

Large-scale patterns in forest growth rates are mainly driven by climatic variables and stand characteristics

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ABSTRACT

Comparing the growth rate of natural forest and plantation forest may be useful to better understand rates of carbon sequestration and carbon turnover. However, the large-scale patterns of biomass growth rates in China's forests are still not well defined. We analyzed the growth rates of forest leaves, branches, stems, and roots across forest communities in China by using data collection, collation, and systematic analysis of published research and our unpublished data. The biomass growth rates in all forests exhibited negative latitudinal trends and negative altitudinal trends, with significant influence from climatic variables and stand characteristics. Stand characteristics explained more variation in growth rates of forest biomass than did climatic variables, and growth rates of forest leaves, branches, stems, and roots varied in relation to climate, stand characteristics, and forest origin. The cross-validated results of stepwise multiple regression (SMR) models and neural network models (NNM) indicated that the prediction accuracy of growth rate of forest biomass by NNM was better than that of the SMR models. Our results improve understanding of the environmental factors affecting Chinese forest growth and inform efforts to model dynamics of carbon accumulation in China's forests.

1. Introduction

In past decades, the global average temperature increased 0.027 °C per year and is expected to increase 1.8–4.0 °C by 2050, depending on the carbon emissions scenario (Nilsson and Schopfhauser, 1995; Houghton, 2007). Global climate changes will affect the net carbon absorption of terrestrial ecosystems by affecting the structure and function of terrestrial ecosystems (Dixon et al., 1994; Fang et al., 2001). Forests are the largest part of the terrestrial carbon pool, storing 80% of the above ground carbon and 40% of the underground carbon, and thus, play an irreplaceable role in the global carbon cycle and in mitigating global climate change (Reich et al., 2014). Forest biomass is the balance of photosynthesis and respiration and can be influenced by resource supply, climate, and plant age (Poorter et al., 2009; 2012). The biomass growth rate, as the ratio between dry biomass and stand age, can reflect the accumulation of vegetation biomass and may provide background data to explore the temporal features of the forest carbon cycle. Thus, knowledge about the growth rate of forest biomass is

important for the accuracy of global carbon cycle accounting and modeling (Hui et al., 2012).

Despite advances in the understanding of forest biomass growth at the individual tree scale, there is still strong debate about the roles of tree size/age, climate, and stand characteristics on the rates of absolute forest growth and forest carbon accumulation (Weiner and Thomas, 2001; Meinzer et al., 2011). The metabolic scaling theory postulates that the biomass growth rate should increase with tree biomass, regardless of forest type, stand age, and other environmental factors. A few site-specific studies also supported the prediction of metabolic scaling theory (Enquist et al., 1999; Sillett et al., 2010). However, some single-species studies were consistent with a widely held assumption that the growth rate of individual trees decreases with increasing tree biomass or size (Ryan et al., 1997). In addition, forest net primary productivity (NPP), the net chemical energy captured by photosynthesizing plants, which reflects the forest carbon sink strength, is regulated by climate, CO₂ concentration, nitrogen deposition, topography, soil, deforestation, pests, fire, and other factors (Pretzsch et al.,

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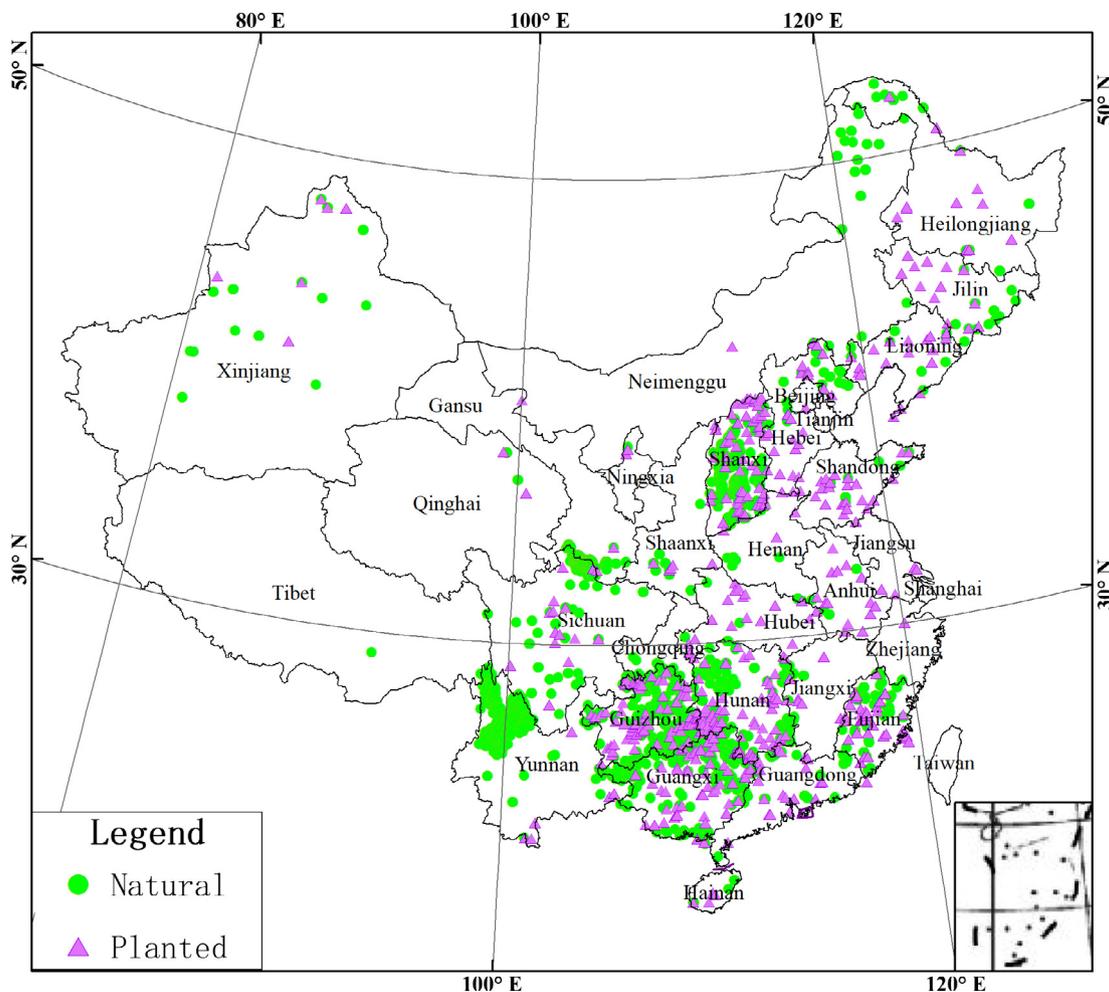


Fig. 1. Distribution of plots across China's forests.

