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Root:shoot ratios across China's forests: Forest type and climatic effects

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ABSTRACT

Using a new above-ground biomass (AGB) and below-ground biomass (BGB) dataset of 649 paired observations from China's forests, root:shoot ratios (RSRs) and BGB–AGB models (where BGB is a function of AGB) were analyzed by forest groups, phylogenies, leaf habits and forest origins. RSRs were lower in coniferous forests than broadleaved forests. RSRs were also lower in evergreen forests than deciduous forests, and lower in plantations than natural forests. Decreasing RSRs with mean annual temperature (MAT) were found in the whole dataset as well as in three separate forest types (coniferous forests, deciduous broadleaved forests and evergreen broadleaved forests) and three genera (*Cunninghamia*, *Pinus* and *Quercus*). However, RSRs showed different trends with mean annual precipitation (MAP) across different groups including: a U-shaped pattern for coniferous forests, *Larix* forest and *Pinus* forest covering wide MAP ranges; a decreasing trend for deciduous broadleaved forests and *Quercus* forest covering ranges with low MAP; and no trend for evergreen broadleaved forest and *Cunninghamia* forest covering ranges with high MAP. Our results support the existence of different AGB–BGB allocation strategies for optimum tree growth which are in line with optimal partitioning theory applied at a broad scale.

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1. Introduction

Relationships between above-ground biomass (AGB) and below-ground biomass (BGB) are important to a range of ecological studies such as plant life-history, plant evolution and ecosystem behaviors (including carbon fluxes, water fluxes, and community dynamics) (Mokany et al., 2006; Niklas and Enquist, 2002; Reich, 2002). The AGB–BGB relationship is commonly described by root:shoot ratio (RSR) or BGB–AGB models (where BGB is a function of AGB) (Brown, 2002; Li et al., 2003; Mokany et al., 2006). Compared to AGB, BGB is more difficult and time-consuming to measure and there are no generally standardized methods (Brown, 2002; Reich, 2002). Moreover, BGB is a major source of uncertainty in large-scale biomass (carbon) estimation, largely due to limitations in the methods for estimating BGB and limited data availability (Brown, 2002; Mokany et al., 2006). Generic RSR and BGB–AGB models provide practical and cost-effective tools for estimating BGB from the easily measured AGB at different scales (ecosystem, landscape, region and biome) (Brown, 2002; Li et al., 2003; Mokany et al., 2006), and are also recommended for forest carbon accounting such as National Greenhouse Gas Inventory and forest carbon

mitigation projects (IPCC, 2006; Ravindranath and Ostwald, 2008). However, it is preferable for RSR parameters and BGB–AGB models to be specified for forest type, region and nation because of their significant variations.

A body of local studies has demonstrated that various factors influence AGB–BGB allocation including stand development, species characteristics (e.g. life form and leaf trait), origin and climate (see reviews in Cairns et al. (1997), Mokany et al. (2006) and Reich (2002)). Most studies reflect optimal partitioning theory (OPT) in that plants preferentially allocate biomass to the organ that acquires the limiting resources (Bloom et al., 1985; Reich, 2002). Previous broad-scale studies have investigated variations of RSRs associated with forest origin, phylogeny (coniferous vs. broadleaved), leaf habit (deciduous vs. evergreen), climate (temperature and precipitation) and soil texture at regional and global scales (Cairns et al., 1997; Jackson et al., 1996; Mokany et al., 2006; Wang et al., 2008), but they reported inconsistent findings. Moreover, the generality of responses of RSRs to climate has not been examined within forest types and within genera. Therefore, evidence is still quite limited at broad scales as to whether there are general patterns of AGB–BGB allocation in relation to biotic and environmental variations as suggested by OPT.

China has various forest types ranging from tropical rainforests to boreal forests across broad geographical regions and environmental gradients. Data collated from across China provide an important opportunity to examine RSRs in relation to tree species

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and climate. Wang et al. (2008) conducted a pioneering study of RSRs in forests of northeast China, but it is doubtful whether their findings could be extrapolated to a national scale. The latest Inter-governmental Panel on Climate Change Guidelines provide RSR defaults for ecological zones based on data from nations and regions other than China (IPCC, 2006). Thus, these defaults cannot be guaranteed to be suitable for estimation of BGB and carbon accounting for China's forests. Using a new AGB–BGB dataset from China's forests, we: (i) determined RSR defaults specific to forest types; (ii) examined variations of RSRs with forest type, phylogeny (coniferous vs. broadleaved), leaf habit (deciduous vs. evergreen) and forest origin (natural forests vs. plantations); and (iii) analyzed the responses of RSRs to climate, especially mean annual temperature (MAT) and mean annual precipitation (MAP) across all forests, within forest types and within genera.

2. Materials and methods

2.1. Dataset

By collecting 511 sources published between 1978 and 2008 from libraries and databases (i.e. National Library of China, Forestry Library of China, CNKI Databases, CQVIP Database and Wanfang Databases), a large AGB–BGB dataset was established including 1554 AGB–BGB paired measurements for ~250 forest types from 343 sites across China. The sampling sites covered a MAT range from -5.1 to 23.6 °C and a MAP range from 222 to 2150 mm. It should be noted that our dataset excluded data for economic forests (stands for producing fruits, edible oils, industrial raw materials, medicinal herbs, etc.), agroforestry systems (stands integrated with crops and/or animals), forested wetlands (e.g. mangroves and swamps), recently disturbed stands (e.g. pruned, coppiced and fertilized), and other stands grown in urban, polluted or atypical environments (e.g. desert, riverine, treeline, heavily eroded and man-made soil, and elevated CO₂ or greenhouse).

