package of *piecewiseSEM*.

To simplify the SEM structure and avoid colinearity among variables, we excluded some variables based on the results of bivariate analysis and Bayesian information criterion (BIC), and retained one variable for each hypothesized driver in SEM (Supporting information). 1) Successional stage was excluded from SEM, because it was highly colinear with species composition, plot biomass metrics and some other factors. 2) For environmental factors, soil water content, pH, SOC, N and P were excluded from SEM because they were not significantly related to any fine-root scaling exponent. Soil bulk density was retained in SEM because it was a good surrogate of soil fertility and had a significant influence on root distribution in the soil (Zhang et al. 2012). 3) For stand factors, we selected stand density as the proxy of competition intensity in SEM. H_{\max} was excluded from SEM, because it had little explanatory power for fine-root scaling exponents in our study. Although TBA was well related to some exponents in bivariate analysis, it was highly colinear with plot biomass and thus actually reflected the effect of tree size in this study. Consequently, TBA was also excluded from SEM. 4) For species composition, we selected MDS1 because it was much better in discriminating successional stages than MDS2 (Fig. 2f). 5) The three species diversity indices had no effects on each scaling exponent, and thus were not considered in the SEM. 6) For tree size, we selected total biomass because it is in concept a better indicator of the overall tree

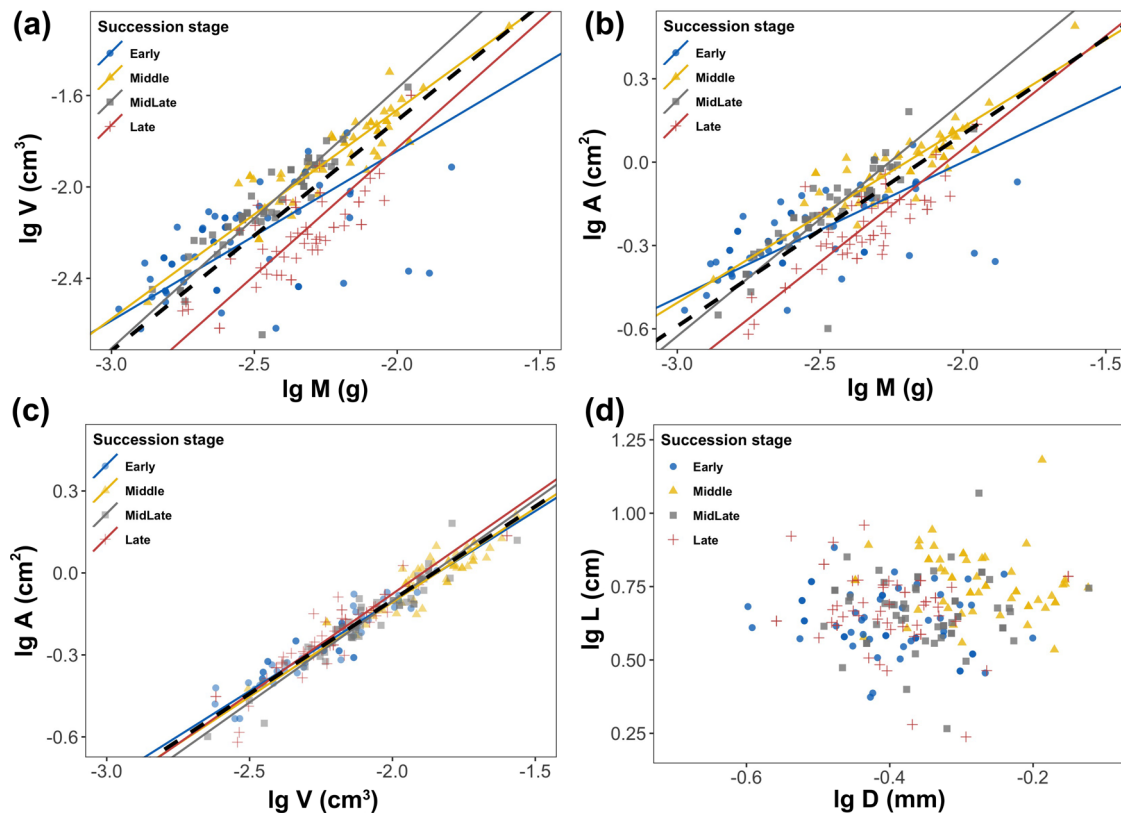


Figure 1. Allometric relationships for fine-root data from 24 plots across four successional stages, fitted with standard major axis regression. (a) Fine-root volume (V) versus mass (M); (b) fine-root surface area (A) versus mass (M); (c) fine-root surface area (A) versus volume (V); (d) fine-root length (L) versus diameter (D). The black dashed line denotes the overall trend.

size within a plot, and also has the strongest effect on fine-root scaling exponents. In a final step, we explained each fine-root scaling exponent with these selected variables in SEM. The Fisher's C statistic was used to assess the SEM fits, and a p -value > 0.05 suggested that the model has adequately reproduced the hypothesized causal network (Duffy et al. 2016, Lefcheck 2016).

