RESEARCH

Effects of climate, biotic factors, and phylogeny on allometric relationships: testing the metabolic scaling theory in plantations and natural forests across China

Han Sun[1], Xiangping Wang[1]* and Dayong Fan[2]*

Abstract

Background: Metabolic scaling theory (MST) is still in debate because observed allometric exponents often deviate from MST predictions, and can change significantly depending on environment, phylogeny, and disturbance. We assembled published scaling exponents from literatures for three allometric relationships linked to biomass allocation: leaf biomass-diameter (L-D), stem biomass-diameter (S-D), and root biomass-diameter (R-D). We used data from natural forests and plantations across China to test the following hypotheses: 1) the allometric relationships of trees support the predictions of MST on a broad scale; 2) the observed deviations from MST predictions are caused by climate, biotic factors, and/or phylogeny; 3) abiotic and biotic factors influence allometric relationships in plantations and natural forests differently, and different allometric relationships (i.e. L-D, S-D, and R-D) are affected differently. We related these scaling exponents to geographic climate gradient, successional stage, stand density, leaf form and phenology, and phylogeny. We used mixed-effect models to examine the major factors affecting tree allometries.

Results: In natural forests, S-D and R-D scaling exponents were consistent with MST predictions in primary forests, but were significantly lower in secondary forests. Both S-D and R-D scaling exponents in plantations had a medium value that fell between those of the secondary and primary forests, despite plantations being similar in species characteristics and age to secondary forests. The S-D and R-D exponents were significantly affected by factors that are not yet considered in MST, including winter coldness which explained 2.76% – 3.24% of variations, successional stage (7.91% – 8.20% of variations), density (a surrogate for competition, 5.86% – 8.54% of variations), and especially phylogeny (45.86% – 56.64% of variations explained). However, the L-D scaling exponents conformed to MST predictions in primary, secondary, and plantation forests, and was not strongly explained by most factors.

Conclusion: MST is only applicable to primary (steady-state) forests, and climate, biotic factors and phylogeny are causes of the observed deviations of allometric relationships from MST predictions. Forest management practices in plantations have a strong influence on tree allometries. L-D allometry is more strongly controlled by biophysical constraints than S-D and R-D allometries, however, the mechanisms behind this difference still need further examinations.

Keywords: Allometry, Successional stage, Climate, Plantation, Conifer, Broadleaf trees, Metabolic scaling theory

---

* Correspondence: wangxiangping@bjfu.edu.cn; dayong.fan@anu.edu.au
[1]School of Ecology and Nature Conservation, Beijing Forest University, Beijing, China
[2]College of Forestry, Beijing Forest University, Beijing, China

Sun *et al. Forest Ecosystems*   (2020) 7:51

Page 2 of 14

Background

Allometry relationships are not only required in estimating ecosystem carbon sources and sinks (Chave et al. 2005, 2014) and in up-scaling ecological processes from the individual to the ecosystem level (Enquist and Niklas 2001; Brown et al. 2004), but also important for understanding the basic biophysical and evolutionary control of plant organs (West et al. 1999; Apol et al. 2008). Considering its critical roles, allometry has long been a focus of studies in ecology and forestry. To date, several biophysical models on allometry have been proposed (e.g. geometric, elastic, and stress similarity (Rubner 1883; McMahon and Kronauer 1976)). Among these models, metabolic scaling theory (MST) provides a series of testable predictions regarding allometric scaling relationships, based on basic biophysical constraints from the organ, individual to the ecosystem level (West et al. 1997; Brown et al. 2004). Because of its broad theoretical importance, MST has attracted far more attention than other models (Muller-Landau et al. 2006; Price et al. 2009; Poorter et al. 2012; Duncanson et al. 2015).

Nevertheless, MST has been debated since it was proposed, partly because the model has not explicitly taken into account the influence of environmental gradient and different among taxa. In fact, studies have shown that allometries may deviate from MST predictions and can vary as a function of abiotic and biotic factors (Wang et al. 2006; White et al. 2007; Lines et al. 2012; Hulshof et al. 2015). For instance, the height-diameter allometric scaling exponent may decrease with lower temperature so as to avoid xylem cavitation under cold and drought conditions (Wang et al. 2006; Lines et al. 2012). The inclusion of climate and forest type can, therefore, markedly improve the explanatory power of allometric models of biomass allocations (Wang et al. 2008). Biomass distribution scaling exponents may have significant differences in their goodness of fit results before and after species specific characteristics are considered (Wang et al. 2011), suggesting that species identity is also important in affecting scaling relationships. Although these criticisms may not be enough to reject MST in its entirety, it is clear that MST needs to be improved.

Recently, studies have proposed an explanation for why observed scaling exponents deviated from the MST predictions in forests (Rüger and Condit 2012; Duncanson et al. 2015; Sun et al. 2017a). These authors found that measured allometric exponents only agreed with MST predictions in late successional forests, because earlier successional forests were more affected by biotic and abiotic factors. For instance, Duncanson et al. (2015) demonstrated that allometries of trees in younger forests may vary quite substantially, while tree allometries in mature forests taller than 35 m were consistent

with MST predictions. Likewise, Sun et al. (2017a) found that H-D allometric scaling exponents conformed to MST predictions in late-successional broadleaf and Korean pine mixed forests in northeast China, while forests in earlier successional stages revealed greater deviations. These deviations from the predictions of MST may be primarily caused by biotic factors such as light competition and recruitment limitation, while climate may indirectly affect allometric exponents through these biotic factors. However, this hypothesis was only derived from studies in temperate forests. More tests need to be conducted to determine whether it applies to other forest biomes (e.g. subtropical and warm-temperate forests), and is therefore applicable across a broad climatic scale (Duncanson et al. 2015; Sun et al. 2017a).

Previous studies have mainly focused on the allometric relationships in natural forests (Muller-Landau et al. 2006; Price et al. 2009; Poorter et al. 2012). However, plantations are significantly different from natural forests in species composition and forest structure due to forest management (Luo et al. 2012). On the one hand, plantations are mostly dominated by fast-growing tree species, which is similar to early successional natural forests. On the other hand, forest management in plantations can increase the utilization of environmental resources (Binkley et al. 2004) which makes the living conditions steadier, and thus the allometries may be more similar to late successional natural forests (Duncanson et al. 2015). Therefore, the allometric relationships in plantations, whose species identity and age are more comparable to early successional forests, may better fit MST predictions like in mature forests than in early successional forests. One aim of this study is to test this hypothesis.

Allometry is not only important for ecological theory, but also an important method used for carbon storage and flux estimation. One of the most widely-used methods in estimating biomass is based on the allometric relationships between biomass and diameter at breast height (Fang et al. 2006; Wang et al. 2013). In this study, we assembled data on biomass-diameter allometric relationships from the literatures on Chinese natural forests and plantations, in order to compare the scaling exponents of three important allometric relationships: leaf biomass-diameter (L-D), stem biomass-diameter (S-D), and root biomass-diameter (R-D). These allometric relationships are not only critical for forest biomass estimation, but are also important indicators of individual biomass allocation strategies for plants (Luo et al. 2015). Previous studies have shown that the leaf mass fraction increased with increased light competition and nutrients (Poorter et al. 2012). The stem biomass fraction increased significantly with stem density (Poorter et al. 2012), and root biomass was found to be much less

Sun *et al. Forest Ecosystems*   (2020) 7:51

Page 3 of 14

limited by growing-season precipitation compared to shoot biomass (Wang et al. 2008). These different mechanisms may also affect L-D, S-D, and R-D allometric relationships, leading to variability and deviations from MST predictions. So, as a part of this study, we examined the differences among the three allometric relationships.

Here we test three hypotheses: 1) the allometric relationships of trees support the predictions of MST on a broad scale; 2) the observed deviations from MST predictions are caused by climate, biotic factors, and/or phylogeny; 3) abiotic and biotic factors influence allometric relationships in plantations and natural forests differently, and different allometric relationships (i.e. L-D, S-D, and R-D) are affected differently.

