Influences of biotic and abiotic factors on the relationship between tree productivity and biomass in China

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ABSTRACT

The relationship between tree productivity and biomass not only reflects plant adaptation and the interaction of plants and the environment, but also has significant implications in global carbon cycling, climate change, and forest management. However, how biotic factors (e.g. tree age, diameter at breast height [DBH], height) and abiotic factors (e.g. elevation, latitude, and longitude) influence the relationship between tree productivity and biomass has not been well investigated. We analyzed a large database on tree productivity and biomass in China to derive the relationships between these two variables. The entire database was split into different groups by tree age, DBH, height, latitude, longitude and elevation. The relationship between productivity and biomass was developed using both a linear regression model and an allometric equation (i.e. power function) for each group. Differences in model parameters among groupings based on biotic or abiotic factors indicate the effect of each factor on the relationship between productivity and biomass. The slope of the linear regression model decreased with tree age, DBH, height, and elevation, but increased with tree density and longitude. The scaling exponent of the power function varied with tree age, height, and density following a quadratic pattern, but decreased linearly with elevation. Our results indicated that there is a significant relationship between tree productivity and biomass in China, but the relationship varies with some biotic and abiotic factors. To better predict tree productivity from biomass, tree age and size need to be considered.

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1. Introduction

Forest ecosystems play an important role in carbon cycling in terrestrial ecosystems and account for 76% of biomass carbon and 42% of the annual net primary productivity of terrestrial vegetation (Schlesinger, 1991; Dixon et al., 1994; Cairns et al., 1997; Goodale et al., 2002; Niklas and Enquist, 2002; Cheng and Niklas, 2007; Peichl and Arain, 2007; Fan et al., 2008). There are about 638 Gt C stored in forest ecosystems, with 283 Gt C in biomass alone (FAO, 2005; Keeling and Phillips, 2007). Previous studies have shown that both tree productivity and biomass are limited by environmental factors such as temperature, precipitation, and soil nutrient availability (Knapp and Smith, 2001; Malhi et al., 2004; Hui and Jackson, 2006; Raich et al., 2006; Keeling and Phillips, 2007). Thus, the relationship between tree productivity and biomass may reflect plant adaptation and the interaction of trees and environments, and may have significant implications in

global carbon cycling, climate change, and forest management. Therefore, it is quite important to understand the relationship between tree productivity and biomass (Whittaker and Likens, 1973; Niklas et al., 2003; Keeling and Phillips, 2007; Aragão et al., 2009; Cheng et al., 2009).

There have been two general approaches to establishing a relationship between productivity and biomass. The first one uses a direct relationship between productivity and biomass based on the assumption that productivity is the source of biomass (Keeling and Phillips, 2007). A linear regression model has been successfully used to relate productivity and biomass in different forest ecosystems (e.g. Whittaker and Likens, 1973; O'Neil and De Angelis, 1981; Raich et al., 2006; Keeling and Phillips, 2007). For example, Whittaker and Likens (1973) reported a linear relationship between aboveground net primary productivity and the aboveground biomass of 25 forests in the US. Ni et al. (2001) found a similar positive linear relationship of forest productivity and biomass in China. But Keeling and Phillips (2007) reported that a nonlinear regression equation (i.e. quadratic regression or asymptotic model) may fit the biomass and forest productivity relationship better than linear regression, when more productive tropical forests are included.