The following criteria were applied to select measurements used for deriving RSRs. Original sources had to clearly describe the sampling protocols and/or procedures for measuring biomass (oven-dried mass) of tree compartments. Individual tree biomass was measured using destructive harvesting and weighing, and then scaled up to stand level (oven-dried mass per unit area) using average tree, stratified average tree or regression equation methods. Regression equations of biomass with one or more stand variables (e.g. diameter at breast height (DBH), tree height or their combinations) were developed based on individual tree biomass measurements. Only belowground biomass measurements made using full-excavation methods were included in this study, when the excavated area was equal to or larger than the average nutrient area of the sample trees covered and the depth of root sampling reached the maximum root depth. Those BGB data obtained using soil pit methods or full-excavation supplemented with soil pit methods were excluded because of their lack of stump biomass or overestimation of root biomass.

For each paired AGB–BGB measurement, biomass data and supporting information were collected, including all component biomass (stem, bark, branch, twig and foliage, flower and fruit, root stump, coarse and fine roots, and rhizomes, Mg/ha) if available, geographical coordinates (latitude, °; longitude, °), climate (MAT, °C; MAP, mm), stand characteristics (forest type, species composition and forest origin) and stand variables (stand age, yr.; mean DBH, cm; mean tree height, m; and basal area, m²/ha). Missing geographical coordinates were added using the geographical center of the sampling site from Google maps (<http://maps.google.com>). Missing MAT and/or MAP data were extracted from a 30 arc-seconds (c. 1 km at the Equator) resolution global climate database (<http://www.worldclim.org>) (Hijmans et al., 2005).

2.2. Data analysis

For examining the influences of biotic and climatic factors on RSRs, we used only older stands (≥ 20 yrs.) to eliminate the effects of young stages and related disturbances on tree growth and soil. As a result, 649 paired data from 190 sites (Fig. 1) were available for subsequent statistical analyses. RSRs were categorized into 17 forest groups according to similarity in dominant tree species or genera and ecogeography described by China's vegetation classification system (Zhang, 2007). When a forest type had limited observations (generally < 8) and/or was investigated in a narrow ecogeographical range, it was assigned into a forest group with similar functional types and ecological zones. Statistics of RSRs were summarized for each forest group, phylogeny (coniferous vs. broadleaved), leaf habit (deciduous vs. evergreen) and forest origin (natural forests vs. plantations).

Because there was strong correlation between MAT and MAP ($r = 0.78$, $P < 0.0001$, $n = 190$) and MAP has more predictive and mechanistic value than MAT (Mokany et al., 2006; Wang et al., 2008), MAP was chosen as the covariate when examining group differences with an ANCOVA (analysis of covariance) procedure. When group differences were found at a significance level of $\alpha = 0.05$, LSD (least square differences) tests were performed. Regression analyses were conducted to assess the responses of RSRs to climate (MAT and MAP). The generality of RSR–climate relationships was also examined when there were sufficient data in three forest types (coniferous forests, deciduous broadleaved forests and evergreen broadleaved forests) and four genera (*Cunninghamia*, *Larix*, *Pinus* and *Quercus*). RSRs were log₁₀-transformed to reduce the influence of a few sites with exceptionally great RSRs.

The ordinary least-squares method was applied to develop log–log models of BGB with AGB as the independent variable. The log–log model is of the form $\log_{10}(\text{BGB}) = \alpha \cdot \log_{10}(\text{AGB}) + \beta$, where α is the scaling factor and β is the integration factor. This model is widely used in allometry and corrects the heterogeneous variation of the regression (Sprugel, 1983; Warton et al., 2006). A correction factor (CF) was also calculated for each log–log model to correct for the systematic bias introduced by logarithmic transformation (Sprugel, 1983). The effects of forest origin, phylogeny, leaf habit, forest group and climate on BGB–AGB models were tested using an ANCOVA procedure.

All statistical analyses were performed in SPSS for Windows (ver. 13.0, SPSS Inc., Chicago, Illinois).

3. Results

3.1. Root:shoot ratio

RSRs varied between 0.070 and 0.730, with a mean (\pm SD) of 0.233 ± 0.082 (Table 1). Mean RSRs for forest groups ranged from 0.159 (*Pinus massoniana* and *P. taiwanensis* forest) to 0.325 (*Quercus* and other temperate deciduous broadleaved forests) (Table 1). They differed significantly among forest groups ($F(16,631) = 11.25$, $P < 0.0001$), which accounted for 22% of total variability in RSRs (Table 1). RSRs also varied significantly ($P < 0.0001$) with phylogeny, leaf habit and forest origin (Table 1). On average broadleaved forests had larger RSRs than coniferous forests and coniferous–broadleaved mixed forests ($P < 0.0001$), but the latter two forests did not show a difference ($P = 0.44$) (Table 1). Deciduous forests showed larger RSRs than evergreen forests ($P < 0.0001$). RSRs in natural forests were larger than those in plantations ($P < 0.0001$) (Table 1).