Table 1

Site information (e.g., longitude, latitude, and altitude), climate factors (e.g., mean annual temperature (MAT), mean annual precipitation (MAP)) and stand characteristics (e.g., stand age, diameter at breast height (DBH), height, stand density, leaf area index (LAI) and tree species richness) across China's forests.

Forest origins	Natural	Plantation
Longitude (°)	80.6–131.8	81.1–130.2
Latitude (°)	18.2–53.2	18.1–52.5
Altitude (m)	5–4240	5–3930
MAT (°C)	−5.4 to 24.1	−0.6 to 24
MAP (mm)	100–2651	180–2650
Stand age (years)	3–400	4–93
DBH (cm)	2–110	2–70
Height (m)	2.0–54.4	1.7–31.2
Stand density (no./ha)	100–70180	100–48750
Leaf area index	1.07–49.1	1.21–34.2
Tree species richness	1–30	1–6

2014; Liang et al., 2015). At the regional scale, forest inventory data and model simulation are important methods to study the carbon budget of forest ecosystems. Most ecological process models only include the impact of environmental factors (Dufresne et al., 2002; Canadell and Raupach, 2008). Many researchers are trying to add forest age and human disturbance into ecological process models to understand the dynamic changes of forest carbon cycles more accurately (Petritsch et al., 2007; Coursolle et al., 2012; Li et al., 2015). However, up until now, to our knowledge, the relationship between growth rate of forest biomass, climate, and stand characteristics is still unclear.

China has diverse climatic zones, complex topography, and landform, and large areas of diverse forests, which are affected by climate and stand characteristics across different regions (Fang et al., 2001; Guo et al., 2013). These factors pose great challenges for the accurate assessment of the carbon fixation rate and mechanism of China's forest ecosystems. Moreover, forests in China are also impacted by human activity, such as excessive exploitation and vegetation restoration (Ren et al., 2012). Excessive exploitation of forest resources decreased forest coverage in China from about 35% in the 1950s to 14% in the 1980s. Conversely, the forest coverage significantly increased from 13.9% in the 1990s to 21% in the 2010s because of several key national ecological restoration programs. As a result of national vegetation restoration, China has the largest forest plantation area which accounts for 25% of the global forest plantation area (Fang et al., 1996; Guo et al., 2013). Previous researchers also indicated that forest plantations have different undergrowth biodiversity, tree species, and human disturbance from natural forests (Guo and Ren, 2014). By investigating differing growth rates in natural and plantation forest predictions of carbon sequestration and carbon turnover in China can be improved.

In the present research, the growth rates of forests in China were investigated based on the data from multiple sources. The aims of this research were as follows: (1) what is the spatial distribution pattern of the growth rates of China's forests? (2) to examine the relationships of growth rates to climatic factors (e.g., temperature and precipitation) and stand characteristics (e.g., age, density, height, diameter at breast height, and leaf area index), and (3) to compare the accuracy of stepwise multiple regression (SMR) models and neural network models (NNM) for predicting the growth rates of China's forests.

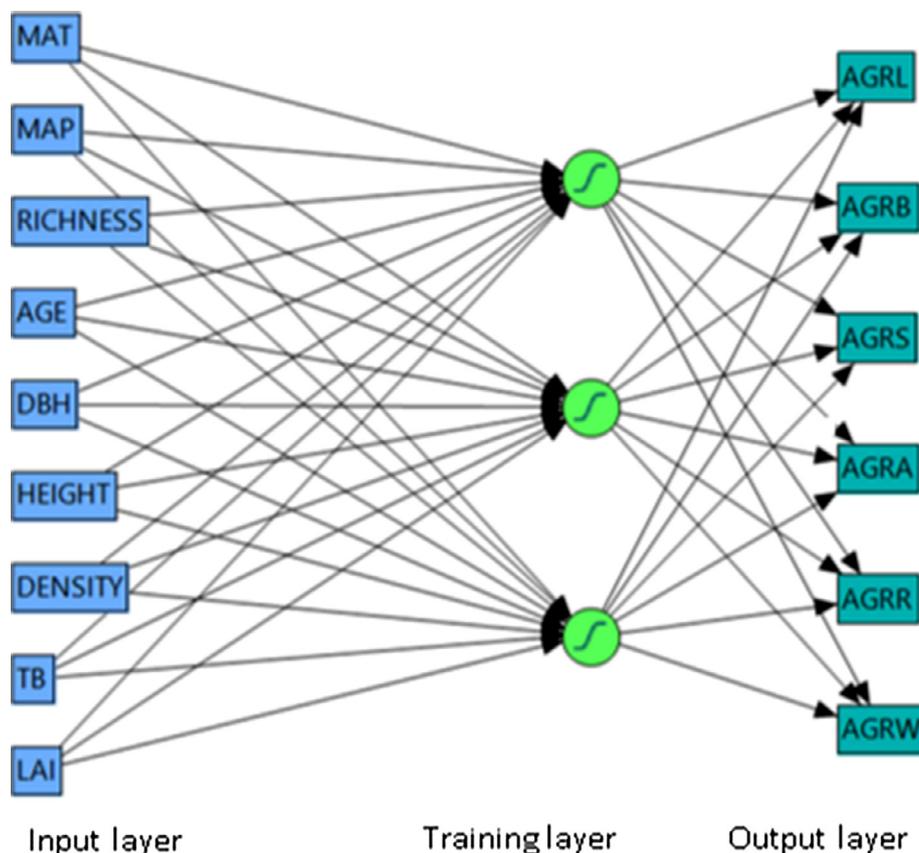


Fig. 2. Diagram of neural network model for the annual growth rate of biomass across China’s forests.

Table 2
Annual growth rate of biomass across China’s forests.

Forest origins	Natural	Plantation
AGRL (Mg/ha/y)	0.0001–4.6	0.0001–4.9
AGRB (Mg/ha/y)	0.0001–11.1	0.0001–7.9
AGRS (Mg/ha/y)	0.001–25.8	0.001–42.0
AGRA (Mg/ha/y)	0.001–41.5	0.001–50.4
AGRR (Mg/ha/y)	0.001–10.7	0.001–14.7
AGRW (Mg/ha/y)	0.002–52.1	0.002–59.5

Note: AGRL annual growth rate of leaf biomass, AGRB annual growth rate of branch biomass, AGRS annual growth rate of stem biomass, AGRA annual growth rate of aboveground biomass, AGRR annual growth rate of root biomass, AGRW annual growth rate of whole tree biomass.

