

REVIEW

Pattern and control of biomass allocation across global forest ecosystems

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Abstract

The underground part of a tree is an important carbon sink in forest ecosystems. Understanding biomass allocation between the below- and aboveground parts (*root:shoot ratios*) is necessary for estimation of the underground biomass and carbon pool. Nevertheless, large-scale biomass allocation patterns and their control mechanisms are not well identified. In this study, a large database of global forests at the community level was compiled to investigate the *root:shoot ratios* and their responses to environmental factors. The results indicated that both the aboveground biomass (AGB) and belowground biomass (BGB) of the forests in China (medians 73.0 Mg/ha and 17.0 Mg/ha, respectively) were lower than those worldwide (medians 120.3 Mg/ha and 27.7 Mg/ha, respectively). The *root:shoot ratios* of the forests in China (median = 0.23), however, were not significantly different from other forests worldwide (median = 0.24). In general, the allocation of biomass between the belowground and aboveground parts was determined mainly by the inherent allometry of the plant but also by environmental factors. In this study, most correlations between *root:shoot ratios* and environmental factors (development parameter, climate, altitude, and soil) were weak but significant ($p < .01$). The allometric model agreed with the trends observed in this study and effectively estimated BGB based on AGB across the entire database.

KEYWORDS

allometric model, belowground biomass, biomass allocation, forest ecosystems, global environmental change, *root:shoot ratios*

1 | INTRODUCTION

The forest ecosystem holds forty percent of the global belowground carbon. It plays key roles in climate change and carbon cycling (Dixon et al., 1994). New biomass produced by photosynthesis is transported to the leaves, stems, roots, and reproductive organs. When new biomass is proportionally allocated to these sinks, it also ensures proportional distribution of new carbon (Reich et al., 2014). Biomass allocation is influenced by both biotic and abiotic factors. Understanding biomass distribution is essential for global carbon cycle modeling and accounting (Hui, Wang, Le, Shen, & Ren, 2012).

The *root:shoot ratios* effectively describe the allocation between aboveground biomass (AGB) and belowground biomass (BGB). They can therefore be used to estimate BGB using the readily measurable AGB (Wang et al., 2014). The *root:shoot ratios* reflect the adaptation of a plant to various environments (Mokany, Raison, & Prokushkin, 2006). This information is a necessary input of carbon modeling. Changes in BGB and C content may be predicted when the driving forces of biomass allocation are identified.

Over the past twenty years, many scholars have used allometry to study biomass allocation in plants (Enquist & Niklas, 2002; West, Brown, & Enquist, 1997; West, Enquist, & Brown, 2009). Their

hypotheses have been corroborated by experimental data (Niklas, 2006; Yang, Fang, Ji, & Han, 2009). Biomass partitioning is described using the allometric model $BGB = aAGB^b$, where a is a normalizing scaling constant, and b is an allometric scaling exponent (Huxley & Tessier, 1936; Niklas & Enquist, 2001). BGB scales nearly isometrically with respect to AGB for both woody and nonwoody plants (Enquist & Niklas, 2001, 2002). This model has been validated across ecologically diverse species worldwide using plants with a wide range of total body mass at the individual plant level. (Niklas, 2005, 2006; Niklas & Enquist, 2002). Similarly, many allometric BGB – AGB models have also been proposed for the major forest types in China (Cheng & Niklas, 2007; Hui et al., 2014; Luo, Wang, Zhang, Booth, & Lu, 2012). These were based on community-level data sets. Some studies indicated that the scaling exponents between AGB and BGB varied by forest origin, phylogeny, leaf habit, forest type, stand age, and climate (Hui et al., 2014; Luo et al., 2012) on different scales. Others reported that using different regression methods might result in scaling exponent differences (Li, Han, & Wu, 2005). Although allometric models may be useful for predicting BGB at specific sites and in particular species (Brown, 2002; Li, Kurz, Apps, & Beukema, 2003; Mokany et al., 2006), more evidence is required to demonstrate a universal scaling relationship. Once this parameter is fully validated, allometric relationships can be applied to predict BGB across wide temporal and spatial scales.

Many studies have indicated that various factors influence AGB – BGB allocation. These include species characteristics, stand development, stand density, resources, and climate (Cairns, Brown, Helmer, & Baumgardner, 1997; Cambui et al., 2011; Poorter & Nagel, 2000). Plants adjust their biomass allocation between the belowground and aboveground parts (*root:shoot ratios*) in ways characteristic of each species (Monk, 1966). Temperature, precipitation, solar radiation, soil texture, and resource availability (such as soil moisture and nitrogen) significantly affect biomass allocation (Mokany et al., 2006; Reich, 2002). In general, environmental stressors force plants to invest their resources in organ growth (Cairns et al., 1997; Cambui et al., 2011; Poorter & Nagel, 2000). Previous studies have investigated variations in the *root:shoot ratios* associated with species characteristics, stand development, stand density, resources, soil texture, and climate at the regional or global level (Cairns et al., 1997; Cambui et al., 2011; Mokany et al., 2006; Poorter & Nagel, 2000; Reich, 2002; Zhang, Song, et al., 2015; Zhang, Wang, et al., 2015), but they reported different findings. More evidence is needed to determine whether the *root:shoot ratios* responds on a large scale to biotic and abiotic factors. Several studies have investigated the forests of China and cited significant findings (Hui et al., 2014; Luo, Wang, Zhang, Ren, & Poorter, 2013; Luo et al., 2012; Wang, Fang, & Zhu, 2008; Zhang, Song, et al., 2015; Zhang, Wang, et al., 2015), but these results may not be consistent with those of the forests elsewhere.