Across all forests, RSRs were negatively correlated with MAT (Fig. 2). The decreasing trend of RSRs with MAT was also observed in three forest types (coniferous forests deciduous broadleaved forests and evergreen broadleaved forests) and three genera

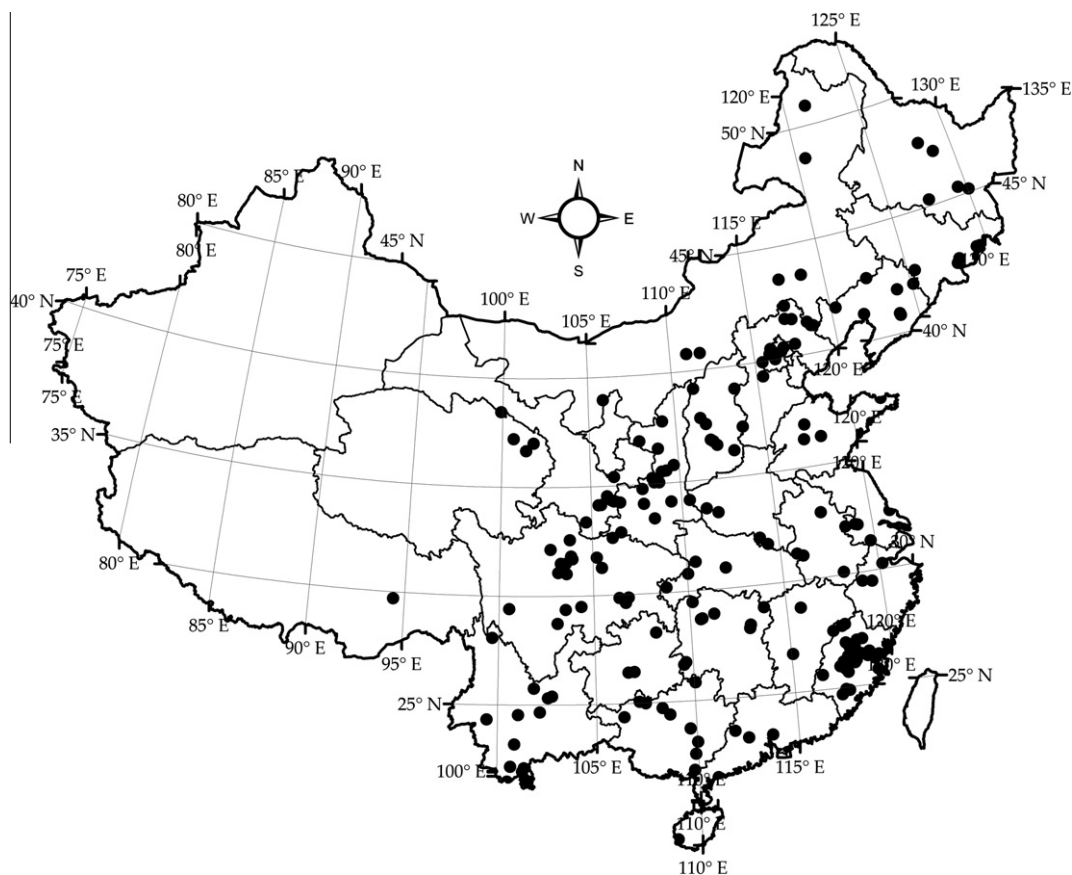


Fig. 1. Spatial distribution of sampling sites used in this study.

(*Cunninghamia*, *Pinus* and *Quercus*), whereas RSRs for *Larix* forest showed a U-shaped pattern with MAT (Fig. 2). A U-shaped relationship between RSRs and MAP was observed in all forests, coniferous forests, *Larix* forest and *Pinus* forest, which covered wide ranges of MAP (Fig. 3). The thresholds from decreasing to increasing trends of RSRs with increasing MAP were c. 1380 mm for all forests and coniferous forests, c. 970 mm for *Larix* forest, and c. 1550 mm for *Pinus* forest, respectively. A decreasing trend of RSRs with MAP was found in deciduous broadleaved forests and *Quercus* forest, which covered ranges with low MAP (Fig. 3). However, there were no trends in evergreen broadleaved forests and *Cunninghamia* forest, which covered ranges with high MAP (Fig. 3).

3.2. BGB–AGB model

The generalized BGB–AGB model created by pooling all data exhibited a highly significant fit ($P < 0.0001$) and explained 76.2% of the variability in BGB data. The scaling factor (α) differed significantly between forest origins ($P = 0.02$) and among forest groups ($P = 0.03$), whereas there were no differences in the scaling factor among phylogenies ($P = 0.07$) and between leaf habits ($P = 0.22$) (Table 1). Inclusion of forest group, forest origin and climate (MAT and MAP) improved the explanatory percentage to 83.4%, although only MAT and forest group were significant ($P < 0.0001$) (Table 2). Forest group-specific models are provided in Table 1, and their explanatory percentage ranged from 48.5% to 89.2% with a mean of 76.2%.

4. Discussion

In this study, we compiled a large AGB–BGB dataset for China's forests based on a survey of the literature, and for the first time

reported RSRs and BGB–AGB models and their variations with climate and biotic factors (e.g. phylogeny and leaf habit) across major China's forests. Our dataset provides a major expansion in comparison to previous biomass datasets available for China's forests (Feng et al., 1999; Luo, 1996; Wang et al., 2008) and so fills an important gap relevant to global studies (Cairns et al., 1997; Jackson et al., 1996; Mokany et al., 2006). Our results will help to understand the responses of plant growth to environmental conditions at broad scales and to improve the accuracy of estimation of root biomass (carbon) in terrestrial ecosystems.

4.1. Influences of biotic factors on root:shoot ratios

Our results about RSRs in China's forests were similar to most previous reports, where there were larger RSRs in broadleaved forests than in coniferous forests (global temperate forests, Jackson et al., 1996; forests of northeast China, Wang et al., 2008), and larger RSRs in deciduous forests than in evergreen forests (global tropical forests, Jackson et al., 1996). This could be explained by plants with higher relative growth rates and photosynthetic rates allocating more biomass to roots to favor survival and growth (Antúnez et al., 2001; Ruiz-Robledo and Villar, 2005) and also to acquire more nutrients and water (Reich, 1998), which would cause higher RSRs. Generally, broadleaved trees show higher relative growth rates and photosynthetic rates than coniferous trees (Lusk et al., 2003; Reich, 1998). Deciduous trees show higher relative growth rates and photosynthetic rates than evergreen trees (Cornelissen et al., 1998; Reich, 1998). The lower levels of RSRs in plantations than in natural forests are likely to be induced by soil conditions (Mokany et al., 2006; Wang et al., 2008). Plantations are usually established in more productive environments (e.g. more fertile and moister soil) than natural forests, which induce a lower proportion of biomass

Table 1

Root:shoot ratios and above- and below-ground biomass models by forest group, forest origin, phylogeny and leaf habit.