Table 3
Mean value and standard error of annual growth rate of biomass across China’s forests.

Annual growth rate	Natural	Plantation
AGRL (Mg/ha/y)	0.117 ± 0.002	0.433 ± 0.011
AGRB (Mg/ha/y)	0.348 ± 0.007	0.801 ± 0.019
AGRS (Mg/ha/y)	1.305 ± 0.020	3.451 ± 0.077
AGRA (Mg/ha/y)	1.770 ± 0.024	4.685 ± 0.097
AGRR (Mg/ha/y)	0.443 ± 0.007	1.085 ± 0.027
AGRW (Mg/ha/y)	2.213 ± 0.035	5.770 ± 0.121

Note: AGRL annual growth rate of leaf biomass, AGRB annual growth rate of branch biomass, AGRS annual growth rate of stem biomass, AGRA annual growth rate of aboveground biomass, AGRR annual growth rate of root biomass, AGRW annual growth rate of whole tree biomass.

2. Materials and methods

2.1. Chinese forest biomass database

We combined forest biomass data from previous database containing 6153 forest stands (Guo and Ren, 2014) and our field work containing 110 forest stands (Wang et al., 2015). In Guo’s forest database, we removed 1140 forests stand with diameter at breast height (DBH) < 2 cm, height < 1.5 m, stand density < 100 no./ha, extremely low leaf area index (LAI), and extremely low mean annual precipitation (MAP). Here, our database includes biomass data from 5123 forest stands (3465 natural forests and 1658 planted forests) ranging from 18.1 to 53.2° N, 75.53 to 131.8° E, and 5 to 4250 m above sea level (Fig. 1; Table 1). Forest component biomass values (leaf, branch, stem, and root), site information (longitude, latitude, and altitude), climatic factors (mean annual temperature (MAT) and MAP) and stand characteristics (stand age, DBH, height, stand density, leaf area index, and tree species richness) across China’s forests are included in this dataset.

For forest biomass estimation in our field work, three 20 × 50 m plots at each site were each divided into ten 10 × 10 m quadrats. In order to avoid underestimation of the forest biomass, the selected plots should be no logging. DBH and height of each individual tree (including dead standing tree) with DBH ≥ 2 cm in each quadrat were recorded. According to the height and DBH data, 5–7 standard trees of each species in one plot were used for cutting and weighing of leaf, branch, stem, and root biomass. The samples of the component parts of standard trees were dried in the laboratory and weighed. The dry biomass coefficient was the ratio of dry biomass to fresh biomass. The dry biomass of leaf, branch, stem, and root in each plot were the sum of the biomass components of all trees in the plot, based on the allometric models of standard trees and the total DBH or height of trees in the plot.

Table 4
Pearson correlations between annual growth rate of biomass across China's forests and site information.

Forest origins	Site information	AGRL	AGRB	AGRS	AGRA	AGRR	AGRW
Natural (n = 3465)	Longitude (E, °C)	-0.115**	-0.040**	-0.082**	-0.078**	-0.041**	-0.071**
	Latitude (N, °C)	-0.282**	-0.345**	-0.296**	-0.321**	-0.172**	-0.296**
	Altitude (m)	-0.107**	-0.234**	-0.185**	-0.200**	-0.153**	-0.195**
Plantation (n = 1658)	Longitude (E, °C)	0.038	0.037	-0.027	-0.009	0.058**	0.003
	Latitude (N, °C)	-0.024**	-0.057**	-0.208**	-0.203**	-0.205**	-0.211**
	Altitude (m)	-0.151**	-0.182**	-0.176**	-0.192**	-0.191**	-0.194**

Note: (1) AGRL annual growth rate of leaf biomass, AGRB annual growth rate of branch biomass, AGRS annual growth rate of stem biomass, AGRA annual growth rate of aboveground biomass, AGRR annual growth rate of root biomass, AGRW annual growth rate of whole tree biomass; (2) ** present $p < 0.05$.

Moreover, for the published data, the tree component of dry biomass per plot or hectare was also collected. In the case of dry biomass data missing for a tree component, the allometric models of standard trees in previous research were used to estimate biomass (Luo et al., 2004).

2.2. Climatic variables and stand characteristics

MAT (°C) and MAP (mm) are regarded as important climatic factors affecting the growth rate of a forest. Here, the MAT and MAP of sites during 2007–2013 were collected for data analysis. If the MAT and MAP data were not present in the literature, they were extracted from the world meteorological database (www.worldclim.org) based on the longitude and latitude information of each site with an accuracy of 30 arcseconds.

Stand age, DBH, height, stand density, leaf area, and tree species richness of sites were collected from the published literature and our field measurements. Stand age of natural forest was determined by the mean age of main tree species and that of plantation forests was determined by the planting date of the stand. The DBH and height of each site were the average value of all tree species in the plots. Stand density was the ratio of individual tree number to the area of the plots. Leaf area index (LAI) of forest stands was the ratio of whole leaf area to stand area. The leaf area was calculated by the leaf biomass/leaf area per unit biomass. The different measured methods of leaf area for forest types can be seen in the Ni et al. (2001). The tree species richness was measured using a previously described method (Hector et al., 1999).

2.3. Statistical analysis

All data were statistically analyzed using JMP 14.1 software from SAS. Biomass growth rates were calculated by dividing each of stand leaf, branch, stem, and root dry mass by stand age, respectively. The different biomass growth rates between natural and plantation forest were also compared using the ANOVA method. Pearson correlations between annual biomass growth rate across China's forests and site information were calculated in JMP. The spatial scale of growth rate along longitudinal, latitudinal, and altitudinal gradients were indicated by the reduced major axis regression slope.

The effect of climatic factors (e.g., MAT and MAP) and stand characteristics (e.g., stand age (AGE), DBH, height (HEIGHT), stand density (DENSITY), LAI, and tree species richness (RICHNESS)) on the forest biomass growth rate were identified by SMR. In addition, a neural network model (NNM) (Fig. 2) was also used to describe the relationship between biomass growth rate, climatic factors and stand characteristics. The determinant coefficient (R^2) and root mean square error (RMSE) were used to compare the prediction accuracy of NNM and SMR models.