The mechanisms by which plants partition photosynthate under environmental stress are incompletely understood. In the short term, the responses of the *root:shoot ratios* to biotic and abiotic factors are predictable for individual species (Chapin, 1980; Hawkins, Kiiskila, & Henry, 1999; Mooney et al., 1988; Vogel et al., 2008). Nevertheless, it is difficult to forecast large-scale biomass allocation patterns in

response to biotic and abiotic stressors, and on a global scale, the results are inconsistent. In the effort to identify large-scale biomass allocation patterns across forest ecosystems, data were gathered from the literature worldwide for *root:shoot ratios*, BGB , and AGB or for standing leaf, stem, flower and fruit dry weights, respectively. Geographical factors, vegetation parameters, and environmental variables were also determined to evaluate biomass allocation in response to biotic and abiotic factors. Data were specifically collected for the forests of China. The following questions were addressed in this study: (1) on a global scale, how do trees partition their biomass between organs and between aboveground and belowground parts? (2) how does the allometric theory hold up at the individual plant and community levels? (3) how do biotic and abiotic variables affect the *root:shoot ratios*? and (4) on a worldwide basis, how well does the allometric theory predict BGB (root biomass)?

2 | MATERIALS AND METHODS

2.1 | Data collections

All correlations between the *root:shoot ratios* and biotic and abiotic factors were analyzed using the data sets of Luo et al. (2012) and Mokany et al. (2006). Luo et al. (2012) reported 1,138 pairs of AGB and BGB measurements for about 250 types of forest at 343 sites across China. They compiled this data set from 511 sources published between 1978 and 2008. In this study, 415 pairs of AGB and BGB measurements were gathered from the published literature. These were added to the Luo et al. (2012) data set. Therefore, in this study, a total of 1,553 pairs of AGB and BGB measurements for the forests of China were collected. The Mokany et al. (2006) data set was compiled for forests worldwide and consisted of 786 pairs of AGB and BGB measurements obtained from 266 sources (books, published reports, and conference reports). Only studies presenting pairs of data for both AGB and BGB were included in Mokany et al. (2006) data set. Biomass data for individual plants and BGB derived from models were excluded.

In the aforementioned data sets, the following factors (where available) were recorded for each sampling site: biomass (Mg/ha); AGB (or leaf, stem, branch, flower, and fruit biomass if available); BGB ; site description (location, longitude, latitude, elevation, soil texture, and soil nutrient profile); climate (mean annual precipitation (MAP), mean annual temperature (MAT), mean annual evapotranspiration (ET), mean annual potential evapotranspiration (PET), and sunshine duration (SH)); vegetation characteristics (forest origin, forest type, and dominant species); and stand parameters (stand age, mean tree height, stem density, and mean diameter at breast height [DBH]). ET and PET were derived from 1 km² land surface ET data sets reported by the Numerical Terra Dynamic Simulation Group at <http://www.ntsg.umd.edu/project/mod16>.

In the Luo et al. (2012) data set, missing MAT , MAP and SH data for each site were estimated by minimum-distance interpolation using 664 ground observation stations across China. The mean MAT , MAP , and SH for 1961–2010 were used in the analysis. Estimates of MAT

and *MAP* were compared with measured values from the literature. The estimated *MAP* was significantly correlated with the measured *MAP* ($R^2 = .92, p < .01$). The estimated *MAT* was also significantly correlated with measured *MAT* ($R^2 = .90, p < .01$). Soil texture data for the forests of China were obtained from texture maps (Institute of Soil Science, Chinese Academy of Sciences, 1986) and were based on the location (longitude and latitude) of the data site. For the Mokany et al. (2006) data set, missing *MAT* and *MAP* were estimated using a Local Climate Estimator (*LocClim*, FAO, 2002). This tool estimates basic climate variables from the latitude, longitude, and altitude. The accuracies of the estimated *MAT* and *MAP* were validated by comparing them with the literature measurements (Mokany et al., 2006).