Methods

Data collection

We assembled scaling exponents from studies that reported the allometric relationships between leaf (L), stem (S) and root (R) biomass and tree diameter at breast height (D) across China. The literatures used different functions to fit the relationship between biomass and D, such as power, logarithm, linear, and quadratic

functions, etc. However, only the power function is consistent with theoretic allometric models and can be used to test MST (West et al. 1997, 1999; Brown et al. 2004). Consequently, we assembled data only from literatures that used the power function (Biomass = aD^b, where b is the scaling exponent). For each record, we also documented the following information whenever available: (1) geographic coordinates, including latitude and longitude of the plantation or forest; (2) forest type, forest origin, species composition, and dominant tree species; and (3) forest structure variables, including the stem density and tree height ranges of each plot measured at the exact time when these organ biomass-diameter power functions exponents were estimated. As a result, our dataset of 284 records included 201 L-D scaling exponents, 259 S-D scaling exponents, and 189 R-D scaling exponents from 143 plots spanning a latitudinal range of 18.7°−52.0° N, and a longitudinal range of 87.2°−130.9° E (Fig. 1). These plots included all the major forest biomes in China. We grouped the plots into two forest origins: natural forest and plantation. We also grouped natural forest plots into two successional stages: secondary natural forest and primary natural forest. Many literatures have described the successional stages of their plots.
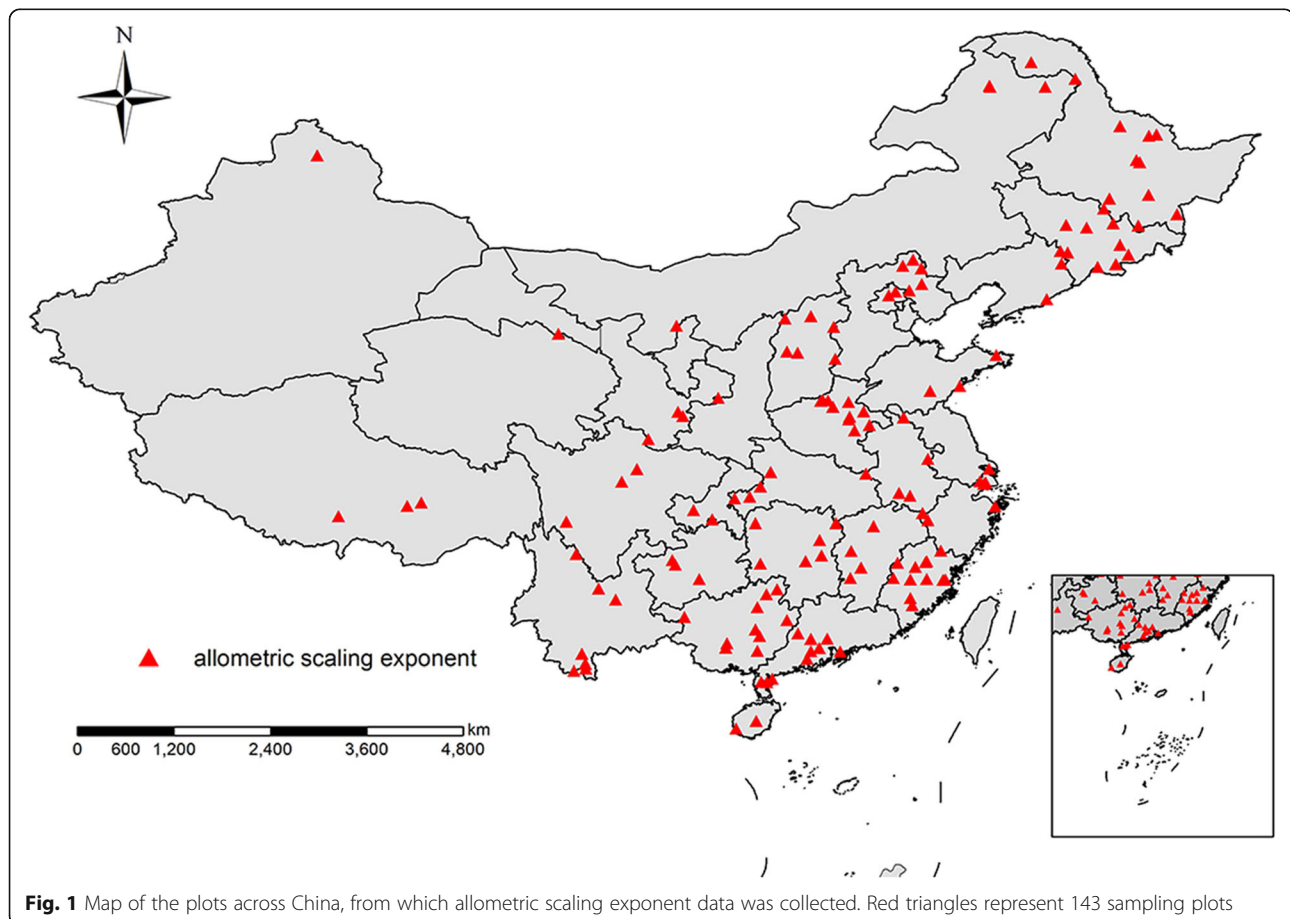

Fig. 1 Map of the plots across China, from which allometric scaling exponent data was collected. Red triangles represent 143 sampling plots

Sun *et al. Forest Ecosystems*   (2020) 7:51

Page 4 of 14

When this information is not explicitly described, the successional stage of some plots can be well judged by species composition and forest age, stock volume, etc., as described by the literatures. In a few cases, there was no enough information to determine whether a plot is a secondary or primary forest. These data were excluded from our dataset (see Appendix 1 and 2 for more detail).

Based on the latitude and longitude of each plot, we extracted the monthly average temperature and precipitation data (means from 1950 to 2000) for each plot from a very high resolution (1 km × 1 km) global climate database using ArcGIS 10.2 (Hijmans et al. 2005). Climatic indices for each plot were calculated using these monthly climate data, including annual potential evapotranspiration (PET) as a measure for energy availability, mean temperature for the coldest month (MTCM) as a proxy for winter coldness, and moisture index (MI, calculated as PET - mean annual precipitation) which is increasingly recognized as a better metric of water availability than commonly-used mean annual precipitation (Fang et al. 2012).

Statistical analysis
To test MST's predictions on the L-D, S-D, and R-D scaling exponents (= 2, 8/3, and 8/3, respectively), we pooled the data together and compared the means and 95% confidence intervals of the three scaling exponents to MST predictions. To test whether allometric relationships changed with successional stage, leaf phenology and leaf forms, we grouped data into three forest types (secondary, primary, or planted forest), two leaf phenology (evergreen vs. deciduous), and two leaf forms (conifer vs. broadleaf) and compared the three scaling exponents in each group with MST predictions.

To determine the effects of climate, biotic factors, and phylogeny on allometric relationships, we explained the L-D, S-D, and R-D scaling exponents with variables as follows: (1) Climate. Previous studies have shown that energy and water availability, and winter coldness can affect allometric relationships (Wang et al. 2006; Lines et al. 2012; Sun et al. 2017a), so we selected PET (energy), MTCM (coldness), and MI (water availability) for statistical analyses. Other climate indices are similar to PET, MTCM, and MI in biological meaning and thus were not used to avoid collinearity. (2) Biotic factors. Studies have shown that competition, species (functional) identity, and forest succession stage can affect allometric exponents, thus we choose stem density, forest age, biome (boreal, temperate, warm-temperate, or subtropical forest), and forest type (primary forest, secondary forest, and plantation) as biotic factors to examine their potential effects on the three scaling exponents. Stem density and forest age were log-transformed to increase normality and homoscedasticity of residuals,