3. Results

3.1. Variation and spatial patterns in forest biomass growth rate

The biomass growth rate across China's forests showed high

variation, ranging from 0.0001 to 4.9 Mg/ha/y for annual growth rate of leaf biomass (AGRL), 0.0001 to 11.1 Mg/ha/y for annual growth rate of branch biomass (AGRB), 0.001 to 42.0 Mg/ha/y for annual growth rate of stem biomass (AGRS), and 0.001 to 14.7 Mg/ha/y for annual growth rate of root biomass (AGRR) (Table 2). The mean values of biomass growth rate in natural forests were 0.117 Mg/ha/y, 0.348 Mg/ha/y, 1.305 Mg/ha/y and 0.443 Mg/ha/y for AGRL, AGRB, AGRS, and AGRR, respectively (Table 3). Moreover, the mean values of biomass growth rate in plantation forest was different from that in natural forests.

Biomass growth rates across all forests exhibited negative latitudinal trends and negative altitudinal trends (Table 4). The growth rate of forest biomass increased from north to south, decreased with increasing altitude. In addition, the biomass growth rate in natural forest decreased from west to east (Table 4).

3.2. Relationship of growth rate with climatic and stand factors

There was a different relationship between biomass growth rate and climatic factors between natural forests and plantation forests (Table 5). For natural forests, AGRB, AGRS, AGRA, and AGRW significantly and positively correlated with MAP, and AGRL and AGRR significantly and positively correlated with MAT and MAP. For plantation forests, AGRL significantly and positively correlated with MAP, while AGRB significantly and negatively correlated with MAP.

SMR modeling showed that all the biomass growth rates in natural forests decreased with AGE, but increased with DENSITY, TB, and LAI (Table 5). AGRL, AGRB, AGRA, and AGRW also increased with DBH, while AGRS and AGRR did not. Except for AGRB, all biomass growth rates in plantation forests decreased with AGE, and all biomass growth rates increased with RICHNESS and TB.

Climatic and stand factors had different contributions to variation in growth rate (Fig. 3). DENSITY, TB, and LAI had positive and high contributions to growth rate in natural forests, and vice versa for the AGE and RICHNESS. AGE had a negative and high contribution on growth rate in plantation forests, while RICHNESS and TB had positive and high contributions to growth rate. Climate explained 0.3–4.6% and 2.2–10.3% of variation in growth rate for natural forests and plantation forests, respectively (Fig. 4). The contributions of stand factors to growth rate were 55.8–66.7% for natural forests, and 34.5–71.6% for plantation forests. Moreover, the climate and stand factors also had obvious and different interactions for variation in growth rates between natural forests and plantation forests (Fig. 4).

3.3. Neural network model for the biomass growth rate

Besides the SMR model, we also built NNM to increase the accuracy of prediction models for the biomass growth rates (Table 6). For natural forests, the range of R^2 and RMSE for NNM training was 0.725–0.936 and 0.044–0.855, respectively. The R^2 and RMSE for the NNM training were different between natural forests and plantation forests. The cross-validated results of the NNM demonstrated that the R^2 and RMSE for the NNM validation were similar with those of NNM training.

Table 5 Stepwise multiple regressions (SMR) between annual growth rate of biomass across China's forests with climate variables and stand characteristics.

Forest origins	Annual growth rate	Equations	P.	R ²	RMSE
Natural	AGRL	AGRL = 0.002 + 0.0009MAT + 0.018MAP - 0.013RICHNESS - 0.046AGE + 0.014DBH + 0.189DENSITY + 0.016TB + 0.130LAI	< 0.001	0.607	0.056
	AGRB	AGRB = -0.0004 + 0.035MAP - 0.087AGE + 0.032DBH + 0.171DENSITY + 0.042TB + 0.107LAI	< 0.001	0.505	0.213
	AGRS	AGRS = 0.0007 + 0.024MAP - 0.079AGE + 0.022HEIGHT + 0.247DENSITY + 0.121TB + 0.023LAI	< 0.001	0.673	0.538
	AGRA	AGRA = 0.003 + 0.022MAP - 0.081AGE + 0.015DBH + 0.019HEIGHT + 0.257DENSITY + 0.110TB + 0.062LAI	< 0.001	0.665	0.934
	AGRW	AGRW = 0.006 - 0.005MAT + 0.016MAP + 0.019RICHNESS - 0.074AGE + 0.012HEIGHT + 0.343DENSITY + 0.102TB + 0.036LAI	< 0.001	0.671	0.215
Plantation	AGRL	AGRL = 0.029 + 0.043MAP + 0.689RICHNESS - 1.002AGE + 0.309DENSITY + 0.145TB + 0.219LAI	< 0.001	0.459	0.191
	AGRB	AGRB = 0.051 - 0.049MAP + 1.003RICHNESS + 0.366TB + 0.138LAI	< 0.001	0.565	0.393
	AGRS	AGRS = 0.047 + 0.771RICHNESS - 1.325AGE - 0.116DBH + 0.120HEIGHT + 0.509TB	< 0.001	0.776	1.009
	AGRA	AGRA = 0.050 + 0.814RICHNESS - 1.429AGE - 0.112DBH + 0.132HEIGHT + 0.541TB	< 0.001	0.694	1.300
	AGRW	AGRW = 0.023 + 1.826RICHNESS - 1.131AGE - 0.120DBH + 0.435TB	< 0.001	0.576	0.419
		AGRW = 0.059 + 1.208RICHNESS - 1.604AGE - 0.187DBH + 0.123HEIGHT + 0.576TB	< 0.001	0.785	1.592

Note: AGRL annual growth rate of leaf biomass, AGRB annual growth rate of branch biomass, AGRS annual growth rate of stem biomass, AGRA annual growth rate of aboveground biomass, AGRW annual growth rate of root biomass, AGRW annual growth rate of whole tree biomass.
 MAT mean annual precipitation, MAP mean annual precipitation, AGE stand age, DENSITY, stand density, RICHNESS tree species richness, DBH diameter at breast height, HEIGHT stand height, TB total biomass, LAI leaf area index.

Moreover, the NNM had higher R² and lower RMSE than the SMR model (Tables 5 and 6), which indicated that the prediction accuracy of the NNM was better than that of the SMR model.