The generality of the allometric partitioning theory was tested using two community-level data sets (i.e., Luo et al. (2012) and Mokany et al. (2006)) and one data set at the individual plant level (Enquist and Niklas (2002)). The latter data set included both woody and nonwoody plants. For woody plants, 346 biomass records were selected from Edwards (1983). Data for nonwoody plants in Enquist and Niklas (2002) were collected from primary literature published between 1987 and 2002. All standing biomass units were converted into kilogram of dry weight per plant. Enquist and Niklas (2002) cited 257 woody and nonwoody species, and more than one thousand dry mass measurements spanning ten orders of magnitude of *AGB* and *BGB*. Only biomass data (leaf, stem, and root biomass in kg dry matter/plant) were presented in the Enquist and Niklas (2002) data set. Therefore, it was only used to analyze allometric relationships in plant organ biomass.

2.2 | Statistical analyses

Linear regression analysis was used to evaluate the relationship between the *root:shoot ratios* and biotic and abiotic factors. Ordinary least squares (*OLS*) were used to establish regression formulas to forecast *BGB* based on *AGB* measurements. The reliability of the *BGB* predicted from *AGB* measurements was determined by calculating the % prediction errors $\text{Pred.Error} = [(\text{Obs.BGB} - \text{Pred.BGB}) / \text{Pred.BGB}] \times 100$ (Smith, 1980).

For woody plants, allometric models predict that standing leaf biomass (M_L) scale as the 3/4 power of both the standing stem biomass (M_S) and the standing *BGB* (M_R), and that the M_R scale is indirectly proportional to M_S (Enquist & Niklas, 2002; Niklas, 2005). Assuming that the roots are the only underground organs, $M_R = M_B$, then, $M_L = \beta M_S^{3/4} = \beta M_R^{3/4}$, $M_S = (\beta_1 / \beta)^{4/3} M_R$ and $\beta_1 M_B^{3/4} + \left(\frac{\beta_1}{\beta} \right)^{4/3} M_B = M_A$.

The regression curve describing the allometric relationship had the form $\log M_1 = \log \beta + \alpha \log M_2$, where M_1 and M_2 are the plant organ biomasses, $\log \beta$ is the y-intercept of the regression curve (the allometric constant in *RMA* analyses), and α is the slope of the regression curve (the allometric scaling exponent in *RMA* analyses). Reduced major axis (*RMA*) regression was applied to establish allometric models for log-transformed data for *BGB* and *AGB* (Enquist & Niklas, 2002; Niklas, 2005). The significance of the differences between slopes (allometric scaling exponent) of the *RMA* regression formulas was evaluated using the univariate analysis of variance function in SPSS V. 17.0.

3 | RESULTS

3.1 | Variations in *AGB*, *BGB*, and *root:shoot ratios*

Both *AGB* and *BGB* varied significantly in the forests of China and worldwide. *AGB* ranged from 0.054 to 1,433 Mg/ha in the forests of China and from 0.058 to 1,736 Mg/ha worldwide. *BGB* ranged from 0.0089 Mg/ha in Chinese forests and from 0.046 to 204 Mg/ha in global forests. Table 1 shows that the standing biomass in the forests of China is significantly lower than that of global forests. The *root:shoot ratios* varied significantly in the forests of China (0.02–0.98) and the rest of the world (0.01–1.20). Nevertheless, *root:shoot ratios* did not significantly differ between the forests of China and those elsewhere; their mean and median values were similar (Figure 1).

3.2 | Factors influencing forest biomass and *root:shoot ratios*

Both *AGB* and *BGB* increased significantly ($p < .01$) with stand height, mean *DBH*, and stand age. On the other hand, both *AGB* and *BGB* were negatively correlated with stand density ($p < .01$). The *root:shoot ratios* decreased significantly ($p < .01$) with increasing stand height and mean *DBH*, and increased slightly with stand density (Figure 2). There was no significant relationship between *root:shoot ratios* and stand age.

The *root:shoot ratios* decreased significantly ($p < .01$) with increasing *MAP* and *ET/PET* (Figure 3a–c). In contrast, the *root:shoot ratios* increased significantly ($p < .01$) with *SH*. Nevertheless, neither *MAT* nor altitude significantly affected the *root:shoot ratios* (Figure 3d–e).

The *root:shoot ratios* in clay and loam soils were significantly lower than those in sandy and sandy loam soils (Figure 3f). Clay loam soil,

TABLE 1 Comparison of *AGB*, *BGB* and the *root:shoot ratios* in global forests and those in China

Forest group	<i>AGB</i> (Mg ha ⁻¹)				<i>BGB</i> (Mg ha ⁻¹)				<i>Root:shoot ratios</i>			
	Mean	Median	SD	n	Mean	Median	SD	n	Mean	Median	SD	n
China's forests	96.78	73.04	85.87	2,010	22.27	17.03	18.34	1,540	0.24	0.23	0.09	1,553
Global forests	161.27	120.34	167.57	566	35.69	27.65	34.16	568	0.29	0.24	0.19	568
Total	110.95	79.35	112.37	2,576	25.88	18.45	24.39	2,107	0.25	0.23	0.13	2,121

AGB, aboveground biomass; *BGB*, belowground biomass; *SD*, standard deviation; *n*, number of observations.