To test the H3 more robustly, in addition to the SEM analyses, we also fitted general linear mixed models (GLMMs) to examine the potential factors affecting allometries. The GLMMs were fitted with the core-level data ($n = 24$ plots \times 9 cores = 216). For each allometric relationship between Y and X (e.g. root mass versus diameter), we explained \log - Y using \log - X together with other explanatory terms as follows: 1) the potential factors affecting allometries we selected above for SEM (i.e. total biomass, MDS1, stand density and soil bulk density); 2) the interactions between \log - X and each of the potential factor, which were used to test whether the allometric exponents were significantly affected by tree size, species composition, competition and environmental factors (Sun et al. 2017a); 3) we also used plot as a random effect in GLMM, because the nine samples cored from a same plot were statistically not fully independent. We conducted GLMM with the R package of lme4 (Bates et al. 2015). Since the GLMMs and SEMs produced very similar results, suggesting the

SEM results fitted with the plot-level data ($n = 24$) were reliable, we presented the GLMM results in the Supporting information.

All statistical analyses were performed with R ver. 4.0.3 (www.r-project.org).

Results

Variations of fine-root scaling relationships in relation to successional stage

When data from all the 24 plots (nine samples per plot) were pooled together (Table 2), the exponents for four scaling relationships revealed 95% confident intervals (CIs) embraced the predictions of MST_w , including the M - D , A - D , V - M and A - M allometries. The 95% CI of A - V scaling exponent was 0.66–0.71, which was also not far from the MST_w 's prediction of 0.75. In contrast, the three scaling relationships associated with fine-root length (L - D , M - L , A - L) showed clear deviations from MST_w 's predictions. Meanwhile, the exponents for eight fine-root scaling relationships rarely embraced the predictions of MST_l , except for the V - M and L - D allometries. However, the V - M scaling exponent of 1 was the basic assumption of MST instead of a specific prediction of MST_l , and the