4. Discussion

4.1. Biogeographic patterns of growth rate and their climatic control

There were significant differences in the spatial distribution of growth rates across China's forests (Table 4). The growth rates of natural forests decreased with longitude, latitude, and altitude, which is consistent with the spatial distribution trend of the national NPP, mainly due to annual precipitation and temperature (Wang et al., 2010; Liang et al., 2015). The growth rate of natural forest in most parts of southern China is greater than those in northern China, and this difference is mainly caused by significant temperature differences (Wang et al., 2011). The growth rate of forest biomass in western regions was higher than that in eastern regions, which indicated that the effect of annual precipitation on growth rates was smaller than other factors, as rainfall is high in eastern China. We recorded large growth rates of forest biomass mainly in the southwest of Yunnan province, a small region in Guangdong province, and Hainan province. These regions belong to the tropics, which with high temperature and precipitation are very suitable for forest growth (Zhou et al., 2002). In addition, plantation forests exhibited similar and significant latitudinal and altitudinal trends in growth rate to natural forest. However, the growth rates of stem and root in plantations were not significantly affected by climatic factors. This result suggests that stem and root growth in plantations may be less sensitive to temperature or precipitation than leaf and branch growth (Sack et al., 2002; Mokany et al., 2006).

4.2. Relationships between biomass growth rates and stand characteristics

Previous researchers demonstrated that the relationship between biomass growth rate, NPP, and tree size is complicated (Stephenson et al., 2014; Li et al., 2016). A global analysis of temperate and tropical tree species indicated that biomass growth rate for most species increases continuously with tree size (Stephenson et al., 2014). However, some research demonstrated that the biomass growth rate of individual trees declines with increasing tree size (Ryan et al., 1997). In this study, our data showed that the biomass growth rate of leaf, branch, stem, and root increased with total biomass, which is similar with the results of the previous global analysis. In addition, the leaf is an important organ for the energy production and material transformation in plants, as well as the main driver of material circulation and energy flow in the ecosystem. Leaf biomass can reflect the photosynthetic capacity of plants, and the rate of absorption of water and nutrients in soil (Zhang et al., 2012). LAI, as a vegetation structure parameter closely related to forest canopy energy and CO₂ exchange, can be inputted into light energy utilization models with climatic variables to estimate changes in NPP (Xu et al., 2016). We noticed that the biomass growth rate increased with LAI (Table 5), which is consistent with some previous research (Waring, 1983; Luo et al., 2004).

Our data indicated that the biomass growth rate decreased with stand age (Table 5), which is consistent with previous studies (Gower et al., 1996). With increasing stand age, the canopy biomass in the upper part of the forest ecosystem increased rapidly with the increase of leaf area. When the leaf area of the forest reached its maximum, the biomass of trees canopy reached its maximum and then rapidly declined (Mao et al., 2011). Some researchers indicate that this decline is a complex process, which may involve many biological and non-biological factors (Ryan et al., 1996; 2004). Besides the leaf area, the soil fertility, stand density, and growth rate of individual trees all have an important influence on the growth rate of the forest (Kaufmann and Ryan, 1986; Yoder et al., 1994). Under high soil fertility, stand density, and tree age conditions, the biomass of forest stands will rapidly reach

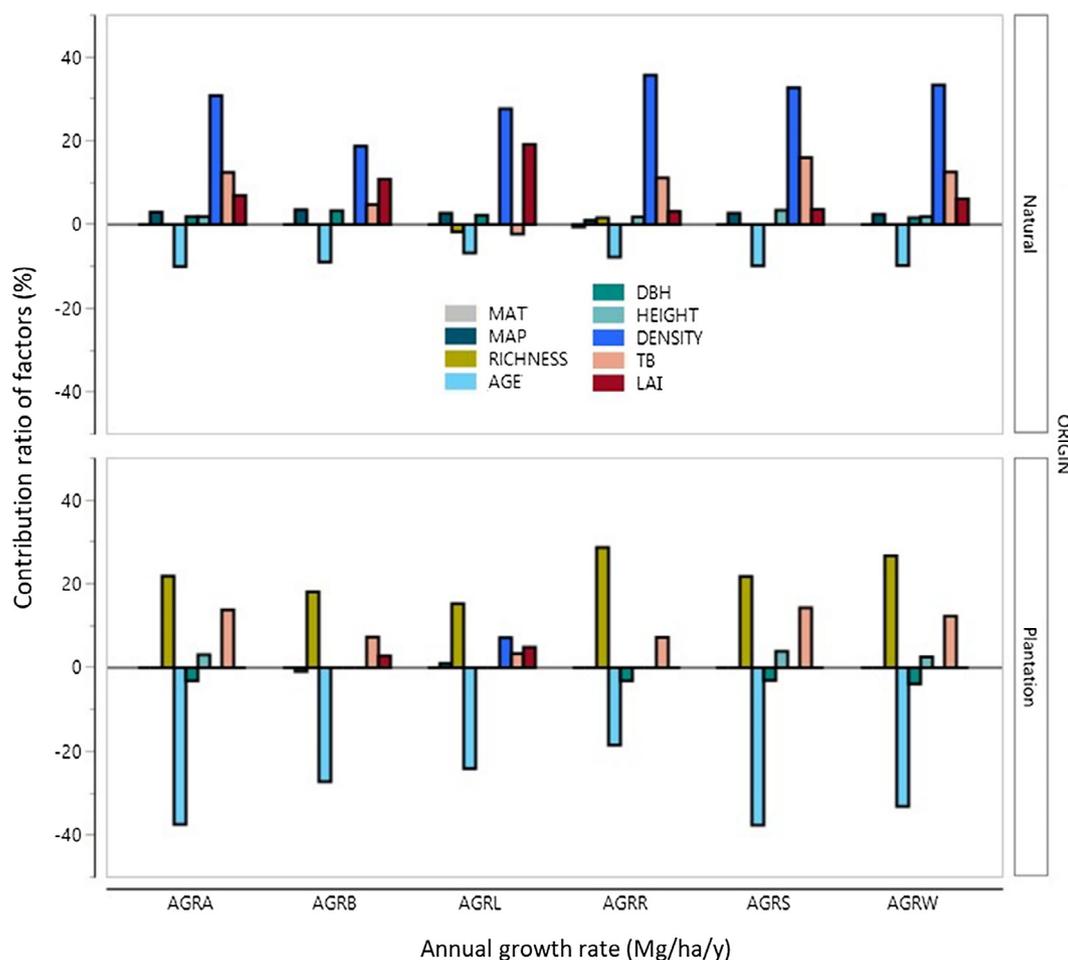


Fig. 3. Contribution ratio of climate variables and stand characteristics to the annual growth rate of biomass across China's forests.

their maximum and then the growth rate declines. Moreover, the increase of water transport resistance to the forest canopy reduces the photosynthetic capacity of trees (Ryan et al., 2004; Woodruff et al., 2004). The loss of nutrients in forest soil leads to an increase in root biomass allocation, resulting in a decrease of forest leaf area and tree photosynthesis (Ryan et al., 1996; Ebel et al., 2000; Basile et al., 2003). Competition for resources changes the species of trees and reduces the utilization rate of resources (Martin and Jokela, 2004). Photosynthetic capacity, forest leaf area and resource utilization, as well as increased root biomass allocation are the key factors of forest growth decline, while forest respiration and forest senescence have little effect (Weiner and Thomas, 2001; Mao et al., 2011).