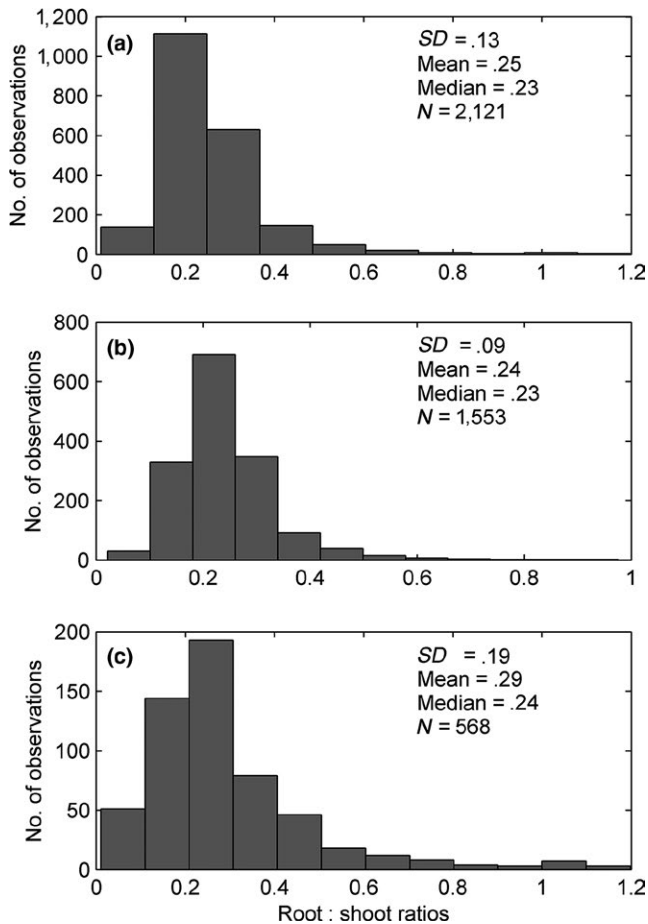


FIGURE 1 Distribution of *root:shoot ratios* for (a) all forests including those in China (b) Chinese forests (c) global forests. Mean and Median, the mean and median values of the *root:shoot ratios*, respectively; SD, the standard deviation; N, number of observations. Summary of statistics provided in Table 1

however, had significantly higher *root:shoot ratios* than those of any other soil texture.

Overall, climate factors (MAP, MAT, SH, and ET/PET) and soil texture explained 34 percent of the variability in *root:shoot ratio* data, and all relationships were significant ($p < .01$) except for MAP (Table 2).

3.3 | Allometric models

The scaling exponent of the allometric model for M_B and M_A ranged from 0.75 to 1.00 for woody plants (Enquist & Niklas, 2001; Niklas, 2005). These predictions (α_{Pred} in Table 3) aligned with the trends in the entire database (Table 3). In general, data presented at the individual plant level (kg dry matter/plant)—fit best with the allometric model (Figure 4; Table 3).

Although there were significant differences (Sig. $p = 0$) in the allometric slopes for M_L versus M_S , M_R versus M_S , and M_R versus M_L (Figure 4a–c), no significant differences (Sig. $p = .05$) were found for M_B versus M_A (Figure 4d) between the individual plant and community-level data sets (Figure 4).

4 | DISCUSSION

4.1 | Variations in AGB, BGB, and *root:shoot ratios*

Both biotic and abiotic factors (species, stand development, origin, human activities, resources, and climate) accounted for wide variations in AGB, BGB, and *root:shoot ratios* in both global and Chinese forests. Table 1 shows that both AGB and BGB of the forests of China were much lower than those of global forests. Local studies indicated that the biomass of typical forests in China is roughly on the same level as that of the rest of the world (Fang, Liu, & Xu, 1996; Peng & Zhang, 1994). Most original zonal forests of China are replaced by secondary forests with lower biomass. Moreover, in China, the tropical forests of China are situated near the northern edge of the tropical zone, and the temperate forests are drought-prone. These environmental disadvantages may explain the fact that the forests of China have lower AGB and BGB than typical global tropical and temperate forests (Fang et al., 1996).

4.2 | Factors influencing forest biomass and *root:shoot ratios*

The response of *root:shoot* to various biotic and abiotic factors was examined. The variables included stand height, stand density, mean DBH, stand age, precipitation, temperature, ET, SH, altitude, and soil type. Previous reports have indicated that *root:shoot ratios* are either positively or negatively correlated with annual precipitation at the local or regional scale (Kang et al., 2013; Li et al., 2012; Wang et al., 2008) but decreased with increasing precipitation on the global scale (Mokany et al., 2006). Temperature also influenced the *root:shoot ratios* differently with region and vegetation type (Luo et al., 2013; Read & Morgan, 1996). Soil texture, nutrient availability, vegetation type, and plant structure also influenced the *root:shoot ratios* across ecosystems and regions (Mokany et al., 2006). Data sets based on specific regions and precise classifications may account for general tendencies in *root:shoot ratio* variations and explain the regional differences in the responses of the *root:shoot ratios* to the same factor.