Categories	n	Root:shoot ratio ^a					BGB–AGB model ^b				
		Mean	SD	Min	Max	Sig	α	β	r^2	SEE	CF
All forests	649	0.233	0.082	0.070	0.730		0.859	−0.370	0.762	0.137	1.051
<i>Forest group</i>											
<i>Abies, Picea and Sabina</i>	32	0.229	0.077	0.115	0.390	bcd	0.945	−0.549	0.613	0.147	1.059
<i>Cunninghamia</i>	83	0.193	0.038	0.110	0.318	de	0.798	−0.294	0.819	0.077	1.016
<i>Cupressus and Fokienia</i>	24	0.209	0.057	0.095	0.317	cde	1.047	−0.790	0.892	0.129	1.045
<i>Larix</i>	46	0.234	0.079	0.132	0.516	bcd	0.763	−0.160	0.599	0.124	1.042
<i>Pinus koraiensis</i>	33	0.227	0.057	0.126	0.345	bcde	0.993	−0.644	0.857	0.116	1.036
<i>P. massoniana</i> and <i>P. taiwanensis</i>	55	0.159	0.049	0.072	0.281	e	0.779	−0.338	0.735	0.119	1.038
<i>P. tabulaeformis</i>	100	0.239	0.092	0.094	0.731	bcd	0.811	−0.307	0.693	0.131	1.047
Other temperate pines and conifers ^c	22	0.250	0.057	0.137	0.360	bcd	0.793	−0.251	0.485	0.105	1.030
Other subtropical pines and conifers ^d	24	0.207	0.051	0.104	0.330	cde	1.024	−0.745	0.847	0.112	1.034
<i>Alnus, Betula and Populus</i>	22	0.290	0.093	0.168	0.546	ab	0.887	−0.366	0.841	0.130	1.046
<i>Quercus</i> and other temperate deciduous broadleaved forests ^e	66	0.323	0.097	0.153	0.573	a	0.877	−0.266	0.742	0.130	1.046
Other subtropical deciduous broadleaved forests ^f	10	0.205	0.046	0.150	0.274	cde	0.802	−0.283	0.802	0.092	1.023
<i>Castanopsis, Cyclobalanopsis and Lithocarpus</i>	23	0.265	0.064	0.157	0.433	abc	0.902	−0.365	0.802	0.101	1.027
Other evergreen broadleaved forests	46	0.265	0.078	0.131	0.435	abc	0.800	−0.177	0.793	0.118	1.038
Tropical forests	17	0.228	0.047	0.125	0.358	bcde	0.949	−0.531	0.816	0.094	1.024
Temperate coniferous–broadleaved mixed forest	15	0.221	0.068	0.100	0.331	cde	1.024	−0.728	0.840	0.154	1.065
Subtropical coniferous–broadleaved mixed forest	31	0.208	0.040	0.137	0.303	cde	1.001	−0.691	0.780	0.084	1.019
<i>Forest origin</i>											
Natural forests	211	0.260	0.091	0.080	0.573	a	0.903	−0.408	0.753	0.149	1.061
Planted forests	438	0.220	0.074	0.072	0.731	b	0.804	−0.288	0.773	0.122	1.040
<i>Phylogeny</i>											
Coniferous forests	420	0.214	0.072	0.072	0.731	b	0.820	−0.332	0.765	0.126	1.043
Broadleaved forests	183	0.283	0.088	0.131	0.573	a	0.857	−0.275	0.826	0.124	1.042
Coniferous–broadleaved mixed forests	46	0.212	0.051	0.100	0.331	b	1.012	−0.711	0.822	0.108	1.031
<i>Leaf habit^g</i>											
Deciduous forests	144	0.281	0.098	0.132	0.573	a	0.837	−0.253	0.729	0.140	1.053
Evergreen forests	459	0.220	0.073	0.072	0.731	b	0.870	−0.415	0.792	0.131	1.047

^a n, the number of observations; SD, standard deviation; Min, minimum; Max, maximum. Sig indicates statistical differences and different small letters denotes statistical significant differences between forests within a category at $P < 0.05$.

^b Models are of log–log form $\log_{10}(\text{BGB}) = \alpha \log_{10}(\text{AGB}) + \beta$, where AGB and BGB are above- and below-ground biomass (Mg/ha), and α and β are the scaling factor and is the integration factor. r^2 , coefficient of determination; SEE, standard error of the estimate in logarithmic units; CF, the logarithmic correction factor. All regression relations were significant ($P < 0.0001$).

^c Forests dominated by *Pinus densiflora*, *P. sylvestrisformis*, *P. sylvestris* var. *mongolica*, *P. thunbergii* and *Platycladus orientalis*, and coniferous mixed forests in temperate zone.

^d Forests dominated by *Cryptomeria fortunei*, *Keteleeria davidiana*, *P. armandii*, *P. densata*, *P. elliotii*, *P. henryi*, *P. kesiya* var. *langbianensis*, *P. rigida* var. *serotina*, *P. yunnanensis* and *Taiwania flousiana*, and coniferous mixed forest in subtropical zone.

^e Forests dominated by *Quercus* spp., *Fraxinus mandshurica*, *Juglans mandshurica* and *Robinia pseudoacacia*, and deciduous broadleaved mixed forests in temperate zone.