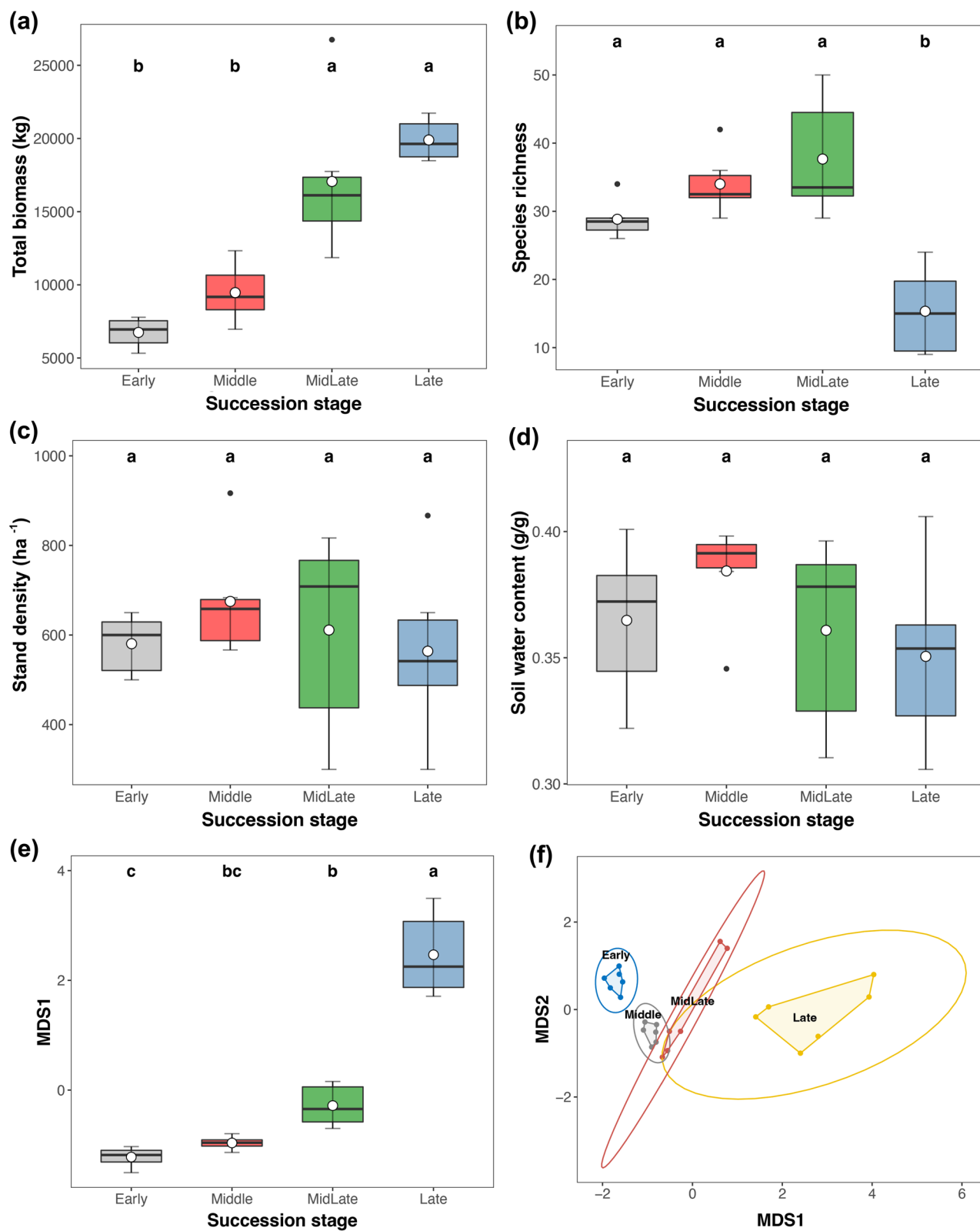


Figure 2. Variations of some biotic and abiotic factors with four successional stages. (a) Tree size (total biomass); (b) species diversity (species richness); (c) competition (stand density); (d) soil water content; (e) species composition (MDS1); (f) NMDS plot for non-metric multi-dimensional scaling, which was used to quantify the species composition based on the plot-species data. MDS1 and MDS2 were the plot scores on the first two axes. For (f), we connected plots from the same successional stage with sequence lines, and an ellipse denoting the 95% confidence interval.

Table 2. Testing the predicted exponents of eight fine-root scaling relationships by MST's model for woody organs (MST_w) and by MST's model for leaf (MST_l), using log-transformed data and standard major axis (SMA) regression. The analysis was conducted for all data pooled together (All), and for each successional stage separately. For each scaling relationship, the first variable is dependent variable, and the exponent predicted by MST was listed. The SAM slopes with a superscript of 'W' or 'L' denote that the 95% confidence intervals (CI) embrace MST_w or MST_l predictions, respectively. M–D, fine-root mass versus diameter; A–D, fine-root surface area versus diameter; V–M, fine-root volume versus mass; A–M, fine-root surface area versus mass; A–V, fine-root surface area versus volume; L–D, fine-root length versus diameter; M–L, fine-root mass versus length; A–L, fine-root surface area versus length.

	Group	R ²	p	Slope	CI _{low}	CI _{high}
M–D (MST_w : 2.67; MST_l : 3.25)						
All		0.21	0.000	2.59 ^W	2.30	2.92
Successional stage	Early	0.03	0.230	3.07 ^{W/L}	2.34	4.02
	Middle	0.26	0.000	2.63 ^{W/L}	2.07	3.33
	Mid-Late	0.28	0.000	2.32 ^W	1.84	2.94
	Late	0.15	0.004	2.23 ^W	1.73	2.88
A–D (MST_w : 2.00; MST_l : 3.00)						
All		0.38	0.000	1.79 ^W	1.61	2.00
Successional stage	Early	0.27	0.000	1.50	1.19	1.90
	Middle	0.22	0.000	1.66 ^W	1.30	2.12
	Mid-Late	0.20	0.001	1.96 ^W	1.53	2.51
	Late	0.16	0.003	1.82 ^W	1.41	2.34
V–M (MST_w : 1.00; MST_l : 1.00)						
All		0.55	0.000	1.01 ^{W/L}	0.92	1.10
Successional stage	Early	0.23	0.000	0.74	0.58	0.95
	Middle	0.79	0.000	0.91 ^{W/L}	0.81	1.04
	Mid-Late	0.79	0.000	1.14 ^{W/L}	1.00	1.29
	Late	0.64	0.000	1.11 ^{W/L}	0.94	1.32
A–M (MST_w : 0.75; MST_l : 0.92)						
All		0.59	0.000	0.69 ^W	0.63	0.75
Successional stage	Early	0.31	0.000	0.49	0.39	0.62
	Middle	0.75	0.000	0.63	0.55	0.73
	Mid-Late	0.74	0.000	0.84 ^{W/L}	0.73	0.97
	Late	0.68	0.000	0.81 ^{W/L}	0.70	0.95
A–V (MST_w : 0.75; MST_l : 0.92)						
All		0.91	0.000	0.69	0.66	0.71
Successional stage	Early	0.86	0.000	0.66	0.59	0.73
	Middle	0.86	0.000	0.69 ^W	0.62	0.77
	Mid-Late	0.91	0.000	0.74 ^W	0.68	0.81
	Late	0.86	0.000	0.73 ^W	0.66	0.81
L–D (MST_w : 0.67; MST_l : 1.25)						
All		0.01	0.102	1.33 ^L	1.16	1.52
Successional stage	Early	0.02	0.284	–1.22	–1.60	–0.93
	Middle	0.01	0.381	–1.38	–1.82	–1.05
	Mid-Late	0.00	0.761	1.61 ^L	1.22	2.11
	Late	0.02	0.308	–1.60	–2.10	–1.22
M–L (MST_w : 4.00; MST_l : 2.60)						
All		0.39	0.000	1.95	1.76	2.17
Successional stage	Early	0.23	0.000	2.51 ^L	1.97	3.20
	Middle	0.30	0.000	1.90	1.51	2.40
	Mid-Late	0.45	0.000	1.45	1.18	1.78
	Late	0.41	0.000	1.40	1.13	1.73
A–L (MST_w : 3.00; MST_l : 2.40)						
All		0.68	0.000	1.35	1.25	1.46
Successional stage	Early	0.53	0.000	1.23	1.02	1.48
	Middle	0.62	0.000	1.20	1.01	1.43
	Mid-Late	0.77	0.000	1.22	1.07	1.40
	Late	0.68	0.000	1.14	0.97	1.33