A key contribution of this study is the investigation of the response of *root:shoot* to biotic and abiotic factors using a large worldwide database. The *root:shoot ratios* were negatively correlated with MAP and MAT and positively correlated with SH (Figure 3). A comprehensive ET/PET index may best describe the response of the *root:shoot ratios* to climate. The *root:shoot ratios* also increased slightly with altitude. This finding is consistent with previous studies (Leuschner, Moser, Bertsch, Roderstein, & Hertel, 2007; Luo et al., 2005). Changes in climate with altitude may cause variations in the *root:shoot ratios*.

In general, the *root:shoot ratios* increased with forest soil coarseness (from clay to sand). The *root:shoot ratios* were significantly higher in sand and sandy loam soils than those in clay and loam soils. The relatively lower water content and nutrient availability of coarse soil may explain the large *root:shoot ratios*. It is easier to sample root biomass from sandy than finer soils, and this property may also account for the higher *root:shoot ratios* in coarser soils (Mokany et al., 2006).

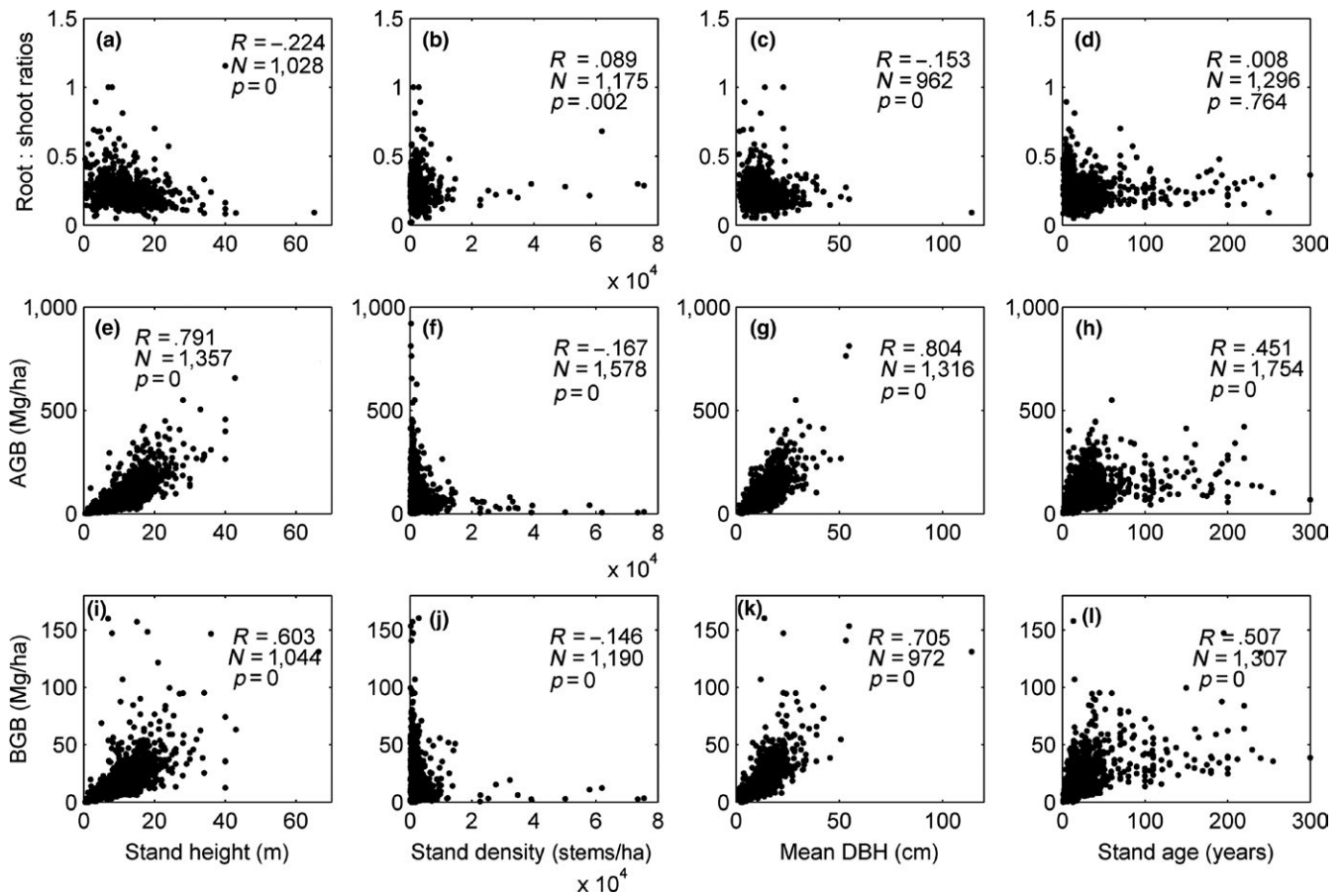


FIGURE 2 Variations in root:shoot ratios (a–d), AGB (e–h), and BGB (i–l) with tree height, stand density, mean diameter at breast height (DBH), and stand age. R, correlation coefficient; p, statistical significance; N, number of observations