^f Forests dominated by *Choerospondias axillaris*, *Fagus engleriana*, *Liquidambar formosana*, *Pistacia chinensis*, *Platycarya strobilacea*, and *Sassafras tzumu*, and deciduous broadleaved mixed forests in subtropical zone.

^g The data of coniferous and broadleaved mixed forests were excluded in this category.

to be allocated to roots. As suggested by OPT, plants preferentially allocate biomass to the organ that acquires the limiting resources (Bloom et al., 1985; Reich, 2002). However, our results differed from those obtained by Mokany et al. (2006), who found that RSRs did not vary with phylogeny and forest origin based on a pooled dataset of global forests and woodlands. Their results may have been affected by large biotic and abiotic discrepancies between forests and woodlands in factors such as stand canopy, stand density and growth environments.

In China, traditional practices such as selected harvesting and thinning are usually employed for forestry production, and have potential to influence AGB–BGB allocation. For instance, coppiced stands that sprout from roots after harvesting aboveground parts of trees may have larger RSRs than non-coppiced stands. Zeng (1984) found large RSRs for *Cunninghamia lanceolata* coppiced stands (0.583 ± 0.242 (SD), $n = 6$) at Xijiang Forest Farm (Guangdong). However, the paucity of field observations available for these forests prohibited further analyses in this study.

It should be noted that young stands (<20 yrs.) were not included in this study, because young stands are more sensitive than older stands to planting practices (especially density) and local soil conditions other than climate (King et al., 2007; Sheng and Fan, 2005). On average, young stands (<20 yrs.) had greater RSRs

(0.253) than older stands (≥ 20 yrs.) (0.233) (t -test, $P < 0.0001$), although the differences were significant only for seven forest groups (Table 3). Moreover, young stands exhibited larger variation in RSR ranges than older stands (Tables 1 and 3). Therefore, using RSRs for old stands will cause the underestimation of root biomass carbon in newly established forests.

4.2. Influences of climate on root:shoot ratios

Although Mokany et al. (2006) and Wang et al. (2008) separately reported that there were no significant trends of RSRs with MAT in global forests and woodlands and in forests of northeast China, the RSRs were negatively related with MAT for all forests, three forest types and three genera in this study (Fig. 2) and in global upland forests in Cairns et al. (1997). This negative relationship could be explained by the factor that less biomass is allocated into roots at higher temperatures because the increasing temperature enhances water and nutrient availability and thus less water and nutrients are demanded by roots to maximize tree growth rate.

Our study found three trends of RSRs with increasing MAP: a decreasing pattern in low precipitation regions (roughly less than 1200 mm in MAP), a U-shaped pattern in regions with wider precipitation ranges, and no trends in high precipitation regions

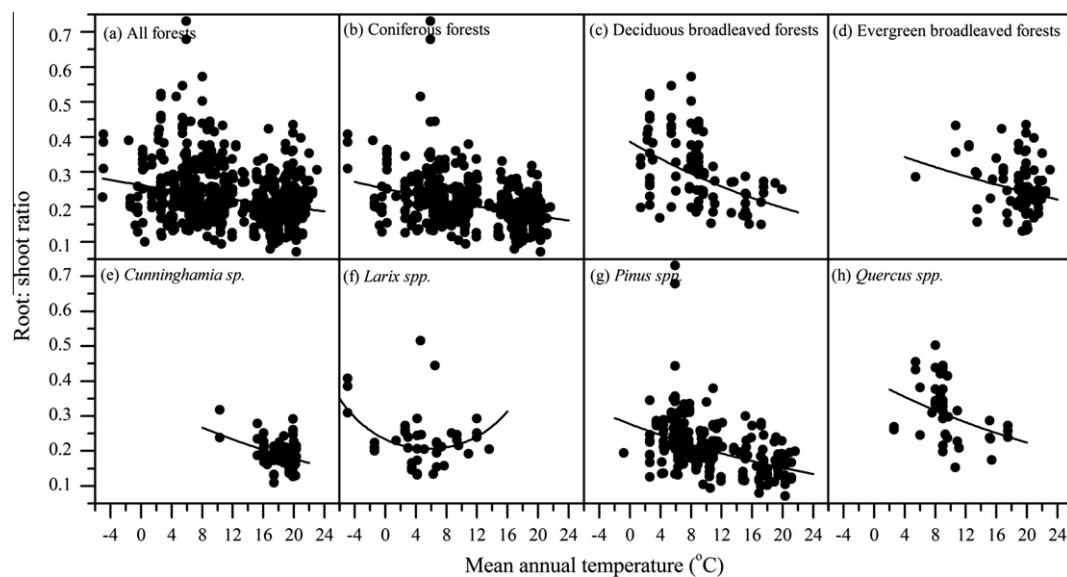


Fig. 2. The relationships between root:shoot ratios and mean annual temperature for (a) all forests ($r^2 = 0.08$, $P < 0.0001$, $n = 649$), (b) coniferous forests ($r^2 = 0.15$, $P < 0.0001$, $n = 420$), (c) deciduous broadleaved forests ($r^2 = 0.22$, $P < 0.0001$, $n = 98$), (d) evergreen broadleaved forests ($r^2 = 0.06$, $P = 0.024$, $n = 87$), (e) *Cunninghamia* forest ($r^2 = 0.12$, $P = 0.001$, $n = 83$), (f) *Larix* forest ($r^2 = 0.15$, $P = 0.030$, $n = 46$), (g) *Pinus* forest ($r^2 = 0.23$, $P < 0.0001$, $n = 219$), and (h) *Quercus* forest ($r^2 = 0.13$, $P = 0.002$, $n = 49$).