Total biomass may increase with increasing stand density up to the suitable stand density (Zhang et al., 2005; 2006). Here, our data demonstrated that the growth rate of natural forests depends on the stand density (Table 5), which is consistent with the relationship between growth rate and total biomass. Over the suitable stand density, average plant biomass will decline with the increasing of stand density by the self-thinning phenomenon (Zhang et al., 2005). Although the relationship between average biomass and stand age may vary with plant genotype, life history, soil fertility, and soil moisture, etc. (Zhang et al., 2010a; 2010b), the total biomass per area may be determined by the total energy (light, temperature, and water) per area (Deng et al., 2006). Compared with the natural forests, the growth rate of plantation forests showed no significant relationship with stand density. It may be a result of plantation forests having the proper stand density under plantation management, and that most of the plantation forests are still in the early stage (Guo and Ren, 2014).

Tree species richness had different and significant effects on the

biomass growth rate in natural forests and plantation forests (Table 5). In plantation forests, increased richness had a strong positive interaction with the biomass growth rate, which is similar with some previous research (Hector et al., 1999; Huang et al., 2018). A manipulation experiment of species composition in grass has shown that community productivity is promoted by plant diversity (Hector et al., 1999). An experiment on 150,000 trees in subtropical plantation forests containing 1–16 species also showed that stand productivity increased with tree species richness (Huang et al., 2018). On the contrary, tree species richness had either positive or negative interactions with the growth rate of natural forests (Table 5), which implies that richness may have a complicated role in the growth rate of natural forests (Guo and Ren, 2014).

The growth rate of forest may be affected by climate, stand conditions and interactions between them. The effect of climate on growth rate is lower than that of stand conditions (Fig. 4), which is consistent with our previous study (Zhang et al., 2016). Although some researchers have shown that the growth of a tree may be dominated by the temperature and tree size, the soil fertility, stand age, stand density, and forest type are also important factors in tree growth at the stand scale (Zhang et al., 2010a; Guo and Ren, 2014). Moreover, our data about the interaction between the climate and stand conditions was similar to some previous research (Han et al., 2011).

4.3. The different growth rate of natural forests and plantation forests

At large scale, the growth rate of forest can be used for the estimation of carbon accumulation per year or integrated into the forest carbon model as an important input parameter (Fang et al., 2001).

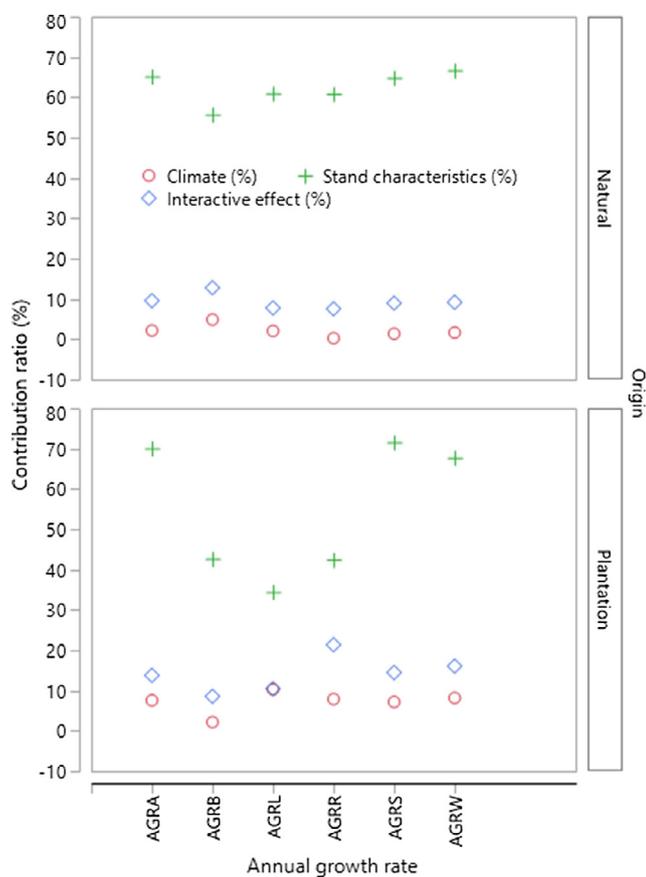


Fig. 4. The independent effects of climate variables, stand characteristics and interactive effects between factors on the annual growth rate of biomass across China's forests.

Table 6

Neural network models (NNM) predicting annual growth rate of biomass across China's forests by climate variables and stand characteristics.

Forest origins	Annual growth rate	NNM-training		NNM-validation	
		R ²	RMSE	R ²	RMSE
Natural	AGRL	0.725	0.044	0.744	0.051
	AGRB	0.740	0.143	0.769	0.195
	AGRS	0.909	0.268	0.852	0.395
	AGRA	0.931	0.855	0.855	0.495
	AGRR	0.774	0.153	0.803	0.166
	AGRW	0.936	0.374	0.872	0.627
Plantation	AGRL	0.592	0.170	0.538	0.140
	AGRB	0.668	0.369	0.636	0.336
	AGRS	0.862	0.475	0.831	0.512
	AGRA	0.886	0.352	0.865	0.446
	AGRR	0.822	0.296	0.759	0.243
	AGRW	0.893	0.288	0.883	0.362

Note: AGRL annual growth rate of leaf biomass, AGBR annual growth rate of branch biomass, AGRS annual growth rate of stem biomass, AGRA annual growth rate of aboveground biomass, AGRR annual growth rate of root biomass, AGRW annual growth rate of whole tree biomass.