Another approach to the relationship between productivity and biomass comes from the metabolic theory of ecology (e.g. West

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et al., 1999; Niklas and Enquist, 2001; Brown et al., 2004; Cheng et al., 2009). If tree productivity is a reasonable surrogate for metabolic rate, the rate of production P and biomass M can be described by a power function: $P = aM^b$, where a is a normalization constant and b represents an allometric scaling exponent. Whether or not the value of the scaling exponent b is a constant is still debatable, the form of the allometric relationship has been widely accepted (Niklas and Enquist, 2001; Ernest et al., 2003; Li et al., 2005; Hui and Jackson, 2007; Cheng et al., 2009). Several studies found that the scaling exponent for individual trees is approximately 3/4. For example, rates of biomass production in tropical trees appear to scale as $M^{3/4}$ (Enquist et al., 2007). Niklas and Enquist (2001) demonstrated that biomass production rates scale as the 3/4-power of body mass over 20 orders of magnitude of biomass, using a dataset containing unicellular algae, aquatic plants, and terrestrial metaphytes. Other studies have found different values for b. Reich et al. (2006) reported that the scaling exponent of plant respiration and biomass is near 1 in size groupings from very small seedlings to vary large trees. A study of tree productivity and biomass in China found that the scaling exponents of tree productivity and biomass vary from 0.43 in a boreal forest to 1.10 in a sclerophyllous evergreen forest, but the sample sizes of the study were quite small, especially for those with extreme scaling exponents (Li et al., 2005). Glazier (2010) recently proposed the metabolic-level boundaries hypothesis that explains the variation in scaling exponent. However, the influence of biotic factors such as tree age or size and abiotic factors such as geophysical locations on the scaling exponent b have not been systematically investigated.

Trees have a remarkable range of shapes and sizes. Plant size, which can be indexed by age, DBH, or height, is a fundamental aspect of their biology and affects almost all other characteristics (Thomas, 1996; Brown et al., 2004; Cheng et al., 2009). There are strong reasons to expect systematic relationships between ecophysiological characteristics and plant stature. Tree size determines biomechanical requirements for structural support (Niklas, 1994; Thomas, 1996) and exerts a significant influence on plant form, function and life history (Niklas, 1994; Kerkhoff and Enquist, 2006). It has been reported that forest aboveground productivity declines in aging stands, even as biomass increases (Ryan and Waring, 1992; Gower et al., 1996; Berger et al., 2004), which may result in a fundamental change in the relationship between tree productivity and biomass. Enquist et al. (2007) analyzed the scaling relationship between leaf biomass and total biomass and found that small trees have a larger scaling exponent than larger trees. A similar conclusion was reached by Cheng et al. (2010) in a study based on 46 larger trees from China and Japan. In addition, abiotic factors such as climate play an important role in plant growth and productivity (Knapp and Smith, 2001; Raich et al., 2006). As climatic factors are linked to location, trees growing at different latitudes, longitudes or elevations may have different relationships between productivity and biomass. Thus, analyses of size- and location-related variation in the statistical parameters governing tree productivity and biomass patterns are needed (Cheng et al., 2009).

In this paper, we took advantage of a forest productivity and biomass database based on a data management system developed by Tang et al. (1999). The latest update of the database was in 2007. The database includes tree productivity and biomass, and other derivative information such as elevation, altitude and longitude, covering a wide range of forests in China. We attempted to (1) estimate mean and variation of tree productivity and biomass in China; (2) develop an overall relationship of forest productivity and biomass using both a linear regression model and a power function; and (3) determine if the relationship varies with certain biotic factors (i.e. age, size of trees) and abiotic factors (i.e. latitude, longitude and elevation).