L–D scaling relationship was not statistically significant. Thus there was almost no support for MST_l (see details in Table 2).

When data from each successional stage were analyzed separately (Fig. 1, Table 2), the exponents for five scaling relationships (M–D, A–D, V–M, A–M and A–V) revealed

a good consistency with MST_w 's predictions at later successional stages, but seldom at the early stage. Interestingly, scaling exponents varied regularly with forest succession, with SMA slope for M–D decreased towards late successional stage, while those of A–D, V–M, A–M and A–V increased.

For the three scaling relationships associated with fine-root length (L–D, M–L, A–L), again, the exponents were not consistent with MST_w 's predictions for each successional stage (Fig. 1, Table 2). The exponents for M–L and A–L relationships decreased towards late successional stage, while that of L–D did not show a clear trend.

Changes of biotic and abiotic factors during forest succession

Stand total biomass increased markedly towards late successional forests (Fig. 2a, Table 1), and this was also true for above-ground and coarse root biomass, but not for leaf biomass. Among the stand factors, TBA increased significantly during forest succession, but stand density did not differ among successional stages, while H_{max} was lower at the middle stage (Fig. 2c, Table 1).

The NMDS analysis of species composition showed that plots from the four successional stages differed clearly along the first axis (MDS1) but not for the second axis (Fig. 2f), with the MDS1 scores lower at early successional stages and increased significantly towards late successional stage (Fig. 2e). Thus MDS1 scores can be well used as an indicator for species composition change during forest succession in our study. As for species diversity, species richness, Shannon index and Pielou's evenness all showed an increase from early to mid-late successional stages (but did not differ statistically), and were significantly lower at the late successional stage (Fig. 2b, Table 1).

Soil water content, bulk density, SOC and N all did not differ among successional stages, while soil P was significantly

higher and pH was lower at the late successional stage (Fig. 2d, Table 1).

Relative effects of abiotic and biotic factors on fine-root scaling exponents

Bivariate analysis showed that environmental factors revealed rather weak correlations with scaling exponents, except that soil bulk density showed a negative correlation with the A–D scaling exponent ($R^2=0.23$) (Table 3). Successional stage was significant in explaining V–M and A–M scaling exponents ($R^2=0.31$) but not for other allometries. As for plot biomass, V–M and A–M scaling exponents were positively related to total, above-ground and coarse root biomass ($R^2=0.17$ – 0.21) but not leaf biomass. Out of the three stand factors, TBA showed a medium positive relationship with V–M and A–M scaling exponents ($R^2=0.27$ and 0.23 , respectively), while H_{max} showed a weak positive relationship with M–D scaling exponent and stand density revealed no significant correlation. This difference was because TBA was highly correlated with total biomass ($R^2=0.85$) while H_{max} and stand density were not ($R^2=0.09$ and 0.04 , respectively). Despite significant changes in species composition during forest succession, both MDS1 and MDS2 revealed little correlations with various fine-root scaling exponents. And this was also true for species richness, Shannon index and Pielou's evenness.

In summary, out of all the abiotic and biotic factors examined here, tree size (as indicated by plot biomass and TBA) seems to be the major driver of some allometric relationships

Table 3. The R^2 of different factors in explaining the eight fine-root scaling exponents of the 24 plots. '–' denotes negative relationships. Bold numbers denote relationship significant at $p < 0.05$. MDS1 and MDS2, the plot scores on the first two axes of non-metric multidimensional scaling analysis. For other abbreviations, see Table 1 and 2.