Here, we compared the growth rate of natural forests and that of plantation forests (Table 3). The mean value of growth rate in plantation forest was higher than that of natural forest, indicating that the plantation forest per area may have the higher accumulation rate of ecological service in carbon storage, timber production, water conservation, water and soil conservation, wind prevention, sand fixation, and climate regulation than that of natural forest (Guo et al., 2013). This difference may result from the fact that most plantation trees

belong to highly productive species (Guo and Ren, 2014). The plantation forests were also younger than the natural forests, and the growth rate may decline with increasing stand age. Moreover, unlike natural forests, plantation forests only had a few species when the stand was created. The reasonable collocation between species significantly affects the growth rate of plantations (Huang et al., 2018). Our data showed that tree species richness has a more positive role on growth rates in plantation forests than in natural forests (Table 5). In practice, the reasonable mixing of tree species in plantations may produce a forest structure with multiple layers and a thick canopy, which can improve the productivity of the forest, resource use efficiency and the stability of the forest (Hui et al., 2012). Finally, we were also aware that biomass growth rates calculated by dividing each of components dry mass by stand age with only one-time investigation was imperfect. To remedy that insufficiency, the more resource data from multi-time investigation will be needed in the future research.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2018.12.054>.

References

Basile, B., Marsa, L.J., DeJong, T.M., 2003. Daily shoot extension growth of peach trees growing on rootstocks that reduce scion growth is related to daily dynamics of stem water potential. *Tree Physiol.* 23, 695–704.

Canadell, J.G., Raupach, M.R., 2008. Managing forests for climate change mitigation. *Science* 320, 1456–1457.

Coursolle, C., Margolis, H.A., Giasson, M.A., Bernier, P.Y., Amiro, B.D., Arain, M.A., Barr, A.G., Black, T.A., Goulden, M.L., McCaughey, J.H., Chen, J.M., Dunn, A.L., Grant, R.F., Lafleur, P.M., 2012. Influence of stand age on the magnitude and seasonality of carbon fluxes in Canadian forests. *Agri. For. Meteorol.* 165, 136–148.

Deng, J.M., Wang, G.X., Morris, E.C., Wei, X.P., Li, D.X., Chen, B.M., Zhao, C.M., Liu, J., Wang, Y., 2006. Plant mass–density relationship along a moisture gradient in north-west China. *J. Ecol.* 94, 953–958.

Dixon, R.K., Solomon, A., Brown, S., Houghton, R., Trexler, M., Wisniewski, J., 1994. Carbon pools and flux of global forest ecosystem. *Science* 265 171–171.

Dufresne, J.L., Fairhead, L., Le Treut, H., Berthelot, M., Bopp, L., Ciais, P., Friedlingstein, P., Monfray, P., 2002. On the magnitude of positive feedback between future climate change and the carbon cycle. *Geophys. Res. Lett.* 29 43-1–43-4.

Ebel, R.C., Cayor, A.W., Pitts, J.A., Wilkins, B.S., 2000. Mineral nutrition during establishment of golden delicious “smoothee” apples on dwarfing rootstocks and inter-stems. *J. Plant Nutri.* 23 (8), 1179–1192.

Enquist, B.J., West, G.B., Charnov, E.L., Brown, J.H., 1999. Allometric scaling of production and life-history variation in vascular plants. *Nature* 401, 907–911.

Fang, J., Chen, A., Peng, C., Zhao, S., Ci, L., 2001. Changes in forest biomass carbon storage in China between 1949 and 1998. *Science* 292, 2320–2322.

Fang, J.Y., Liu, G.H., Xu, S.L., 1996. Biomass and net productivity of forest vegetation in China. *Acta Ecol. Sin.* 16, 497–508.

Gower, S.T., McMurtrie, R.E., Murty, D., 1996. Aboveground net primary production decline with stand age: potential causes. *Trends Ecol. Evol.* 11, 378–382.

Guo, Z., Hu, H., Li, P., Li, N., Fang, J., 2013. Spatio-temporal changes in biomass carbon sinks in China's forests from 1977 to 2008. *Sci. China Life Sci.* 56, 661–671.

Guo, Q.F., Ren, H., 2014. Productivity as related to diversity and age in planted versus natural forests. *Global Ecol. Biogeogr.* 23, 1461–1471.

Han, W.X., Fang, J.Y., Reich, P.B., Woodward, F.I., Wang, Z.H., 2011. Biogeography and variability of eleven mineral elements in plant leaves across gradients of climate, soil and plant functional type in China. *Ecol. Lett.* 14, 788–796.

Hector, A., et al., 1999. Plant diversity and productivity experiments in european grasslands. *Science* 286 (5442), 1123–1127.