2. Materials and methods

2.1. Tree productivity and biomass database

The database was developed by Dr. Hai Ren and his colleagues at the South China Botanical Garden, Chinese Academy of Sciences, Guangzhou, China (Tang et al., 1999). The data were collected from journal publications and inventory reports of tree productivity and biomass studies in China up to 2007. The database includes 6153 records, ranging from 18.1 to 53.2 N latitude, 11.53 to 131.8 E longitude, and between elevations of 7–4240 m above sea level. Each record includes the site name, source of reference, latitude, longitude, elevation, tree age, height, DBH, density of trees, above- and below-ground productivity and biomass, as well as different component (i.e. leaf, stem, branch, and root) measures of productivity and biomass. The "standard tree" method was most commonly used for productivity and biomass measurements. First, quadrates (plots) were established for each site before sampling. For plantations, eight or more 10×10 m plots were established. For natural forests, at least twenty 10×10 m plots were established. Height and DBH of each individual tree as well as the total number of individuals in each plot were recorded. Second, five to seven standard trees for each species within a plot were selected for cutting and weighing of the component parts. The selection of a tree was based on the height and DBH measured above. Three individuals with mean sizes, one or two smaller trees, and one or two bigger trees were selected. The stems, branches and leaves of the standard trees were weighed respectively. The coarse roots of the tree were dug and weighed and the fine roots were estimated. Some of the different component parts of standard trees were taken back to laboratory and dried for calculating the rate of dry to fresh weights. Total biomass was then calculated based on total tree numbers. The biomass was either measured directly by harvesting standing vegetation or estimated using the regression techniques considering DBH and/or height. Net primary productivity of the tree was estimated by adding annual increments of tree leaf, stem, branch and root, respectively. The detailed description of the methodology of biomass measurement and production estimation for the database can be found in Luo (1996), Tang et al. (1999) and Ni et al. (2001).

2.2. Data analysis

In this study, we focused on the relationship between productivity and biomass and how tree age, size and location (latitude, longitude, and elevation) influence the relationship. The total productivity and biomass were calculated as total productivity and biomass of stem, leaf, branch, and root.

We applied two models to determine the relationship between productivity and biomass of forests in China. The first was a linear regression model: $P = a + bM$; where a and b were intercept and slope of the linear regression. Slope b indicates that productivity will increase b t ha^{-1} year^{-1} on average when biomass increases by 1 t ha^{-1}. The second was an allometric model (i.e. power function): $P = aM^b$. To facilitate the comparison of model parameters with other studies, we used reduced major axis (RMA) regression analyses to estimate the scaling exponents and normalization constants (Hui and Jackson, 2007). When the power function was linearized using a log transformation, the scaling exponent b was the slope in the log–log linear regression model.