which is a common practice in statistical analysis (Quinn and Keough 2002; Crawley 2007; He et al. 2009; Wang et al. 2009). (3) Phylogeny. To test for a phylogenetic effect, we used family, genus, and species as explanatory terms, which have been shown to be good surrogates for phylogenetic relationships among taxa (He et al. 2009). This is because some species cannot be found in the existing phylogenetic database (Zanne et al. 2014), and thus we were not able to construct a phylogenetic tree for the species in our study.
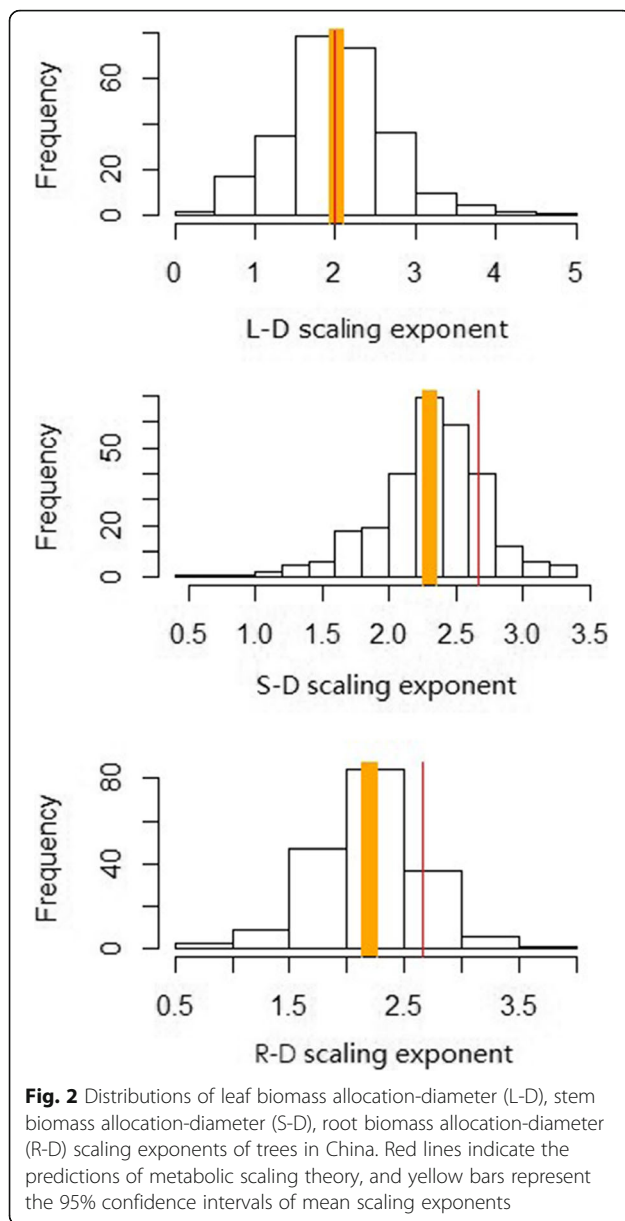
We used bivariate analyses and multivariate mixed-effect models to explain the L-D, S-D, and R-D allometric exponents with above-mentioned abiotic and biotic factors. In mixed models, we used genus as a random effect for the fixed effect of species, while family was used as random effect for that of genus (for details, see e.g. He et al. 2009). Records missing forest age or stem density were excluded from the mixed-model analysis, and thus 125 records including 123 L-D scaling exponents, 125 S-D scaling exponents, and 81 R-D scaling exponents were retained in this analysis. To identify the major factors affecting the three allometric relationship, we refined our model using the Akaike Information Criterion (AIC) to drop unnecessary variables (Johnson and Omland 2004). All statistical analyses were performed with R 3.5.1 (R Core Team 2014).

Results
When data were pooled together, the mean L-D scaling exponent was 2.01 (95% CI: 1.908–2.212), which agrees with the MST prediction of 2. The mean of the S-D and R-D scaling exponent was 2.303 (95% CI: 2.253–2.353) and 2.194 (95% CI: 2.125–2.263), respectively, both were lower than the MST predictions of 8/3 (Fig. 2).

When examined for each forest type separately (Fig. 3), the L-D scaling exponent again agreed with the MST prediction in all the three forest types: secondary and primary natural forests, and plantations. However, both S-D and R-D scaling exponents showed greater deviation from MST predictions in secondary forests, and were close to MST predictions in primary forests, while plantations revealed medium exponents between secondary and primary forests. The L-D scaling exponents also agreed with the MST prediction irrespective of leaf phenology or leaf forms (Fig. 4). However, the S-D and R-D scaling exponents were lower than MST predictions when examined in each category grouped by leaf phenology or leaf forms.

Some climate, biotic factors, and phylogeny were significantly related with scaling exponents (Table 1, Figs. 5, 6 and Table A1). Although some r^2 were not very strong, significant relationships could still reflect the trends. In fact, low r^2 but significant relationships were often found in previous studies of allometric scaling

Fig. 2 Distributions of leaf biomass allocation-diameter (L-D), stem biomass allocation-diameter (S-D), root biomass allocation-diameter (R-D) scaling exponents of trees in China. Red lines indicate the predictions of metabolic scaling theory, and yellow bars represent the 95% confidence intervals of mean scaling exponents

Fig. 3 Variations of L-D, S-D, and R-D with primary and secondary forests and plantations. Red lines indicate the predictions of metabolic scaling theory, and a, b, and ab above the plots indicate whether there are significant differences between two groups