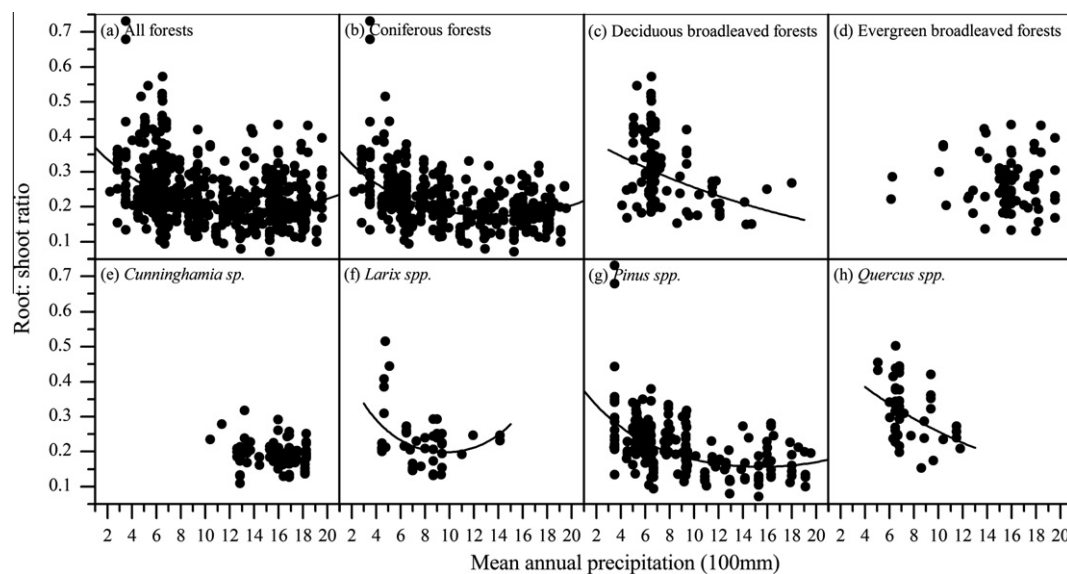


Fig. 3. The relationships between root:shoot ratios and mean annual precipitation for (a) all forests ($r^2 = 0.13$, $P < 0.0001$, $n = 649$), (b) coniferous forests ($r^2 = 0.22$, $P < 0.0001$, $n = 420$), (c) deciduous broadleaved forests ($r^2 = 0.17$, $P < 0.0001$, $n = 98$), (f) *Larix* forest ($r^2 = 0.17$, $P = 0.020$, $n = 46$), (g) *Pinus* forest ($r^2 = 0.28$, $P < 0.0001$, $n = 219$), and (h) *Quercus* forest ($r^2 = 0.18$, $P = 0.002$, $n = 49$).

Table 2

Results of analysis of covariance with belowground biomass (BGB, \log_{10} -transformed) as dependent variable; aboveground biomass (AGB, \log_{10} -transformed), mean annual temperature (MAT) and mean annual precipitation (MAP) as covariates; and forest origin and forest group as the factors. df, degrees of freedom; MS, mean square.

Source	df	MS	F-ratio	P value
log(AGB)	1	25.13	1857.86	<0.0001
Forest origin	1	0.03	2.43	0.12
Forest group	16	0.16	11.58	<0.0001
MAT	1	0.19	13.83	<0.0001
MAP	1	0.00	0.03	0.87
Residual	628	0.014		

(Fig. 3). The decreasing pattern has also been reported in studies that investigated limited MAP gradients (mostly less than

1200 mm, Mokany et al. (2006); 380–1050 mm, Wang et al. (2008); 367–1101 mm, Zerihun et al. (2006)). However, Cairns et al. (1997) found that there were no trends of RSRs with MAP in the global upland forests. This finding may have been influenced by data from microenvironments (e.g. treeline and riverine sites) that did not reflect a true precipitation gradient. The U-shaped pattern occurred for all forests, coniferous forests and two genera (*Larix* and *Pinus*), which covered a wide precipitation gradient. The thresholds of U-shaped pattern ranged from c. 970 mm (*Larix* forest) to c. 1550 mm (*Pinus* forest) (Fig. 3), which were close to the optimal conditions for corresponding forest growth. For example, the threshold c. 1550 mm for *Pinus* forest is in the optimum range (1400–1800 mm) for the production of *P. massoniana* and *P. taiwanensis* (Wu, 1999). As precipitation increases, water supply will become sufficient and trees will allocate less biomass to roots for

Table 3Root:shoot ratios for young stands (<20 yrs.) by forest group.^a

Forest group	n	Mean	SD	Min	Max	P-value
All forests	905	0.253	0.096	0.064	0.745	<0.0001
<i>Abies</i> , <i>Picea</i> and <i>Sabina</i>	8	0.217	0.151	0.135	0.587	0.75
<i>Cunninghamia lanceolata</i>	237	0.259	0.079	0.098	0.685	<0.0001
<i>Cupressus</i> and <i>Fokienia</i>	25	0.229	0.050	0.089	0.325	0.19
<i>Larix</i>	37	0.259	0.102	0.125	0.668	0.21
<i>Pinus koraiensis</i>	8	0.220	0.041	0.162	0.270	0.76
<i>P. massoniana</i> and <i>P. taiwanensis</i>	76	0.196	0.048	0.106	0.331	<0.0001
<i>P. tabulaeformis</i>	18	0.181	0.088	0.064	0.403	0.01
Other temperate pines and conifers ^b	10	0.334	0.124	0.221	0.648	0.01
Other subtropical pines and conifers ^c	71	0.266	0.102	0.097	0.611	<0.001
<i>Alnus</i> , <i>Betula</i> and <i>Populus</i>	51	0.254	0.139	0.134	0.745	0.27
<i>Quercus</i> and other temperate deciduous broadleaved forests ^d	22	0.306	0.113	0.163	0.626	0.51
Other subtropical deciduous broadleaved forests ^e	13	0.297	0.096	0.176	0.449	<0.001
<i>Castanopsis</i> , <i>Cyclobalanopsis</i> and <i>Lithocarpus</i>	14	0.364	0.160	0.142	0.696	0.04
Other evergreen broadleaved forests	216	0.249	0.091	0.078	0.656	0.26
Tropical forests	9	0.234	0.059	0.179	0.380	0.78
Temperate coniferous–broadleaved mixed forest	3	0.224	0.074	0.138	0.267	0.95
Subtropical coniferous–broadleaved mixed forest	87	0.266	0.093	0.135	0.626	<0.0001