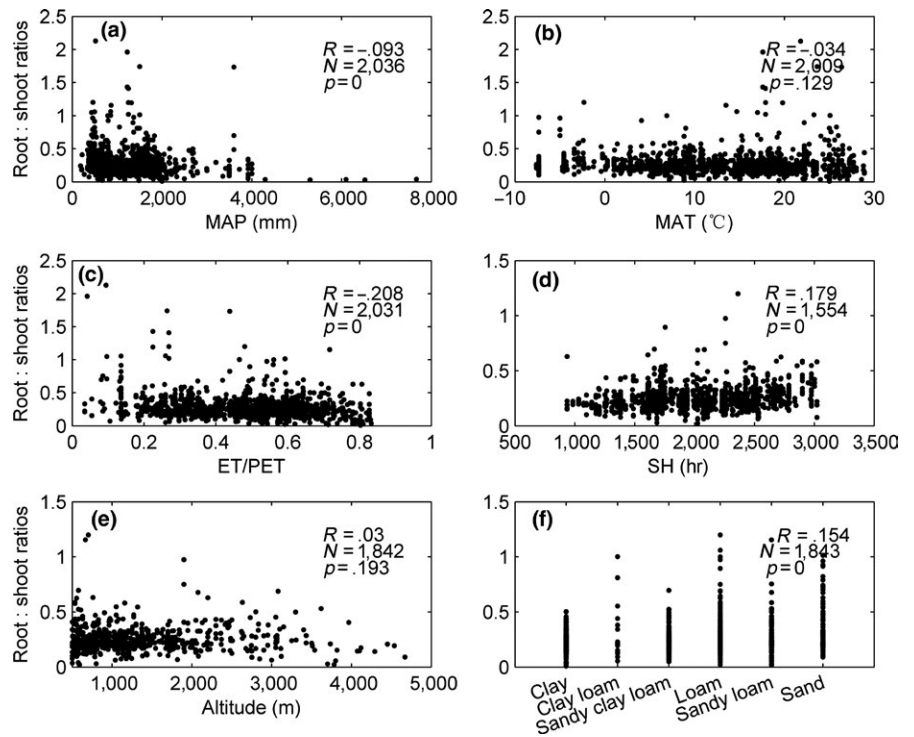


FIGURE 3 Root:shoot ratios as a function of (a) MAP, (b) MAT, (c) ET/PET, (d) SH, and (e) Altitude. (f) Soil texture. R, correlation coefficient; p, statistical significance; n, number of observations

TABLE 2 Results of the analysis of covariance using the *root:shoot ratios* as the dependent variable, the mean annual precipitation (MAP), mean annual temperature (MAT), sunshine hours (SH), and *ET/PET* as covariates, and the soil texture as the factor. df, degrees of freedom; MS, mean square

Source	df	MS	F-ratio	P value
Soil texture	5	168.90	18.56	<.0001
MAP	1	9.20	1.01	.315
MAT	1	248.97	27.36	.0001
SH	1	107.85	11.85	.001
ET/PET	1	883.33	97.06	.0001
Residual	2,046	9.10		

Although both *AGB* and *BGB* had high positive correlations with stand height, mean *DBH*, and stand age, these factors were only weakly (but significantly) correlated with the *root:shoot ratios* (Figure 2). Therefore, the *root:shoot ratios* may be genetically stable despite multiple environmental stressors.

Young plantation stands (<10 years) were included in all analyses although they are affected by traditional practices such as selected harvest and thinning which may influence the *root:shoot ratios* (King et al., 2007; Sheng and Fan, 2005; Luo et al., 2012). The lack of field observations for these forests, however, prohibited further analysis in this study. Fortunately, there were very few young plantations included in the analysis, and so the effects of selected harvest and thinning on the *root:shoot ratios* can be safely ignored here.

Plants tend to adapt to environment variations by adjusting their *root:shoot ratios* (Friedlingstein, Joel, Field, & Fung, 1999; McConaughay & Coleman, 1999). The analyses of this study indicated that biomass allocation between the belowground and aboveground parts is determined mainly by the inherent allometric relationships in the plant but also environmental factors. Most of the correlations between the *root:shoot ratios* and environmental parameters were significant ($p < .01$) but weak. Biomass allocation has been changing for

thousands of years, whereas documented measurements of biomass, climate, and soil properties span only several decades. Most of the earlier studies on environment allocation correlations were based on data from sporadic experiments. One or two factors were studied, whereas the others were fixed or suppressed (Agren & Franklin, 2003; Gholz et al., 1991; Kellomaki & Wang, 1996; Li et al., 2012; Matsui, Fukuda, Inoue, & Matsushita, 2003; Read & Morgan, 1996). Nevertheless, biomass allocation is the result of complex environmental factors that short-term studies cannot represent. For this reason, despite decades of research, no strong or general correlations were found between biomass allocation and environment factors at the global scale.