factors at large scale (Luo et al. 2012). In climate factors, the temperature indices (PET and MTCM) were significantly and negatively correlated with the L-D scaling exponent ($r^2 = 0.02$–0.03, $p < 0.05$), while the moisture index (MI) had a significant negative relationship with the S-D scaling exponent ($r^2 = 0.02$, $p < 0.05$). As for biotic factors, stem density was significantly related with the L-D scaling exponent ($r^2 = 0.05$, $p < 0.01$), while forest type was significant in explaining the S-D scaling exponent ($r^2 = 0.03$, $p < 0.05$), and leaf form had a significant effect on the R-D scaling exponent ($r^2 = 0.02$, $p < 0.05$). In comparison, phylogeny (family, genus and species) revealed much stronger effects on the S-D and R-D scaling exponents ($r^2 = 0.25$–0.58, $p < 0.05$).
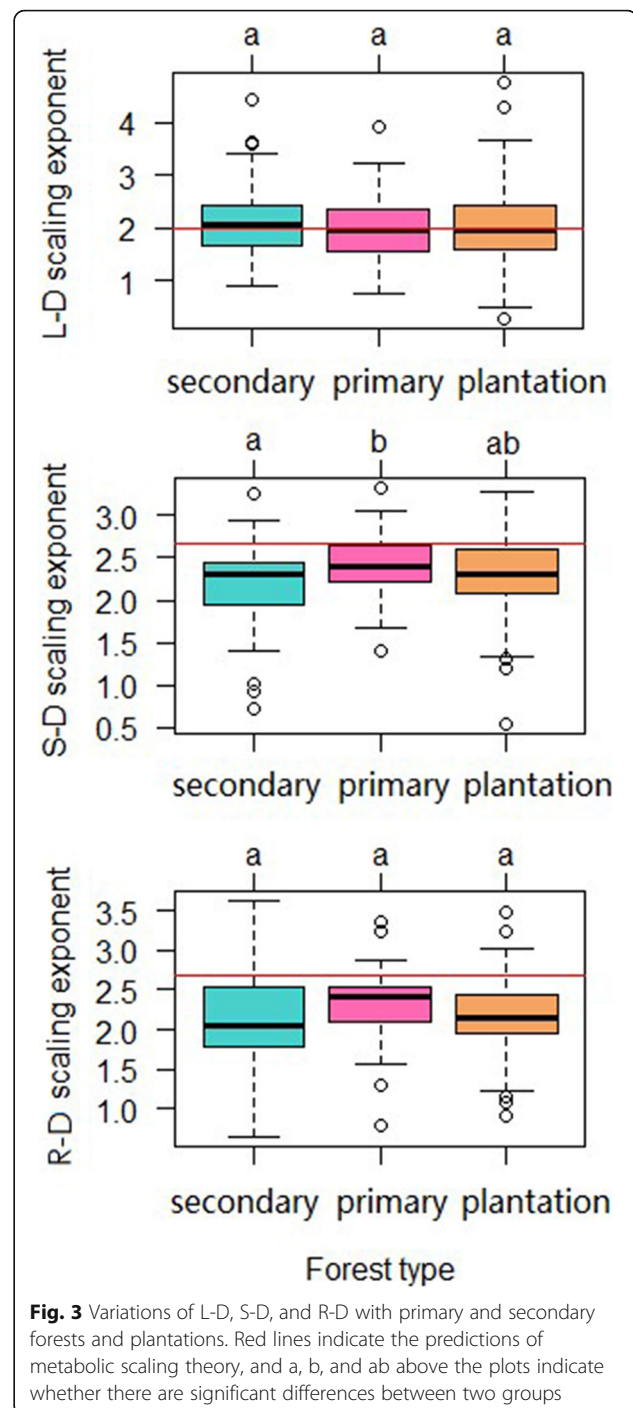
There were clear differences in the main correlates of allometric relationships between plantations and secondary forests. Scaling exponents were related to only a few factors in plantations: stem density was positively correlated with the L-D scaling exponent ($r^2 = 0.05$, $p < 0.05$), genus was significant in explaining the S-D scaling exponent ($r^2 = 0.28$, $p < 0.05$), while MTCM was negatively correlated with the R-D scaling exponent ($r^2 = 0.05$, $p < 0.05$). However, scaling exponents in the natural forests
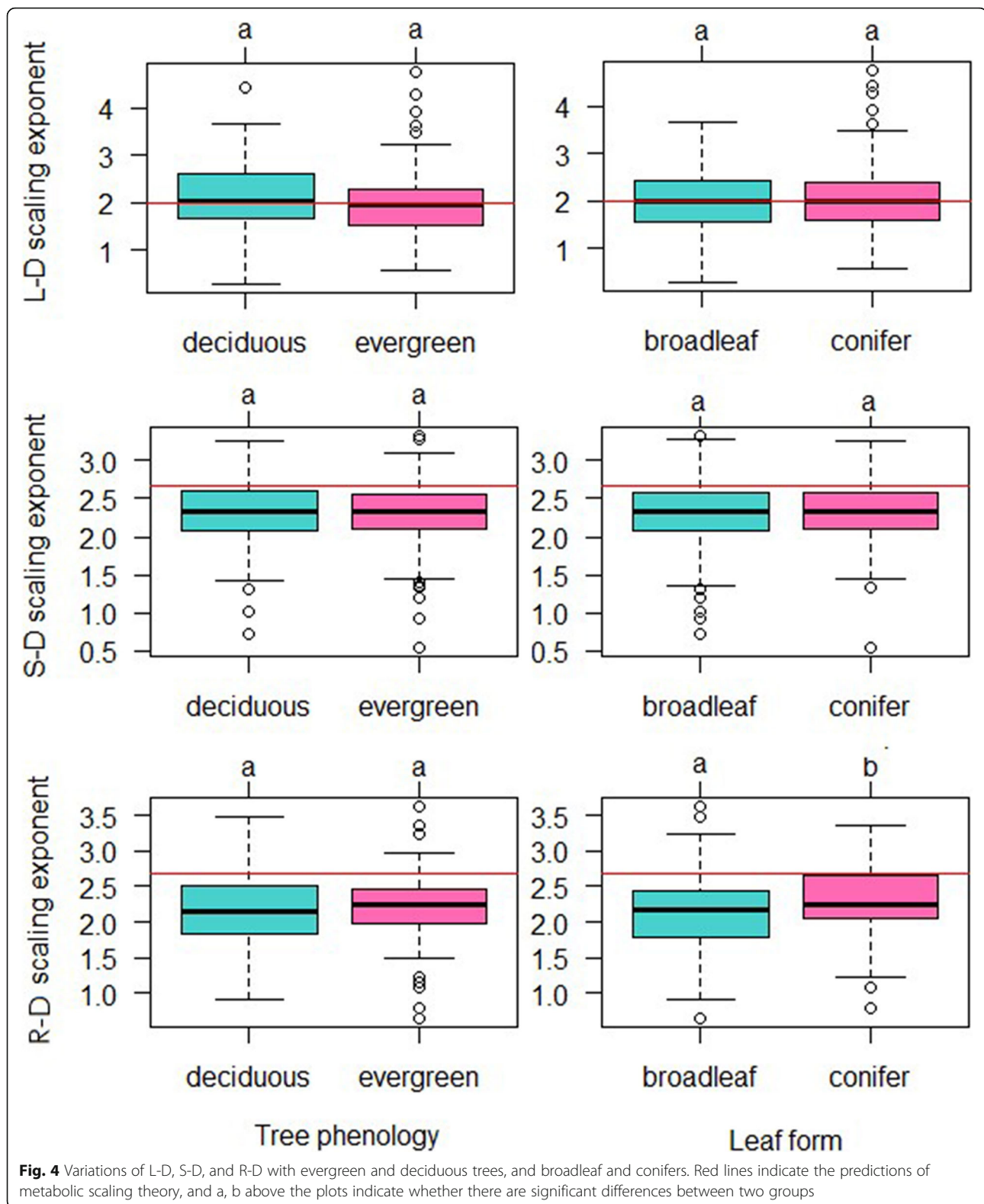
Fig. 4 Variations of L-D, S-D, and R-D with evergreen and deciduous trees, and broadleaf and conifers. Red lines indicate the predictions of metabolic scaling theory, and a, b above the plots indicate whether there are significant differences between two groups

were affected by more factors: the L-D scaling exponent was affected by climate (PET and MTCM, $r^2 = 0.09$–0.10, $p < 0.01$) and biotic factors (leaf phenology, $r^2 = 0.07$, $p <$ 0.05); and the S-D scaling exponent was affected by forest type ($r^2 = 0.07$, $p < 0.01$) which means that successional stage had a significant effect on scaling exponents in a

Table 1 The r^2 of each climate, biotic factors and phylogeny in explaining the scaling exponent for allometric relationships of leaf, stem and root biomass with diameter at breast height (L-D, S-D, and R-D, respectively). Negative r^2 represents negative correlation while others represent positive correlation. Significant relationships ($p < 0.05$) were boldfaced. *Abbreviations*: *PET* annual potential evapotranspiration, *MTCM* mean temperature for the coldest month, *MI* moisture index

	Overall		Plantation		Natural forest	
	r^2	p	r^2	p	r^2	p
L-D scaling exponent						
Climate						
PET	**−0.02**	**0.043**	0.00	0.823	**−0.09**	**0.005**
MTCM	**−0.03**	**0.008**	0.00	0.356	**−0.10**	**0.003**
MI	−0.01	0.250	−0.01	0.232	0.00	0.717
Biotic factors						
Biome	0.02	0.136	0.00	0.917	0.09	0.060
Forest type	0.01	0.425	–	–	0.01	0.291
Leaf form	0.00	0.393	0.00	0.422	0.01	0.394
Leaf phenology	0.01	0.106	0.00	0.826	**0.07**	**0.014**
Stem density	**0.05**	**0.010**	**0.05**	**0.024**	0.05	0.188
Forest age	0.01	0.232	0.02	0.137	−0.02	0.409
Phylogeny						
Family	0.14	0.347	0.16	0.153	0.17	0.787
Genus	0.26	0.166	0.22	0.257	0.40	0.467
Species	0.43	0.102	0.40	0.120	0.58	0.381
S-D scaling exponent						
Climate						
PET	0.00	0.243	0.01	0.260	0.00	0.664
MTCM	0.00	0.990	0.00	0.983	0.00	0.899
MI	**−0.02**	**0.030**	0.00	0.457	**−0.06**	**0.012**
Biotic factors						
Biome	0.01	0.297	0.01	0.551	0.03	0.410
Forest type	**0.03**	**0.011**	–	–	**0.07**	**0.004**
Leaf form	0.00	0.307	0.00	0.450	**0.08**	**0.003**
Leaf phenology	0.00	0.664	0.00	0.352	0.00	0.748
Stem density	0.00	0.493	−0.01	0.328	0.00	0.622
Forest age	0.00	0.511	0.00	0.707	0.00	0.982
Phylogeny						
Family	**0.25**	**0.000**	0.17	0.106	**0.45**	**0.000**
Genus	**0.39**	**0.000**	**0.28**	**0.030**	**0.70**	**0.000**
Species	**0.53**	**0.000**	0.42	0.074	**0.77**	**0.000**
R-D scaling exponent						
Climate						
PET	0.00	0.782	−0.02	0.084	0.02	0.223
MTCM	−0.01	0.336	**−0.05**	**0.015**	0.01	0.387
MI	−0.00	0.846	0.00	0.801	0.00	0.937
Biotic factors						
Biome	0.01	0.428	0.06	0.051	0.05	0.332
Forest type	0.01	0.433	–	–	0.02	0.306
Leaf form	**0.02**	**0.037**	0.02	0.139	**0.06**	**0.044**