^a n, the number of observations; SD, standard deviation; Min, minimum; Max, maximum. P-value indicates statistical differences in root:shoot ratios between young (<20 yrs.) and older stands (≥20 yrs.) using t-test.

^b Forests dominated by *Pinus densiflora*, *P. sylvestrisformis*, *P. sylvestris* var. *mongolica*, *P. thunbergii* and *Platycladus orientalis*, and coniferous mixed forests in temperate zone.

^c Forests dominated by *Cryptomeria fortunei*, *Keteleeria davidiana*, *Metasequoia glyptotroboideis*, *P. armandii*, *P. densata*, *P. elliotii*, *P. fanzeliana*, *P. henryi*, *P. kesiya* var. *langbianensis*, *P. rigida* var. *serotina*, *P. taeda*, *P. yunnanensis* and *Taiwania flousiana*, and coniferous mixed forest in subtropical zone.

^d Forests dominated by *Quercus* spp., *Fraxinus mandshurica*, *Juglans mandshurica* and *Robinia pseudoacacia*, and deciduous broadleaved mixed forests in temperate zone.

^e Forests dominated by *Choerospondias axillaris*, *Fagus engleriana*, *Liquidambar formosana*, *Liriodendron chinensis*, *Paulownia fortunei*, *Pistacia chinensis*, *Platycarya strobilacea*, *Sassafras tzumu*, *Tapiscia sinensis*, *Zenia insignis*, and deciduous broadleaved mixed forests in subtropical zone.

absorbing soil moisture, so RSRs show a decreasing trend with MAP. When the increasing precipitation exceeds the threshold of water forest demands, forests will be not limited by water but may be by soil nutrient availability, so more biomass will be allocated into roots for more nutrient uptake from the soil.

Apart from climate, soil characteristics may be important factors influencing RSRs. Local studies have demonstrated shifts in AGB–BGB allocation induced by soil characteristics (e.g. soil moisture and nutrients), but evidence is generally lacking for regional or global trends (Beets et al., 2007; Cairns et al., 1997; Reich, 2002). Soil characteristics have covarying changes with climate and vegetation in China (Fang et al., 2002; Yang et al., 2007a,b). Both climate (MAT and MAP) and vegetation could explain c. 78% and 75% of the total variances in soil organic carbon and nitrogen, respectively (Yang et al., 2007a,b). Considering the above covariation and the lack of soil data in the original sources, therefore, the influences of soil characteristics were not analyzed in this study.

4.3. Methods for root biomass estimation

We used generalized RSR and group-specific RSRs (Table 1) to predict BGB values from AGB measurements for older stands (≥20 yrs.) in our dataset. Group-specific RSRs generated higher r^2 (0.787) between the predicted and observed values and lower mean relative difference (8.0%) than generalized value (0.691 and 11.5%). Note that relative difference (%RD_i) between the *i*th observed (O) and predicted (P) values was calculated using %RD_i = $(-P_i - O_i)/O_i \times 100\%$. The group-specific BGB–AGB models also produced higher r^2 (0.805) between the predicted and observed BGB values and lower mean relative difference (7.4%) than the generalized model (0.690 and 10.8%). Therefore, both group-specific RSRs and models performed better than their corresponding generalized ones.

5. Conclusion

Although RSR and BGB–AGB models are very important ecological parameters and practical tools in carbon accounting for estimating BGB from AGB, prior to the present study there have

been limited analyses available for China. To the best of our knowledge, this study is the first to review forest RSRs and BGB–AGB models across China and to provide critical parameters for China's carbon accounting. Due to significant variations in RSRs with forest groups, phylogenies, leaf habits and forest origins, different RSRs should be applied in carbon accounting for different forest groups, phylogenies, leaf habits and forest origins. The variability of RSRs with climate such as MAP and MAT with forest group should be considered in carbon accounting. Our study found that the variations of RSRs with MAP depend on MAP ranges forests cover. These results demonstrated different AGB–BGB allocation strategies for optimum tree growth as suggested by OPT at a broad scale.

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References

- Antúnez, I., Retamosa, E.C., Villar, R., 2001. Relative growth rate in phylogenetically related deciduous and evergreen woody species. *Oecologia* 128, 172–180.
- Beets, P.N., Pearce, S.H., Oliver, G.R., Clinton, P.W., 2007. Root/shoot ratios for deriving below-ground biomass of *Pinus radiata* stands. *New Zeal. J. For. Sci.* 37 (2), 267–288.
- Bloom, A.J., Chapin, F.S., Mooney, H.A., 1985. Resource limitation in plants: an economic analogy. *Ann. Rev. Ecol. Syst.* 16, 363–392.
- Brown, S., 2002. Measuring carbon in forests: current status and future challenges. *Environ. Pollut.* 116, 363–372.
- Cairns, M.A., Brown, S., Helmer, E.H., Baumgardner, G.A., 1997. Root biomass allocation in the world's upland forests. *Oecologia* 111, 1–11.
- Cornelissen, J.H.C., Castro-Díez, P., Carnelli, A.L., 1998. Variation in relative growth rate among woody species. In: Lambers, H., Poorter, H., van Vuuren, M.M.I. (Eds.), *Inherent Variation in Plant Growth: Physiological Mechanisms and Ecological Consequences*. Backhuys Publishers, Leiden, The Netherlands, pp. 363–392.
- Fang, J.-Y., Song, Y.-C., Liu, H.-Y., Piao, S.-L., 2002. Vegetation–climate relationship and its application in the division of vegetation zone in China. *Acta Bot. Sin.* 44, 1105–1122.
- Feng, Z.-W., Wang, X.-K., Wu, G., 1999. *Biomass and Productivity of Forest Ecosystems in China*. Science Press, Beijing, 241 pp.

- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* 25, 1965–1978.
- IPCC (Intergovernmental Panel on Climate Change), 2006. 2006 IPCC Guidelines for National Greenhouse Gas Inventories (Vol. 4): Agriculture, Forestry and Other Land Use. Institute for Global Environmental Strategies, Hayama, Japan.
- Jackson, R.B., Canadell, J., Ehleringer, J.R., Mooney, H.A., Sala, O.E., Schulze, E.D., 1996. A global analysis of root distribution for terrestrial biomes. *Oecologia* 108, 389–411.
- King, J.-S., Giardina, C.P., Pregitzer, K.S., Friend, A.L., 2007. Biomass partitioning in red pine (*Pinus resinosa*) along a chronosequence in the Upper Peninsula of Michigan. *Can. J. For. Res.* 37, 93–102.
- Li, Z., Kurz, W.A., Apps, M.J., Beukema, S.J., 2003. Belowground biomass dynamics in the carbon budget model of the Canadian forest sector: recent improvements and implications for the estimation of NPP and NEP. *Can. J. For. Res.* 33, 126–136.
- Luo, T.-X., 1996. Patterns of net primary productivity for Chinese major forest types and their mathematical models. Ph. D. dissertation, The Commission for Integrated Survey of Natural Resources, The Chinese Academy of Sciences, Beijing, 211pp.
- Lusk, C.H., Wright, I., Reich, P.B., 2003. Photosynthetic differences contribute to competitive advantage of evergreen angiosperm trees over evergreen conifers in productive habitats. *New Phytol.* 160, 329–336.
- Mokany, K., Raison, R.J., Prokushkin, A.S., 2006. Critical analysis of root:shoot ratios in terrestrial biomes. *Global Change Biol.* 12, 84–96.
- Niklas, K.J., Enquist, B.J., 2002. Canonical rules for plant organ biomass partitioning and annual allocation. *Am. J. Bot.* 89 (5), 812–819.
- Ravindranath, N.H., Ostwald, M., 2008. Carbon Inventory Methods: Handbook for Greenhouse Gas Inventory, Carbon Mitigation and Roundwood Production Projects. Springer, Dordrecht, The Netherlands, 304 pp.
- Reich, P.B., 1998. Variation among plant species in leaf turnover rates and associated traits: implications for growth at all life stages. In: Lambers, H., Poorter, H., van Vuuren, M.M.I. (Eds.), *Inherent Variation in Plant Growth: Physiological Mechanisms and Ecological Consequences*. Backhuys Publishers, Leiden, The Netherlands, pp. 467–487.
- Reich, P.B., 2002. Root–shoot relations: optimality in acclimation and adaptation or the “Emperor’s New Clothes”? In: Waisel, Y., Eshel, A., Kafkafi, U. (Eds.), *Plant Roots: The Hidden Half*, third ed. Marcel Dekker, Basel, Switzerland, pp. 205–220.
- Ruiz-Robledo, J., Villar, R., 2005. Relative growth rate and biomass allocation in ten woody species with different leaf longevity using phylogenetic independent contrasts (PICs). *Plant Biol.* 7 (5), 484–494.
- Sheng, W.-T., Fan, S.-H., 2005. Long-term Productivity of Chinese Fir Plantations. Science Press, Beijing, 251 pp.
- Sprugel, D.G., 1983. Correcting for bias in log-transformed allometric equations. *Ecology* 64 (1), 209–210.
- Wang, X., Fang, J., Zhu, B., 2008. Forest biomass and root–shoot allocation in northeast China. *For. Ecol. Manag.* 255, 4007–4020.
- Warton, D.I., Wright, I.J., Falster, D.S., Westoby, M., 2006. Bivariate line-fitting methods for allometry. *Biol. Rev.* 81, 259–291.
- Wu, Z.-L., 1999. China’s Forests: Coniferous Forest. China Forestry Publishing House, Beijing, pp. 922–941.
- Yang, Y.-H., Mohammad, A., Feng, J.-M., Zhou, R., Fang, J.-Y., 2007a. Storage, patterns and environmental controls of soil organic carbon in China. *Biogeochemistry* 84, 131–141.
- Yang, Y.-H., Ma, W.-H., Mohammad, A., Fang, J.-Y., 2007b. Storage, patterns and controls of soil nitrogen in China. *Pedosphere* 17 (6), 776–785.
- Zeng, T.-X., 1984. Investigation of *Cunninghamia lanceolata* stands mixed with *Pinus elliotii* in Xijiang Forest Farm (Guangdong). *Tropical For. (Chinese)* 4, 1–13.
- Zerihun, A., Montagu, K.D., Hoffmann, M.B., Bray, S.G., 2006. Patterns of below- and aboveground biomass in *Eucalyptus populnea* woodland communities of northeast Australia along a rainfall gradient. *Ecosystems* 9, 501–515.
- Zhang, X.-S., 2007. Vegetation Map of China and Its Geographic Patterns. Geological Publishing House, Beijing, pp. 91–124.