4.3 | Allometric models

The regression slopes across the entire database at the individual plant level were predicted by models (α_{pred} ; Niklas, 2005; Niklas & Enquist, 2001, 2002) and used in comparisons across the data sets from this study. RMA regression analysis showed that the slope ($\alpha_{RMA} = 0.938$) of the regression curve M_B versus M_A for the community-level data set is not significantly different ($p > .01$) from that predicted by the allometric model ($\alpha_{pred} = 3/4-1$). This finding confirmed the hypothesis that M_B versus M_A relationships at the community and individual plant levels share the same scaling exponents (RMA regression curve slopes). Niklas (2005); Niklas and Enquist (2002) constructed their allometric model based on a wide range of data for woody and nonwoody plants worldwide. When the nonwoody species data were excluded, the relationships observed for M_B versus M_A were even more consistent with the allometric model prediction. Unfortunately, the Enquist and Niklas (2002) data set did not present a definitive standard distinguishing woody from nonwoody species. When it was combined with the Enquist and Niklas (2002) data set, the related regression curve coefficients improved (Table 3).

It is apparent that the allometric theory is completely empirical. The slopes and regression curve constants vary with region and vegetation type. Various data sets yield different slope and constants (Cheng & Niklas, 2007; Luo et al., 2012; Mokany et al., 2006; Yang et al., 2009).

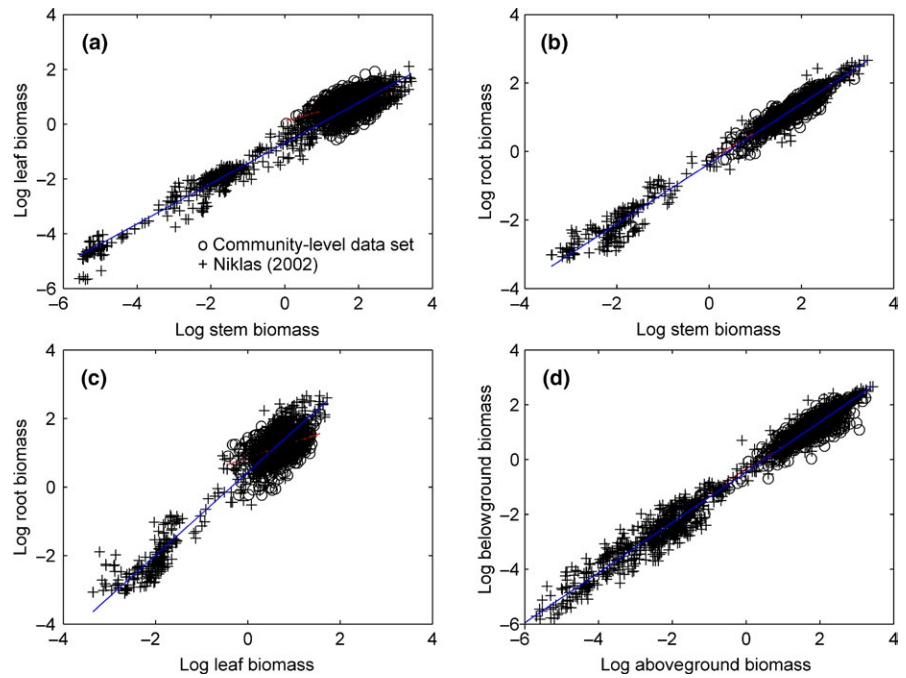
TABLE 3 RMA analysis of log-transformed data for organ biomass

	α_{pred}	$\alpha_{RMA} \pm SD$	95% CI	$\log \beta_{RMA} \pm SD$	95% CI	n	r^2
Across entire database							
M_B versus M_A	3/4-1	0.920 ± 0.01	0.915–0.924	−0.479 ± 0.01	−0.492 to −0.466	3,109	.980
M_B versus M_S	1.0	0.882 ± 0.00	0.875–0.889	−0.375 ± 0.01	−0.388 to −0.362	1,616	.974
M_B versus M_L	4/3	1.189 ± 0.01	1.169–1.209	0.323 ± 0.01	0.302–0.344	1,621	.882
M_L versus M_S	3/4	0.775 ± 0.01	0.766–0.783	−0.653 ± 0.01	−0.662 to −0.643	2,546	.927
Across community-level database							
M_B versus M_A	3/4-1	0.938 ± 0.01	0.918–0.957	−0.521 ± 0.01	−0.557 to −0.484	2,105	.811
M_B versus M_S	1.0	0.887 ± 0.01	0.865–0.909	−0.392 ± 0.02	−0.433 to −0.351	1,101	.817
M_B versus M_L	4/3	1.088 ± 0.03	1.029–1.146	0.355 ± 0.03	0.305 to 0.404	1,101	.166
M_L versus M_S	3/4	0.867 ± 0.02	0.827–0.906	−0.783 ± 0.04	−0.854 to −0.712	1,549	.176

All cases were significant ($p < .01$).