Sun *et al. Forest Ecosystems*   (2020) 7:51

Page 8 of 14

Table 1 The r^2 of each climate, biotic factors and phylogeny in explaining the scaling exponent for allometric relationships of leaf, stem and root biomass with diameter at breast height (L-D, S-D, and R-D, respectively). Negative r^2 represents negative correlation while others represent positive correlation. Significant relationships ($p < 0.05$) were boldfaced. *Abbreviations: PET* annual potential evapotranspiration, *MTCM* mean temperature for the coldest month, *MI* moisture index *(Continued)*

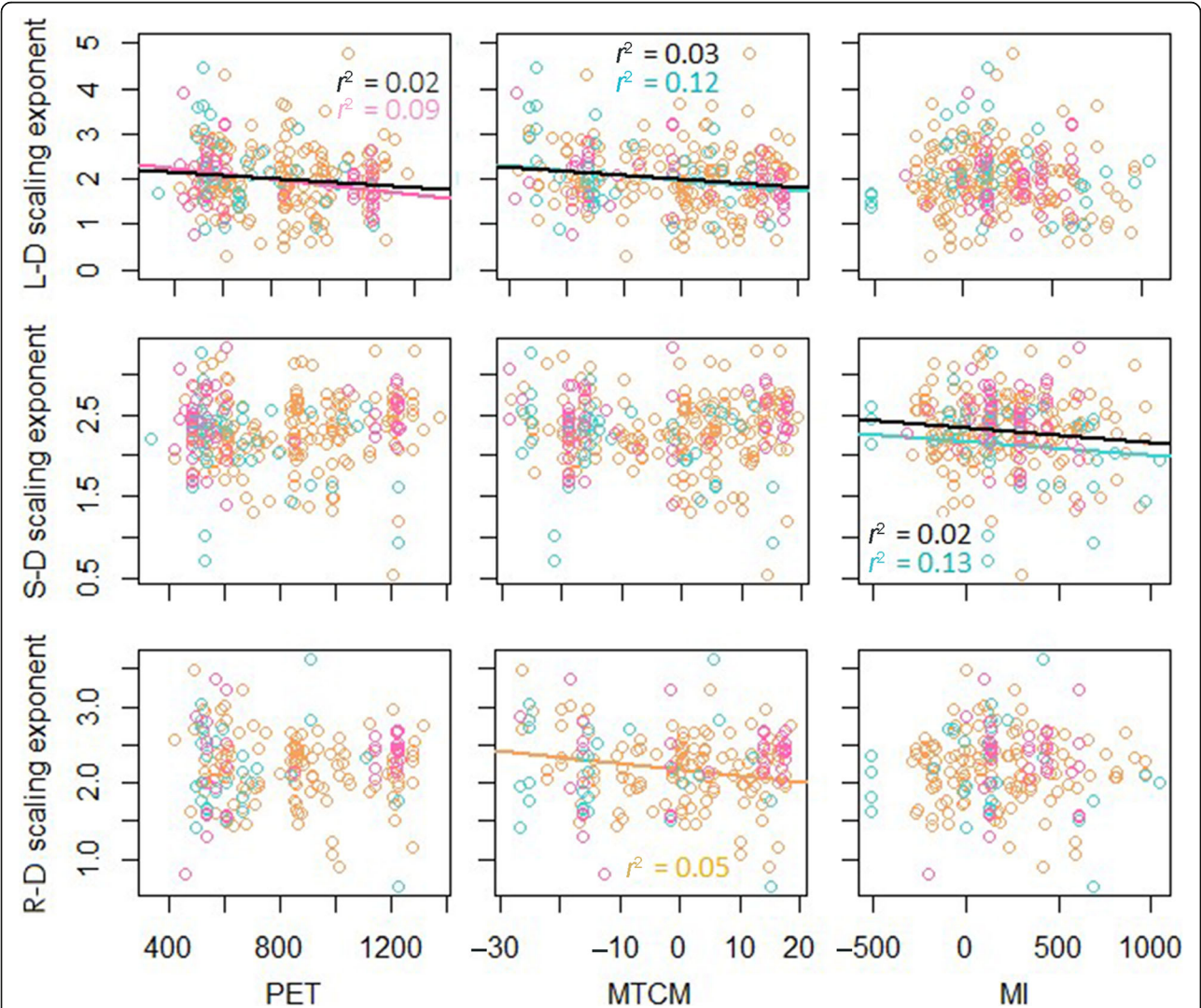|	Overall		Plantation		Natural forest	
	r^2	p	r^2	p	r^2	p
Leaf phenology	0.00	0.704	0.00	0.621	0.02	0.262
Stem density	−0.02	0.222	0.00	0.770	−0.10	0.128
Forest age	0.00	0.816	0.01	0.270	−0.02	0.494
Phylogeny						
Family	**0.26**	**0.013**	0.17	0.394	0.41	0.054
Genus	**0.41**	**0.004**	0.24	0.447	**0.76**	**0.000**
Species	**0.58**	**0.003**	0.47	0.161	**0.82**	**0.005**

Fig. 5 Relationships of L-D, S-D, and R-D scaling exponents with climate indices (PET, MTCM, and MI). Regression lines were given for relationships scaling exponents that were significant ($p < 0.05$). Green circles and regression lines represent trees in secondary forests, pink circles and regression lines represent trees in primary forests, and brown circles and regression lines represent trees in plantations. Black regression lines are given when relationships at overall level were significant
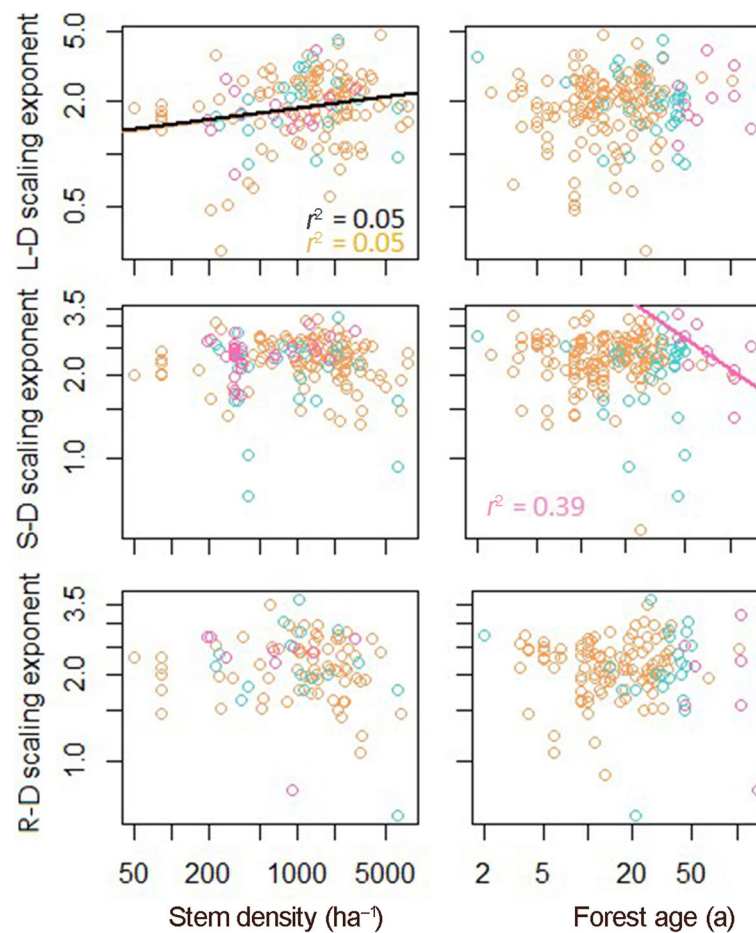
Fig. 6 Relationships of L-D, S-D, and R-D scaling exponents with biotic factors (stem density and forest age). Regression lines are given for relationships for scaling exponents that were significant ($p < 0.05$). Green circles and regression lines represent trees in secondary forests, pink circles and regression lines represent trees in primary forests, and brown circles and regression lines represent trees in plantations. Black regression lines are given when overall relationships were significant

natural forests. Both S-D and R-D scaling exponents were significant affected by leaf form ($r^2 = 0.06–0.08$, $p < 0.05$) and phylogeny ($r^2 = 0.45–0.82$, $p < 0.01$).