Factors	M–D	A–D	V–M	A–M	A–V	L–D	M–L	A–L
Environmental factors								
Soil water content	0.00	–0.02	–0.01	0.00	0.03	–0.04	0.00	0.00
Soil bulk density	–0.01	–0.23	–0.06	–0.12	–0.03	0.00	0.03	0.00
Soil pH	0.01	0.07	0.01	0.02	0.00	–0.02	–0.05	–0.04
SOC	0.02	–0.05	–0.15	–0.13	0.00	0.00	0.04	0.00
Soil N	0.01	0.01	0.00	0.00	0.00	–0.11	–0.04	–0.05
Soil P	0.00	0.03	0.06	0.09	0.03	–0.02	–0.08	–0.02
Successional stage	0.16	0.08	0.31	0.31	0.04	0.04	0.21	0.06
Tree size								
Leaf biomass	0.00	0.00	0.15	0.13	0.00	0.01	–0.01	0.03
Above-ground biomass	–0.01	0.01	0.21	0.19	0.00	0.00	–0.15	–0.04
Coarse root biomass	–0.01	0.02	0.17	0.17	0.00	0.00	–0.16	–0.06
Total biomass	–0.01	0.01	0.20	0.19	0.00	0.00	–0.16	–0.04
Diversity								
Richness	–0.06	–0.03	0.12	0.09	0.00	0.06	0.00	0.09
Shannon index	–0.07	–0.04	0.04	0.04	0.00	0.01	0.00	0.01
Pielou's evenness	–0.05	–0.02	0.01	0.02	0.01	0.00	0.00	0.00
Stand factors								
Density	0.00	–0.01	0.00	0.00	0.02	0.00	0.02	0.09
H_{max}	0.17	0.01	0.00	0.00	0.00	–0.04	0.01	0.00
TBA	–0.03	0.01	0.27	0.23	0.00	0.00	–0.14	–0.01
Species composition								
MDS1	0.00	0.05	0.02	0.03	0.01	–0.01	–0.08	–0.05
MDS2	0.03	0.03	–0.03	–0.04	–0.01	0.00	0.01	–0.03

(Fig. 3). In the SEMs of V–M and A–M (Fig. 4c, d), total biomass had a strong and direct positive effect on scaling exponents, with path coefficients as high as 0.78–0.90. On the other hand, MDS1 (species composition) had no significant direct effect on the two scaling exponents, but showed an indirect effect via total biomass. Stand density (a proxy for competition) and soil bulk density revealed no significant direct or indirect effects on these scaling exponents, except that soil bulk density showed a negative direct effect on A–M scaling (but the path coefficient (0.41) was much lower than that of biomass (0.78)). In the GLMMs of V–M and A–M allometries (Supporting information), only total biomass showed a significant positive effect on scaling exponent. Overall, both allometric relationships supported H3, and showed that the variation of fine-root allometry during forest succession was mainly due to changes in tree size, while species composition affected allometric exponents indirectly via tree size.

However, the SEM of A–D and the GLMM of A–V only showed a significant negative effect of soil bulk density on scaling exponent (Fig. 4b, Supporting information), which was not consistent with H3. In addition, none of the other four allometries (M–D, M–L, L–D and A–L) showed significant pathways affecting the scaling exponents (Fig. 4, Supporting information).

Discussion

Fine roots are not ‘leaves underground’ in terms of allometry

There have been many studies on the scaling relationships of trees, but most of them focus on woody organs (e.g. trunks and branches) and leaves instead of fine roots (West et al. 1999, Niklas and Enquist 2002b, Price et al. 2007). Further, no studies yet have tested whether fine roots conform to the MST’s predictions for leaves (MST_l) or woody organs (MST_w). Among the eight fine-root allometric relationships in our study, most provided supports to MST_w but rarely to

MST_l (Table 2). Therefore, from the perspective of allometry, fine roots are more like woody organs rather than leaves.

Leaves differ markedly from woody organs and fine roots in geometry as plant vascular networks typically fill three-dimensional space. Leaf networks are closer to two dimensional, behaving more like ‘leaky pipes’, which may reduce the efficiency of delivering resources within the leaf networks (Canny 1990, 1993). Compare to the networks of roots and stems, water and nutrients transportation faces greater resistance inside the leaf to reduce the water loss through leaf surface (Canny 1990, 1993). However, in order to accomplish sufficient exchange with external environment, the leaf cross-sectional area would increase, which lead to changes in the scaling of leaf morphology (Sack et al. 2003). Overall, these differences in internal vascular network structure may be a major reason why leaf allometries differ from that of fine roots and woody organs.