M_A , aboveground biomass; M_B , belowground or root biomass; M_S , stem biomass; M_L , leaf biomass; *SD*, standard deviation; *n*, number of observations; α_{pred} , model-predicted scaling components constructed by Niklas (2005) and Niklas and Enquist (2001, 2002).

FIGURE 4 Allometric plots of log-transformed data for (a) leaf and stem biomass (Sig. $p = 0$), (b) root and stem biomass (Sig. $p = 0$), (c) root and leaf biomass (Sig. $p = 0$), and (d) below- and aboveground biomass (Sig. $p = 0$). Solid lines represent OLS regression curves for the Niklas (2005) and Niklas and Enquist (2002) and community-level data sets. All correlations are significant at $p < .01$. Sig. p indicates the significance of difference in the slopes of the linear regression between two data sets. Sig. $p > .05$ means no significant difference in regression slopes; Sig. $p < .05$ means significant difference in regression slopes



This study predicted the community-level BGB from the AGB using the M_B versus M_{AOLS} regression formula across the entire database. It was found that the allometric relationship reasonably estimates BGB (Figure 5a). The percentage error of the BGB predicted by AGB using OLS regression formula decreased as AGB increased (Figure 5b). That is, the reliability of the OLS regression formula increased with AGB (or plant size) across global forest communities. The precise estimation of allocation patterns is essential for predicting global carbon budget and climate change, and for ecosystem modeling. Although many carbon allocation schemes were constructed in the last few decades, none of them accurately described the long-term allocation dynamics in various environments. The allometric theory empirically evaluates global root biomass but its scaling components vary with environmental conditions. It also indicates that it will be possible to trace biomass allocation and determine when it reaches homeostasis.

5 | CONCLUSION

Using a large database of global forest ecosystems, the *root:shoot ratios* and their responses to environmental factors were investigated in this study. Both aboveground and belowground biomass in the forests of China were lower than those of global forests. Nevertheless, the *root:shoot ratios* were not significantly different from each other. They were determined primarily from the inherent allometric relationships of plants, but they were significantly affected by developmental parameters, climate variables, altitude, and soil ($p < .01$).

The *root:shoot ratios* responded to changes in mean annual temperature, mean annual precipitation, and the potential water deficit index. They were negatively correlated with mean annual precipitation, mean annual temperature, and potential water deficit. Soil texture, developmental parameters, and climatic conditions influenced

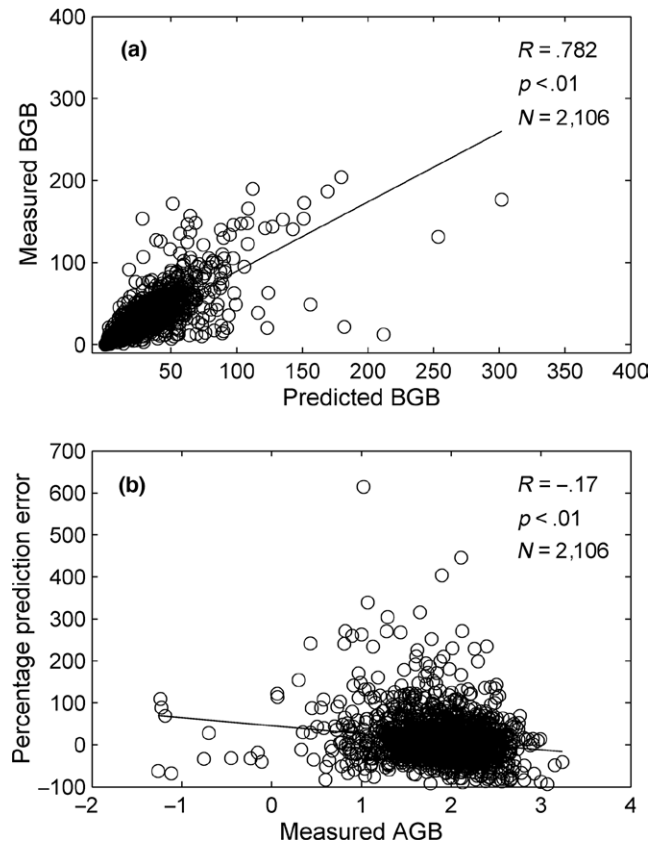


FIGURE 5 Accuracy of OLS regression formulas in predicting BGB based on AGB. (a) correlation analysis between measured and predicted BGB, and (b) variation in percentage prediction error with AGB

the magnitudes of the *root:shoot ratios*. The allometric theory aligned with the trends observed in this study and correctly estimated BGB based on AGB for the entire database.

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CONFLICT OF INTEREST

None declared.

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