The aforementioned results suggested that climate, biotic factors, and phylogeny all can have significant influence on allometric exponents. Indeed, many of these variables were retained in the final mixed-models and had significant explanatory power (Table 2). However, the result of mixed-models suggested that the major factors influencing the three allometric relationships were different. L-D scaling exponent was only significantly affected by MTCM, which explained 3.24% of variation ($p < 0.05$). On the other hand, S-D and R-D scaling exponents were affected by many factors including climactic, biotic, and phylogenetic factors. The S-D scaling exponent was significantly affected by MTCM (i.e. climate index, %SS = 2.76, $p < 0.05$), forest types and stem density (i.e. biotic factors, %SS = 7.32–5.86, $p < 0.01$), and family (i.e. phylogeny, %SS = 26.43, $p < 0.05$). The R-D

scaling exponent was significantly affected by forest types, stem density (%SS = 8.20–8.54, $p < 0.01$) and family (%SS = 36.16, $p < 0.05$).

Discussion

Allometries vary with successional stage in natural forests

Previous criticism of MST theory has focused on the fact that many observations do not support MST predictions. Our results show that S-D and R-D scaling exponents deviated from theory predictions when examine all data together. However, a further analysis showed that all the L-D, S-D and R-D exponents supported the MST predictions in primary forests, while the S-D and R-D exponents deviated more from MST predictions in secondary forests. This is consistent with some studies (Enquist et al. 2009; Duncanson et al. 2015; Sun et al. 2017a) which found that the MST predictions may be only supported in late successional forests, while forests in earlier successional stages revealed greater deviations. Note that

Table 2 Summary of mixed-models for the effects of climate (PET, MTCM, MI, and biome), leaf form (conifer or broadleaf), leaf phenology (evergreen or deciduous), forest types (secondary natural forest, primary natural forest, and plantation), stem density, forest age, and phylogeny groups (family, genus, and species) on L-D, S-D, and R-D allometric relationships. Bold indicates $p < 0.05$. Unnecessary variables were dropped based on AIC. %SS, percentage of sum squares explained; *df* degree of freedom, *MS* mean square

	df	MS	p	%SS
L-D scaling exponent				
MTCM	1	2.68	**0.042**	3.24
Biome	3	1.35	0.101	4.87
Stem density	1	1.87	0.089	2.26
Residuals	117	0.63		89.63
S-D scaling exponent				
PET	1	0.02	0.669	0.09
MTCM	1	0.70	**0.024**	2.76
Biome	3	0.67	**0.003**	7.91
Forest types	2	0.93	**0.002**	7.32
Stem density	1	1.49	**0.001**	5.86
Family	23	0.29	**0.010**	26.43
Genus	10	0.16	0.899	6.12
Species	24	0.14	0.985	13.30
Residuals	59	0.13		30.21
R-D scaling exponent				
MI	1	0.00	0.957	0.00
Forest types	2	0.95	**0.010**	8.20
Stem density	1	1.97	**0.002**	8.54
Family	20	0.42	**0.017**	36.16
Genus	5	0.22	0.904	4.78
Species	17	0.21	0.876	15.71
Residuals	34	0.18		26.61

Enquist et al. (2009) presented a zeroth-order model based on MST theory and predicted that deviations of scaling exponents from theory predictions should be greater in earlier successional stages. After that, Duncanson et al. (2015) and Sun et al. (2017a) demonstrated that the allometric exponents of tree height vs. trunk diameter, and tree size distribution, both deviated more from MST predictions as a function of successional status in North America and northeast China. Interestingly, here we found stem and root biomass-diameter allometric relationships have the same variation with successional progress. Our results provided clear evidence that the regular change of allometric exponent during forest succession is a general pattern, for various scaling relationships, across biomes from boreal to tropical forests.

Although according to our results, allometries in primary forests did not fully support MST predictions, which seems inconsistent with MST, it still cannot be rejected. We found that the data were not well estimated by reduced major-axis (RMA) regressions, and that when using an ordinary least squares (OLS) regression for fitting the slope (i.e. scaling exponent), the allometry exponent values were underestimated (note that OLS regression is recommended when predicting Y from X while RMA is recommended when test if the slope equals a specific value for the line best describing the relationship between Y and X (Warton et al. 2006; Price et al. 2007)). The scaling exponents of allometric relationships in primary forest would therefore be affected leading to lower statistical results. Therefore, the allometric relationships in primary forest might better support the predictions of MST if the underestimates of traditional regressions are accounted for. Thus, our results were consistent with the predictions of MST.

Differences in allometries between plantations and natural forests

Our results showed that forest origin influenced allometries. Scaling exponents deviated more in secondary natural forests and were close to theoretical predictions in primary natural forests, while plantations fell somewhere in the middle. These are consistent with the results of Wang et al. (2008), which demonstrated that root–shoot allocation scaling exponents in plantations were in between those of primary and secondary forests. However, both of our results contrast with Mokany et al. (2006) who reported no significant difference in the ratios of root to shoot biomass between plantations and natural forests. It may be because that Mokany et al. (2006) did not analyze natural forests at different stages of succession separately. Our results suggest that, if succession stages are ignored and data from early and late successional forests are pooled together, the result may be close to the intermediate value that is observed in plantations. The importance of distinguishing between successional stages when examining allometric relationships in natural forests (see also Duncanson et al. 2015; Sun et al. 2017a), as well as comparing allometries between natural forests and plantations, is clearly illustrated by our findings.

Plantations are generally established in more fertile and moister soil than natural forests, and comprehensive forest management practices can further ensure them more appropriate living conditions, compared with other types of forests. Because of sufficient soil moisture and nutrient availability in plantations, trees do not need to increase their allocation to root biomass to get more nutrients and water (Mokany et al. 2006; Wang et al. 2008). Consequently, plantations generally have lower

root to shoot biomass ratios than natural forests (Luo et al. 2012). Although Luo et al. (2012) did not look into age but used stands over 20 years and did not analyze the age effect, our results showed that the effect of forest age is weak. Furthermore, forest management practices in plantations such as thinning and selected harvesting affect the biotic factors that are important for tree allometries, which lead to different allometries between plantations and natural forests (Luo et al. 2012, 2014; Zhang et al. 2015). For example, thinning reduces stem density, which reduces the competition for light (Rüger and Condit 2012; Sun et al. 2017a), and thus promotes the accumulation of biomass in woody tissues (Poorter et al. 2012), while pruning reduces the branches and leaves of the trees which affects the accumulation of leaf biomass (but not necessarily the most active part of the tree foliage ("unproductive leaf mass") and can also affect the diameter development if in extreme conditions.

Additionally, our result showed that phylogeny have few significant effects on allometries in plantations. This may be due to management practices involving species selection. Such species selection may make biodiversity in plantations lower than natural forests (Brockerhoff et al. 2008). This may be the reason that phylogeny did not have a significant effect in plantations. Consequently, forest management practices may lead to different patterns of allometries in plantations than those in natural forests, and it must be considered when conducting research on allometric relationships in plantations.

More importantly, the differences between allometric relationships in plantations, secondary and primary natural forests mean that the estimation of stand biomass requires the use of relevant allometric relationships measured from the same forest type. But this has not been paid attention to in biomass estimation yet, which may lead to errors in biomass estimation.

Factors determining allometric variation

In our multivariate models, MTCM, biome, forest type, stem density, and species significantly affected allometric exponents. These results, examining abiotic and biotic effects on allometries, are consistent with previous broad-scale studies (Duncanson et al. 2015).

Authors have found that climate can have a weak indirect effect on allometric relationships (Wang et al. 2006; Lines et al. 2012). In our study, winter temperature had a significant effect on L-D and S-D scaling exponents. Trees may adopt particular allometric relationships to survive cold temperatures in winter (Lines et al. 2012). Thus, winter coldness may become an important constraint for allometric relationships. Our results are in line with previous studies showing that higher stem density intensifies light competition between trees (Getzin et al. 2006; Wang et al. 2016). Competition for

light has been known to explain the highest proportion of the variations in the D-H allometric exponent (Poorter et al. 2012). Our study further confirmed that the S-D and R-D scaling exponents were linked to light competition too. However, we also found that these effects were weak, which means that biophysical constraints still strongly influence allometric relationships. This may explain why the effect of external factors was almost insignificant over a small gradient in some studies (Poorter et al. 2012; Sun et al. 2017b).