Although, as mentioned above, fine roots and leaves have some similarities (e.g. both located at the terminal part of the plant vascular network, with low proportion of secondary woody tissue, high turnover rate and physiologically more active), there are also many differences in morphological structure and physiological function between them. Further, the abiotic and biotic environment of fine roots and leaves are also different, such as soil texture, physical obstacles, ambient temperature and moisture, and competition for water and nutrients (Robinson et al. 2003, Price and Enquist 2007, Weemstra et al. 2016). Natural selection can differentiate the functional requirements of fine roots (water acquisition) and leaves (photosynthesis) via optimizing their internal vascular networks, and thus their allometries may differ as well (West et al. 1999, Price and Enquist 2007, Ma et al. 2018).

In our study, we used the average individual root data to test the MST models for individual leaf or woody organ, which is a commonly used approach in many studies on above-ground allometries. We made an analogy between individual fine root and individual leaf from the perspective of allometry, and found clear differences between them. However, Chen et al. (2019) proposed that fine roots were

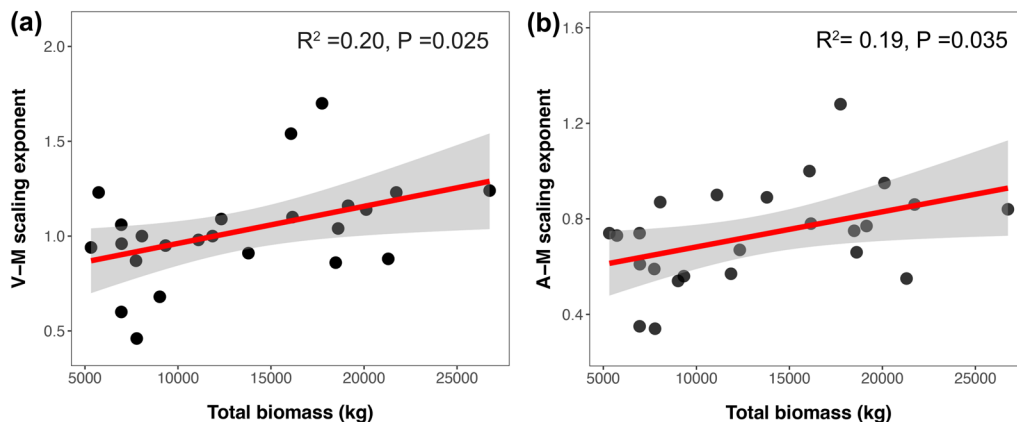


Figure 3. Relationship of V–M (a) and A–M (b) scaling exponent with tree size (total biomass). V–M, fine-root volume versus mass; A–M, fine-root surface area versus mass.