- Houghton, R.A., 2007. Balancing the global carbon budget. *Annu. Rev. Earth Pl. Sc.* 35, 313–347.
- Hui, D., Wang, J., Le, X., Shen, W.J., Ren, H., 2012. Influences of biotic and abiotic factors on the relationship between tree productivity and biomass in China. *For. Ecol. Manage.* 264, 72–80.
- Huang, Y.Y., et al., 2018. Impacts of tree species richness on productivity in a large-scale subtropical forest experiment. *Science* 362, 80–83.
- Kaufmann, M.R., Ryan, M.G., 1986. Physiographic, stand, and environmental effects on individual tree growth and growth efficiency in subalpine forests. *Tree Physiol.* 2 (1/2/3), 47–59.
- Li, D.Q., Zhang, C.H., Ju, W.M., Liu, L.J., 2016. Forest net primary productivity dynamics and driving forces in Jiangxi Province, China. *Chin. J. Plant Ecol.* 40, 643–657.
- Li, M.Z., Wang, B., Fan, W.Y., Zhao, D.D., 2015. Simulation of forest net primary production and the effects of fire disturbance in Northeast China. *Chin. J. Plant Ecol.* 39, 322–332.
- Liang, W., Yang, Y., Fan, D., Guan, H., Zhang, T., Long, D., Zhou, Y., Bai, D., 2015. Analysis of spatial and temporal patterns of net primary production and their climate controls in China from 1982 to 2010. *Agri. For. Meteorol.* 204, 22–36.
- Luo, T.X., Pan, Y.D., Ouyang, H., Shi, P.L., Luo, J., Yu, Z.L., Lu, Q., 2004. Leaf area index and net primary productivity along subtropical to alpine gradients in the Tibetan Plateau. *Global Ecol. Biogeogr.* 23, 1461–1471.
- Mao, P.L., Cao, B.H., Tian, W.X., Meng, F.Z., 2011. Advances in research on the mechanisms of age-related productivity decline of planted forests. *Acta Ecol. Sin.* 31 (11), 3208–3214.
- Martin, T.A., Jokela, E.J., 2004. Stand development and production dynamics of loblolly pine under a range of cultural treatments in north-central Florida USA. *For. Ecol. Manage.* 192 (1), 39–58.
- Meinzer, F.C., Lachenbruch, B., Dawson, T.E. (Eds.), 2011. Size- and Age-Related Changes in Tree Structure and Function. Springer.
- Mokany, K., Raison, R.J., Prokushkin, A.S., 2006. Critical analysis of root:shoot ratios in terrestrial biomes. *Glob. Chang. Biol.* 13, 345–358.
- Ni, J., Zhang, X., Scurlock, J.M., 2001. Synthesis and analysis of biomass and net primary productivity in Chinese forests. *Ann. Forest Sci.* 58, 351–384.
- Nilsson, S., Schopfhauser, W., 1995. The carbon sequestration potential of a global afforestation program. *Clim. Change* 30, 267–293.
- Petritsch, R., Hasenauer, H., Pietsch, S.A., 2007. Incorporating forest growth response to thinning within biome-BGC. *For. Ecol. Manage.* 242, 324–336.
- Poorter, H., Niinemets, Ü., Poorter, L., Wright, I.J., Villar, R., 2009. Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. *New Phytol.* 182, 565–588.
- Poorter, H., Niklas, K.J., Reich, P.B., 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.
- Pretzsch, H., Biber, P., Schütze, G., Uhl, E., Rotzer, T., 2014. Forest stand growth dynamics in Central Europe have accelerated since 1870. *Nat. Commun.* 5, 4967.
- Ren, H., Lu, H., Wang, J., Liu, N., Guo, Q.F., 2012. Forest restoration in China: advances, obstacles, and perspectives. *Tree For. Sci. Biotech.* 6, 7–16.
- Reich, P.B., Luo, Y.J., Bradford, J.B., Poorter, H., Perry, C., Oleksyn, J., 2014. Temperature drives global patterns in forest biomass distribution in leaves, stems, and roots. *Proc. Nat. Acad. Sci. USA* 111, 13721–13727.
- Ryan, M.G., Hubbard, R.M., Pongracic, S., Raison, R.J., McMurtrie, R.E., 1996. Foliage, fine-root, woody-tissue and stand respiration in *Pinus radiata* in relation to nitrogen status. *Tree Physiol.* 16, 333–343.
- Ryan, M.G., Binkley, D., Fownes, J.H., 1997. Age-related decline in forest productivity: pattern and process. *Adv. Ecol. Res.* 27, 213–262.
- Ryan, M.G., Binkley, D., Fownes, J.H., Giardina, C.P., Senock, R.S., 2004. An experimental test of the causes of forest growth decline with stand age. *Ecol. Monogr.* 74 (3), 393–414.
- Sack, L., Maranon, T., Grubb, P.J., 2002. Global allocation rules for patterns of biomass partitioning. *Science* 296 A1923–A1923.
- Sillett, S.C., et al., 2010. Increasing wood production through old age in tall trees. *For. Ecol. Manage.* 259, 976–994.
- Stephenson, N.L., et al., 2014. Rate of tree carbon accumulation increases continuously with tree size. *Nature* 507, 90–95.
- Wang, B., Huang, J., Yang, X., Zhang, B., Liu, M., 2010. Estimation of biomass, net primary production and net ecosystem production of China's forests based on the 1999–2003 National Forest Inventory. *Scandinavian J. For. Res.* 25, 544–553.
- Wang, S., Zhou, L., Chen, J., Ju, W., Feng, X., Wu, W., 2011. Relationships between net primary productivity and stand age for several forest types and their influence on China's carbon balance. *J. Environ. Manage.* 92, 1651–1662.
- Wang, Z.C., Du, H., Song, T.Q., Peng, W.X., Zeng, F.P., Zeng, Z.X., Zhang, H., 2015. Allometric models of major tree species and forest biomass in Guangxi. *Acta Ecol. Sin.* 35 (13), 4462–4472.
- Weiner, J., Thomas, S.C., 2001. The nature of tree growth and the “age-related decline in forest productivity”. *Oikos* 94, 374–376.
- Woodruff, D.R., Bond, B.J., Meinzer, F.C., 2004. Does turgor limit growth in tall trees? *Plant Cell Environ.* 27, 229–236.
- Xu, B.X., Chen, B.Z., Xu, G., Chen, J., Che, M.L., 2016. Estimated gross primary productivity based on global leaf area index. *Acta Ecol. Sin.* 36, 3546–3555.
- Yoder, B.J., Ryan, M.G., Waring, R.H., Schoettle, A.W., Kaufmann, M.R., 1994. Evidence of reduced photosynthetic rates in old trees. *For. Sci.* 40, 513–527.
- Zhang, H., Wang, G.X., Shen, Z.X., Zhao, X.Z., Qiu, M.Q., 2006. Effect of sensitivity to abscisic acid on scaling relationships for biomass production rates and body size in *Arabidopsis thaliana*. *Acta Physiol. Plant.* 28, 373–379.
- Zhang, H., Wang, G.X., Liu, Z.Q., Shen, Z.X., Zhao, X.Z., 2005. Sensitivity of response to abscisic acid affects the power of self-thinning in *Arabidopsis thaliana*. *Bot. Bull. Acad. Sin.* 46, 347–353.
- Zhang, H., Wang, G.X., Zheng, K.F., Zhang, W.P., 2010a. Mass-density relationship changes along salinity gradient in *Suaeda* L. *Acta Physiol. Plant.* 32, 1031–1037.
- Zhang, H., Shen, Z.X., Wang, G.X., Dai, X.F., Huang, Q.Q., Zheng, K.F., 2010b. Sensitivity to abscisic acid modulates positive interactions between *Arabidopsis thaliana* individuals. *J. Integr. Plant Bio.* 52, 340–346.
- Zhang, H., Song, T.Q., Wang, K.L., Yang, H., Yue, Y.M., Zeng, Z.X., Peng, W.X., Zeng, F.P., 2016. Influences of stand characteristics and environmental factors on forest biomass and root-shoot allocation in southwest China. *Ecol. Eng.* 91, 7–15.
- Zhang, W.P., Jia, X., Morris, E.C., Bai, Y.Y., Wang, G.X., 2012. Stem, branch and leaf biomass-density relationships in forest communities. *Ecol. Res.* 27, 819–825.
- Zhou, G., Wang, Y., Jiang, Y., Yang, Z., 2002. Estimating biomass and net primary production from forest inventory data: A case study of China's *Larix* forests. *For. Ecol. Manage.* 169, 149–157.