Meanwhile, among these factors, phylogeny explained the highest proportion of the variations in the S-D and R-D scaling exponents (Table 2, 26.43% and 36.16% of variation). Wang et al. (2011) found that there were significant deviations in scaling exponents when interspecies differences were considered with the stratified Bayesian method. Our results support their findings. A possible mechanism that phylogeny affects the S-D and R-D scaling exponents is that phylogeny has been shown to be associated with conduit size, i.e., recently evolved species have longer and wider conduits than ancient ones (Savage et al. 2010; Jacobsen et al. 2012), while the size of conduit largely determines the water transport efficiency it can consequently leads to the variations of the S-D and R-D scaling exponents. Therefore, theoretical models such as MST should be extended to include the effect of phylogeny.

Besides, we noted that the influence of phylogeny is mainly reflected in family level (Table 2). This may imply that the allometric relationships are evolutionary conservative at the family level. Previous studies have generally found that conifers had a higher D-H scaling exponent than broadleaf trees because of differences in wood density or branching architecture (Lines et al. 2012; Duncanson et al. 2015; Hulshof et al. 2015). Our results are consistent with these findings.

Different variation rules among L-D, S-D and R-D allometries

Previous studies have shown that the biomass allocation and functional traits of leaves, stems, and roots were affected by various abiotic, biotic and evolutionary factors (Wang et al. 2008; Poorter et al. 2015; Wright et al. 2005, 2017). According to MST, different allometric relationships between traits are connected and can be therefore be deduced from each other, however, our results showed that variations, and the major factors producing those variations, were significantly different for L-D, S-D and R-D relationships. This is consistent with many previous studies (Deng et al. 2006; Poorter et al. 2012). For example, previous studies found that leaf biomass allocation was relatively insensitive, while stem and root biomasses were affected by many factors (Poorter et al. 2012). Deng et al. (2006) showed that during water

shortage, between above-ground biomass and stem density of shrub communities varied significantly with water gradient, while the scaling exponent of total biomass with underground biomass was not only unaffected by moisture gradient but was close to the MST prediction of − 4/3. Our results also showed that in forests, the scaling exponent of the L-D relationship supported MST prediction and had no significant deviations in plantations or secondary forests, while variations observed in the S-D and R-D scaling exponents were relatively large. The L-D scaling exponent was more stable and only weakly affected by MTCM, while the S-D and R-D scaling exponents had similar patterns of variation and were significantly affected by climate, succession, light competition, and phylogeny. Our results and Deng et al. (2006) both showed different responses for different allometric relationships to various factors. Consequently, it is necessary to study multiple allometric relationships simultaneously in order to understand how they are related and how they are influenced by various abiotic and biotic factors.

Our results indicated that L-D exponent is relatively stable, and conform to MST prediction irrespective of successional stage, forest origin, phylogeny, leaf form and phonology. To our knowledge, this difference from S-D and R-D allometries has not been reported before in large scale studies. We propose three potential explanations as follows. First, as the photosynthesizing organ, leaves may have stronger biophysical constraints and thus may be more phylogenetically conserved than the stem or root. Previous studies found that leaves prefer to change shapes and area to adapt to the environment rather than change biomass allocation (Poorter et al. 2012). Our results also showed that phylogeny had no significant effect on the L-D scaling exponent, so our results all support this explanation. Second, trees can shed and regenerate leaves to adapt leaf biomass to their environment (Zanne et al. 2014). This mechanism may also make leaf biomass allocation more stable and closer to theoretical predictions as they maintain optimal metabolism. Third, adding secondary xylem and gradually lost water transport function of earlier developed xylems in the stem and root during growth may change stem and root biomass fractions (Niklas and Spatz 2004). This change may cause further variation in the S-D and R-D scaling exponents. Since leaves have no secondary xylem, the L-D scaling exponent would not be altered by the same mechanism. However, which of these explanations is the major cause of the differences among L-D, S-D, and R-D scaling exponents remains unclear and needs further examination.

Conclusions

In this study, we examined effects of climate, biotic factors, and phylogeny on the allometric relationships of leaf, stem, and root biomass to diameter in plantations and natural forests across China. Our research at a broad scale, including biomes from boreal to tropical forests across China, thus provided strong support to the idea that allometric relationships are also vary with successional stage. Scaling exponents are consistent with MST predictions in primary forests and deviated greater from theoretical predictions in secondary forests. The allometric scaling exponents of plantations were in between secondary and primary natural forests even though the species composition and forest age of a plantation is closer to that of secondary forests, and were affected by fewer factors than in natural forest. These results reflect the influence of forest management practices on allometries. MST cannot explain this variation yet, however, since there is a great amount of plantation area in the world, it is important to do more research on allometries in closely managed plantations. Our study also found that the L-D scaling exponent was relatively insensitive, while the S-D and R-D scaling exponents were significantly affected by climate, biotic factors, and phylogeny. This suggested that L-D allometry is more strongly controlled by biophysical constraints compared with S-D and R-D allometry, however, the mechanisms behind this difference still needs further examination.

Supplementary information

Supplementary information accompanies this paper at https://doi.org/10.1186/s40663-020-00263-y.

Additional file 1.

Additional file 2.

Abbreviations
MST: metabolic scaling theory; H: height; D: diameter; L: leaf biomass; S: stem biomass; R: root biomass; PET: annual potential evapotranspiration; MTCM: mean temperature for the coldest month; MI: moisture index; AIC: Akaike Information Criterion; CI: confidence intervals; RMA regression: reduced major-axis regression; OLS regression: ordinary least squares regression

Authors' contributions
Han Sun, Xiangping Wang and Dayong Fan conceived the study; Han Sun performed the analyses and wrote the first draft; all authors contributed critically to successive drafts and gave final approval for publication.

Availability of data and materials
The datasets used and/or analyzed in during the current study are available from the corresponding author on reasonable request.

Ethics approval and consent to participate
No applicable.

Consent for publication
No applicable.

References

Apol MEF, Etienne RS, Olff H (2008) Revisiting the evolutionary origin of allometric metabolic scaling in biology. Funct Ecol 22:1070–1080

Binkley D, Stape JL, Ryan MG (2004) Thinking about efficiency of resource use in forests. Forest Ecol Manag 193:5–16

Brockerhoff EG, Jactel H, Parrotta JA, Quine CP, Sayer J (2008) Plantation forests and biodiversity: oxymoron or opportunity? Biodivers Conserv 17:925–951

Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Toward a metabolic theory of ecology. Ecology 85:1771–1789

Chave J, Andalo C, Brown S, Cairns MA, Chambers JQ, Eamus D, Fölster H, Fromard F, Higuchi N, Kira T, Lescure J-P, Nelson BW, Ogawa H, Puig H, Riéra B, Yamakura T (2005) Tree allometry and improved estimation of carbon stocks and balance in tropical forests. Oecologia 145:87–99

Chave J, Réjou-Méchain M, Búrquez A, Chidumayo E, Colgan MS, Delitti WBC, Duque A, Eid T, Fearnside PM, Goodman RC, Henry M, Martínez-Yrízar A, Mugasha WA, Muller-Landau HC, Mencuccini M, Nelson BW, Ngomanda A, Nogueira EM, Ortiz-Malavassi E, Pélissier R, Ploton P, Ryan CM, Saldarriaga JG, Vieilledent G (2014) Improved allometric models to estimate the aboveground biomass of tropical trees. Glob Chang Biol 20:3177–3190

Crawley M (2007) The R book. Wiley, Chichester

Deng J, Wang G, Morris EC, Wei X, Li D, Chen B, Zhao C, Liu J, Wang Y (2006) Plant mass-density relationship along a moisture gradient in north-West China. J Ecol 94:953–958

Duncanson LI, Dubayah RO, Enquist BJ (2015) Assessing the general patterns of forest structure: quantifying tree and forest allometric scaling relationships in the United States. Glob Ecol Biogeogr 24:1465–1475

Enquist BJ, Niklas KJ (2001) Invariant scaling relations across tree-dominated communities. Nature 410:655–660

Enquist BJ, West GB, Brown JH (2009) Extensions and evaluations of a general quantitative theory of forest structure and dynamics. PNAS 106:7046–7051