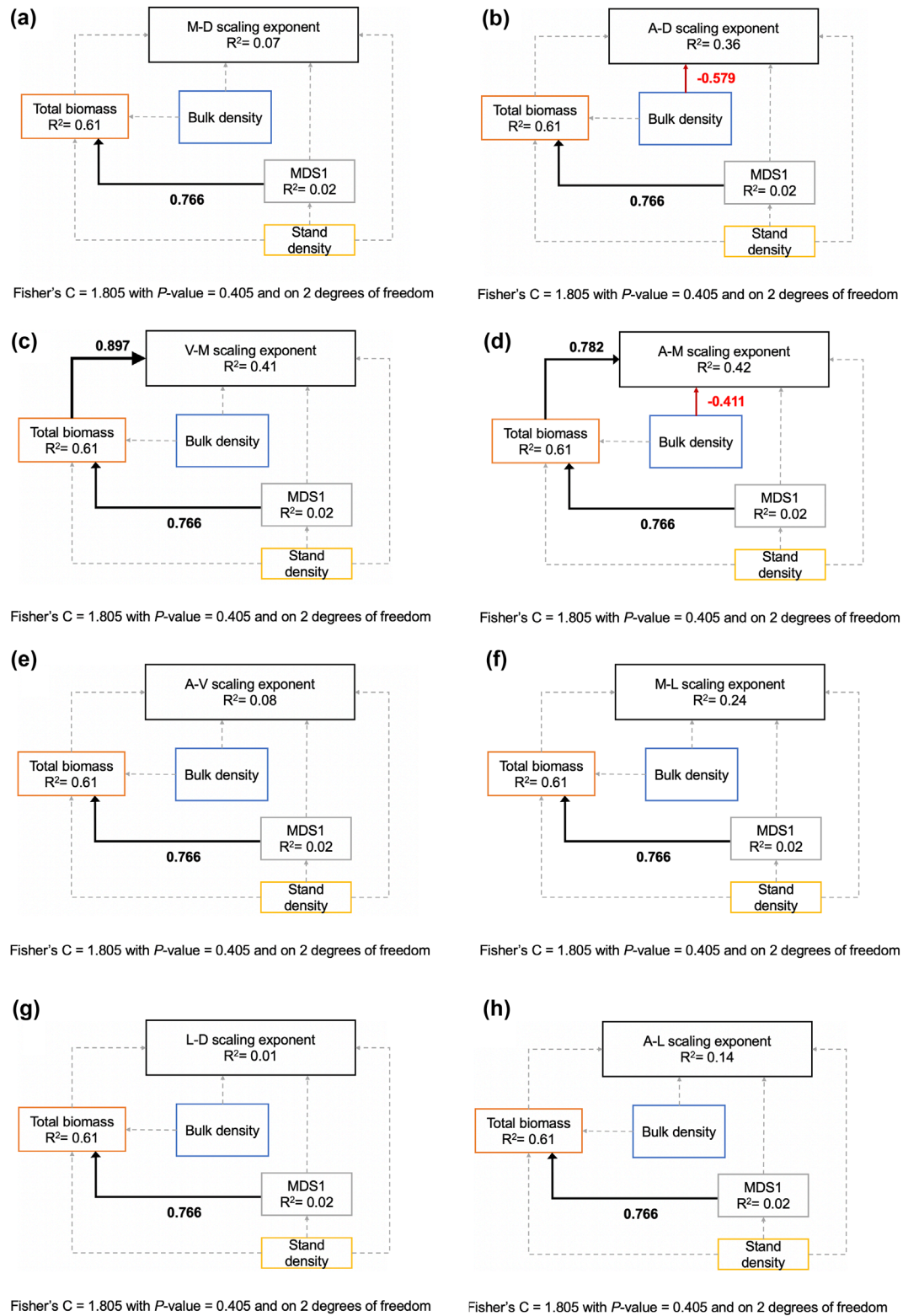


Figure 4. Structure equation models for the effects of environmental factors (soil bulk density), species composition (MDS1), competition (stand density) and tree size (total biomass) on eight allometric exponents across 24 plots. (a) Fine-root mass versus diameter (M–D) relationship; (b) fine-root surface area versus diameter (A–D) relationship; (c) fine-root volume versus mass (V–M) relationship; (d) fine-root surface area versus mass (A–M) relationship; (e) fine-root surface area versus volume (A–V) relationship; (f) fine-root mass versus length (M–L) relationship; (g) fine-root length versus diameter (L–D) relationship; (h) fine-root surface area versus length (A–L) relationship. The gray dotted line denotes no significant effect, black solid line denotes significant positive effect while red solid line for significant negative effect.

analogous to leaves within the plant vascular network at the module scale. A leaf itself is a module containing a vein network while an individual fine root is not, this may lead to the different results between our study and [Chen et al. \(2019\)](#).

Drivers for changes of fine-root allometry across successional stages

We also found that five scaling exponents (M–D, A–D, V–M, A–M and A–V) revealed a well consistency with MST_w 's predictions at the later successional stages, and did show more deviations at the earlier successional stages ([Table 2](#)). Thus, it seems that MST not only provides a good theory for predicting various fine-root allometric relationships (H1), but also can explain variations of allometry across successional stages (H2).

As for why the five scaling exponents (M–D, A–D, V–M, A–M and A–V) deviated from MST_w 's predictions regularly with forest succession, our SEM and GLMM results showed that biomass had the strongest effect on scaling exponents for the V–M and A–M relationships ([Fig. 4](#), Supporting information). This result provided support to the flexible MST, which suggested that tree size, rather than environmental gradient or species composition, is the main driver of changes in allometries ([Niklas and Spatz 2004](#)). However, it should be noted that we also found that the effect of tree size was not significant in the M–D, A–D and A–V allometries ([Fig. 4](#), Supporting information), which may indicate that different fine-root scaling relationships are driven by different mechanisms. Thus, the flexible MST is only partly supported, and deserves further investigation.

In the present study, there was no significant direct effect of species composition and diversity on each allometric exponent ([Fig. 4](#), [Table 3](#)). Meanwhile, among various environmental variables, only soil bulk density had a direct effect on A–D and A–M scaling exponents (note that its effect was much weaker compared with biomass for A–M allometry). Considering the drastic change in species composition during forest succession ([Fig. 2f](#), [Table 1](#)), we concluded that these results lend more supports to the flexible MST, instead of the competing hypothesis that allometric relationships were mainly driven by the difference among taxa and environmental gradient ([Wang et al. 2006](#), [Lines et al. 2012](#), [Poorter et al. 2015](#)). Further, we found that species composition affected some scaling exponents (V–M and A–M) indirectly via tree size, as predicted by the flexible MST. Previous studies have also found support for the flexible MST ([Niklas 2004](#), [Duncanson et al. 2015](#)). Overall, these findings suggest that MST may provide a mechanism to explain changes in allometries across successional series and environmental gradients, though it still needs to be improved to address the unfavorable evidence found in our study (e.g. the M–D, A–D and A–V allometries).

The relationships between stand factors and allometric exponents were also barely significant in our study ([Fig. 4](#), [Table 3](#)), except for TBA, which was likely due to the strong correlation with biomass that actually reflected the effect of tree size. Stand density is a good surrogate for competition

intensity among trees ([Matsuo et al. 2021](#)). Many studies have also shown that stand density has a significant effect on above-ground allometries. For instance, it is well known that trees are slender in stands with higher stand density due to increased competition ([Wang et al. 2006](#), [Lines et al. 2012](#)). [Sun et al. \(2017b, 2020\)](#) further showed that stand density may be a significant cause of deviation from MST_w 's predictions for several scaling relationships (diameter versus height, stem and coarse root biomass allocation). However, this study did not find any significant effect of stand density on fine-root allometries. This may be related to the difference in competition between above-ground and fine-root organs. The competition aboveground is mainly driven by height growth in an effort to compete for light resources, and consequently stand density is important because it significantly affects light availability. On the contrary, competition for soil resources depends on not only rooting depth, but also horizontal root extension and total root length ([Postma et al. 2021](#)). As such, stand density may not be able to reflect the complexity of competition underground.

The allometry associated with fine-root length

Another interesting finding of our study is that, while the above-mentioned five scaling relationships were generally consistent with MST_w 's predictions, the other three scaling relationships associated with fine-root length (M–L, L–D, A–L) were not. There are two possible reasons to explain the inconsistency.

First, the MST_w model assumes that plants allocate resources through a 'fractal branching network', in which the vascular transport resistance is minimized ([West et al. 1999](#), [Enquist et al. 2000](#)). However, studies have shown that the assumption of minimized resistance was not always met ([Price et al. 2007](#)). A major difference between fine roots and above-ground organs is that fine roots are subjected to strong physical pressure from soil. This additional pressure may increase the transport resistance in root conduit system, and thus lead to deviation from MST_w 's predictions. As for why soil pressure affects only the scaling relationships associated with root length rather than other fine-root allometries, we speculate that this may be explained as follows. Hydrodynamic resistance in a pipe is determined by the viscosity (which is a constant), length and inner diameter of the pipe ([West et al. 1999](#)). Since the length of fine roots varies markedly while root diameter does not differ much, it is possible that soil pressure affects hydrodynamic resistance mainly through fine-root length. However, whether this is the case requires further investigation.

Second, the elongation mechanism of fine roots is also different from that of the woody organs and leaves. Fine roots do not need to provide mechanical support during growth, whereas trunks and branches do ([Robinson et al. 2003](#), [Price et al. 2007](#)). In addition, the fine-root length is considered to be an important trait for acquisition ability, and has a tradeoff with the mycorrhizal colonization ([Weemstra et al. 2016](#), [Ma et al. 2018](#)). Thus, interactions

between fine roots and soil fungi may affect the allometries associated with fine-root length, while the woody organs are not affected. However, the specific mechanisms of how these factors affect fine-root allometries are still not clear. Examining these questions may significantly deepen our understanding of plant allometry, so as to improve MST models in the future.

Conclusions

In this study, we tested MST models using fine-root data in tropical forests across different successional stages. From the perspective of allometry, our results showed that fine roots were more like woody organs rather than leaves. These results highlight the great potential of applying MST to estimate fine-root biomass and productivity, so as to better estimate forest carbon storage. However, the existing MST_w model is not suitable to predict the allometric relationships associated with fine-root length, suggesting that there are still unknown differences between the allometric mechanisms of fine roots and woody organs. At the same time, current MST models also need to be improved for quantifying changes in allometry in secondary forests, because the changes of some scaling relationships in our study still remain inconsistency with MST.

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Author contributions

Zijian Guo and **Xingping Wang** contributed equally to this publication. **Zijian Guo**: Conceptualization (lead); Data curation (lead); Methodology (lead); Writing – original draft (lead); Writing – review and editing (lead). **Wenhao Miao**: Writing – review and editing (equal). **Yueming Lyu**: Writing – review and editing (equal). **Han Sun**: Writing – review and editing (equal). **Dayong Fan**: Writing – review and editing (equal). **Xiangping Wang**: Conceptualization (lead); Methodology (lead); Funding acquisition (lead); Writing – original draft (equal); Writing – review and editing (lead).

Data availability statement

The datasets generated and analyzed during the current study are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.crjdfn36v> (Guo et al. 2022).

Supporting information

The Supporting information associated with this article is available with the online version.

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