Fang J, Brown S, Tang Y, Nabuurs GJ, Wang X, Shen H (2006) Overestimated biomass carbon pools of the northern mid- and high latitude forests. Clim Chang 74:355–368

Fang J, Shen Z, Tang Z, Wang X, Wang Z, Feng J, Liu Y, Qiao X, Wu X, Zheng C (2012) Forest community survey and the structural characteristics of forests in China. Ecography 35:1059–1071

Getzin S, Dean C, He F, Trofymow JA, Wiegand K, Wiegand T (2006) Spatial patterns and competition of tree species in a Douglas-fir chronosequence on Vancouver Island. Ecography 29:671–682

He JS, Wang X, Flynn DFB, Wang L, Schmid B, Fang J (2009) Taxonomic, phylogenetic, and environmental trade-offs between leaf productivity and persistence. Ecology 90:2779–2791

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. Int J Climatol 25:1965–1978

Hulshof CM, Swenson NG, Weiser MD (2015) Tree height–diameter allometry across the United States. Ecol Evol 5:1193–1204

Jacobsen AL, Pratt RB, Tobin MF, Hacke UG, Ewers FW (2012) A global analysis of xylem vessel length in woody plants. Am J Bot 99:1583–1591

Johnson JB, Omland KS (2004) Model selection in ecology and evolution. Trends Ecol Evol 19:101–108

Lines ER, Zavala MA, Purves DW, Coomes DA (2012) Predictable changes in aboveground allometry of trees along gradients of temperature, aridity and competition. Glob Ecol Biogeogr 21:1017–1028

Luo Y, Wang X, Lu F (2015) Comprehensive database of biomass regressions for China's tree species. China Forestry Publishing House, Beijing

Luo Y, Wang X, Zhang X, Booth TH, Lu F (2012) Root:shoot ratios across China's forests: forest type and climatic effects. Forest Ecol Manag 269:19–25

Luo Y, Zhang X, Wang X, Ren Y (2014) Dissecting variation in biomass conversion factors across China's forests: implications for biomass and carbon accounting. PLoS One 9:e94777

McMahon TA, Kronauer RE (1976) Tree structures: deducing the principle of mechanical design. J Theor Biol 59:443–466

Mokany K, Raison RJ, Prokushkin AS (2006) Critical analysis of root:shoot ratios in terrestrial biomes. Glob Chang Biol 12:84–96

Muller-Landau HC, Condit RS, Chave J, Thomas SC, Bohlman SA, Bunyavejchewin S, Davies S, Foster R, Gunatilleke S, Gunatilleke N, Harms KE, Hart T, Hubbell SP, Itoh A, Kassim AR, LaFrankie JV, Lee HS, Losos E, Makana J-R, Ohkubo T, Sukumar R, Sun I-F, Supardi MNN, Tan S, Thompson J, Valencia R, Muñoz GV, Wills C, Yamakura T, Chuyong G, Dattaraja HS, Esufali S, Hall P, Hernandez C, Kenfack D, Kiratiprayoon S, Suresh HS, Thomas D, Vallejo MI, Ashton P (2006) Testing metabolic ecology theory for allometric scaling of tree size, growth and mortality in tropical forests. Ecol Lett 9:575–588

Niklas KJ, Spatz HC (2004) Growth and hydraulic (not mechanical) constraints govern the scaling of tree height and mass. PNAS 101:15661–15663

Poorter H, Jagodzinski AM, Ruiz-Peinado R, Kuyah S, Luo Y, Oleksyn J, Usoltsev VA, Buckley TN, Reich PB, Sack L (2015) How does biomass distribution change with size and differ among species? An analysis for 1200 plant species from five continents. New Phytol 208:736–749

Poorter H, Niklas KJ, Reich PB, Oleksyn J, Poot P, Mommer L (2012) Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. New Phytol 193:30–50

Price CA, Enquist BJ, Savage VM (2007) A general model for allometric covariation in botanical form and function. PNAS 104:13204–13209

Price CA, Ogle K, White EP, Weitz JS (2009) Evaluating scaling models in biology using hierarchical Bayesian approaches. Ecol Lett 12:641–651

Quinn G, Keough M (2002) Experimental design and data analysis for biologists. Cambridge University Press, Cambridge

R Core Team (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Rubner M (1883) On the influence of body size on metabolism and energy exchange. Zeitschriftfür Biologie 19:535–562

Rüger N, Condit R (2012) Testing metabolic theory with models of tree growth that include light competition. Funct Ecol 26:759–765

Savage VM, Bentley LP, Enquist BJ, Sperry JS, Smith DD, Reich PB, von Allmen EI (2010) Hydraulic trade-offs and space filling enable better predictions of vascular structure and function in plants. PNAS 107:22722–22727

Sun H, Wang X, Fan Y, Liu C, Wu P, Li Q, Yin W (2017b) Effects of biophysical constraints, climate and phylogeny on forest shrub allometries along an altitudinal gradient in Northeast China. Sci Rep 7:43769

Sun H, Wang X, Wu P, Han W, Xu K, Liang P, Liu C, Yin W, Xia X (2017a) What causes greater deviations from predictions of metabolic scaling theory in earlier successional forests? Forest Ecol Manag 405:101–111

Wang X, Fang J, Sanders NJ, White PS, Tang Z (2009) Relative importance of climate vs local factors in shaping the regional patterns of forest plant richness across Northeast China. Ecography 32:133–142

Wang X, Fang J, Tang Z, Zhu B (2006) Climatic control of primary forest structure and DBH–height allometry in Northeast China. Forest Ecol Manag 234:264–274

Wang X, Fang J, Zhu B (2008) Forest biomass and root-shoot allocation in Northeast China. Forest Ecol Manag 255:4007–4020

Wang X, Ouyang S, Sun OJ, Fang J (2013) Forest biomass patterns across Northeast China are strongly shaped by forest height. Forest Ecol Manag 293:149–160

Wang Y, Chu C, Zhu K, Shen Z (2011) Effects of inter-specific variability on biomass allocation: a hierarchical Bayesian approach. Ecol Inform 6:341–344

Wang Y, Pederson N, Ellison AM, Buckley HL, Case BS, Liang E, Julio Camarero J (2016) Increased stem density and competition may diminish the positive effects of warming at alpine treeline. Ecology 97:1668–1679

Warton DI, Wright IJ, Falster DS, Westoby M (2006) Bivariate line-fitting methods for allometry. Biol Rev 81:259–291

West GB, Brown JH, Enquist BJ (1997) A general model for the origin of allometric scaling laws in biology. Science 276:122–126

West GB, Brown JH, Enquist BJ (1999) A general model for the structure and allometry of plant vascular systems. Nature 400:664–667

White CR, Cassey P, Blackburn TM (2007) Allometric exponents do not support a universal metabolic allometry. Ecology 88:315–323

Wright IJ, Dong N, Maire V, Prentice IC, Westoby M, Díaz S, Gallagher RV, Jacobs BF, Kooyman R, Law EA, Leishman MR, Niinemets Ü, Reich PB, Sack L, Villar R, Wang H, Wilf P (2017) Global climatic drivers of leaf size. Science 357:917–921

Wright IJ, Reich PB, Cornelissen JHC, Falster DS, Groom PK, Hikosaka K, Lee W, Lusk CH, Niinemets Ü, Oleksyn J, Osada N, Poorter H, Warton DI, Westoby M (2005) Modulation of leaf economic traits and trait relationships by climate. Glob Ecol Biogeogr 14:411–421

Zanne AE, Tank DC, Cornwell WK, Eastman JM, Smith SA, Fitzjohn RG, McGlinn DJ, O'Meara BC, Moles AT, Reich PB, Royer DL, Soltis DE, Stevens PF, Westoby M, Wright IJ, Aarssen L, Bertin RI, Calaminus A, Govaerts R, Hemmings F, Leishman MR, Jacek O, Soltis PS, Swenson NG, Warman L, Beaulieu JM (2014) Three keys to the radiation of angiosperms into freezing environments. Nature 506:89–92

Zhang H, Song T, Wang K, Wang G, Liao J, Xu G, Zeng F (2015) Biogeographical patterns of forest biomass allocation vary by climate, soil and forest characteristics in China. Environ Res Lett 10:44014