To detect the influence of tree age, size and geographical location on the relationship between productivity and biomass, we split the entire database into 8 groups, each with a similar sample size. We achieved this by finding the 12.5, 25, 37.5, 50, 62.5, 75,
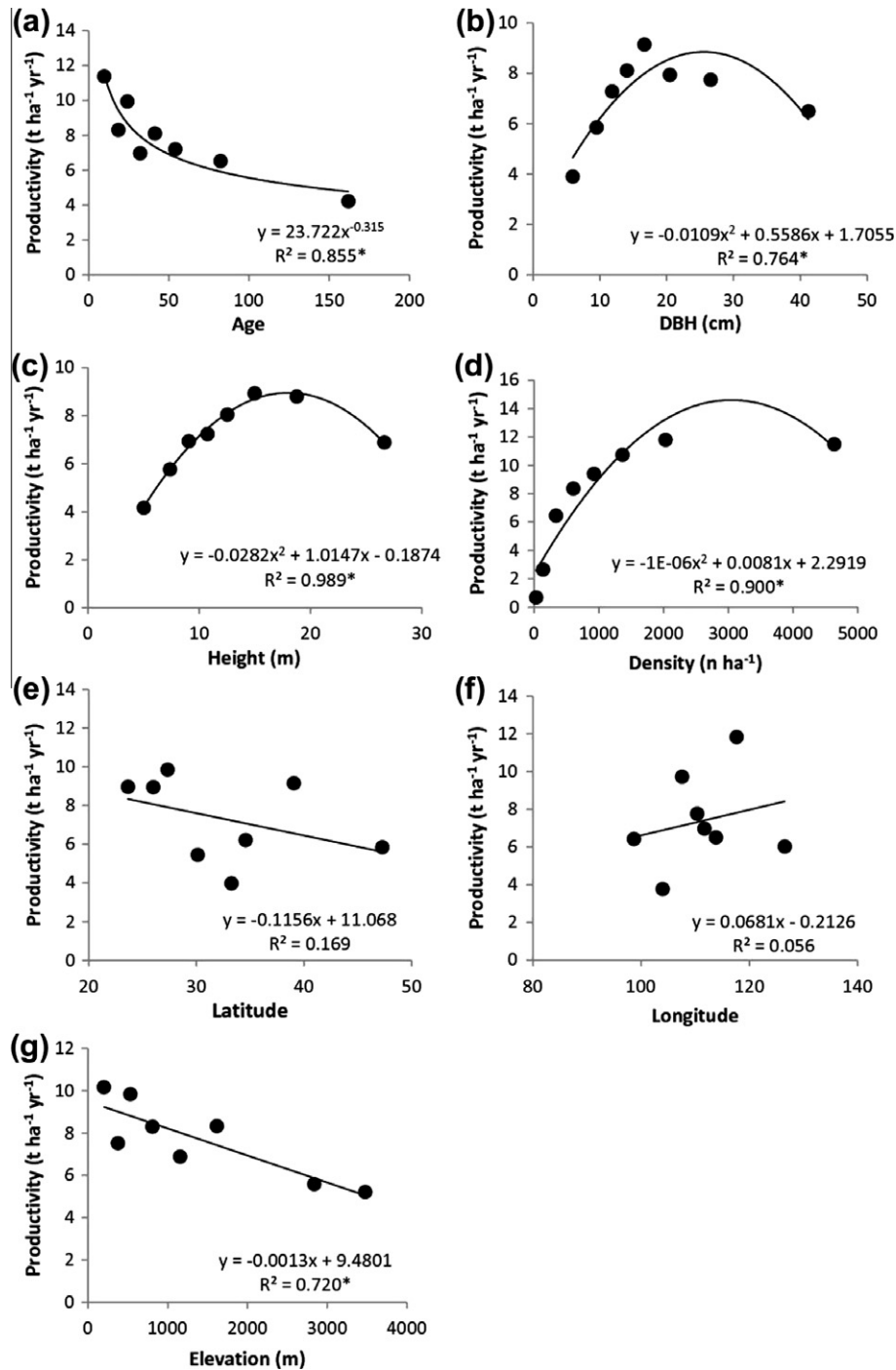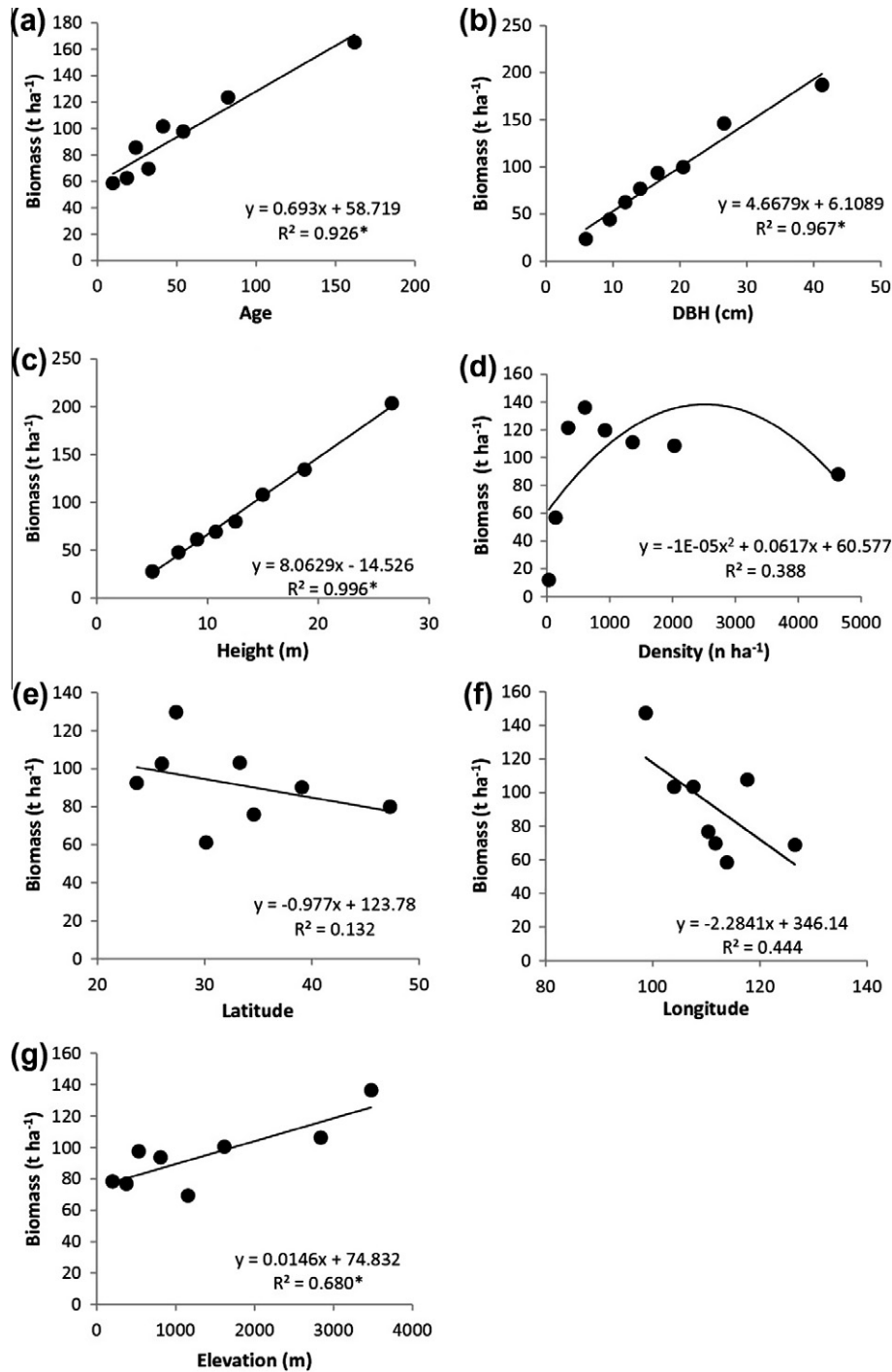
Fig. 1. Relationships between tree productivity and tree age (a), diameter at breast height (DBH, b), height (c), density (d), latitude (e), longitude (f), and elevation (g). The model with the best fit among the linear, quadratic and power function models is presented. * indicates that the model is significant at $\alpha = 0.05$ level. Error bars are too small to be shown.

and 87.5 percentiles and grouped observations into these 8 groups. For example, the corresponding ages for the percentiles above were 15, 20, 28, 35, 47, 60, and 110, respectively. Group 1 included 804 trees with age younger than or equal to 15 years. Group 2 included 756 trees with ages older than 15 years, but younger than or equal to 20. Similarly, group 8 included 730 trees with age older than 110 years. Due to missing productivity or biomass measurements, the sample size for each group was not exactly the same. Those records with unknown ages were grouped into one group and not used in further analysis. The sample procedure was applied to size (i.e. DBH, height, and density) and location (i.e. elevation,

latitude, and longitude). We calculated mean values for productivity and biomass and the corresponding group variables (age, size, or location) for each group. The relationships between productivity and biomass with group variables were developed (Figs. 1 and 2).

The relationship between productivity and biomass for the whole database and for each age, size, or geographical location group was estimated using both linear regression and the allometric scaling method as described above. We further developed the relationship of the regression slope or scaling exponent with mean age, size, density, latitude, longitude, and elevation by fitting the best of a linear, quadratic or power function equation. All data

Fig. 2. Relationships between tree biomass and tree age (a), diameter at breast height (DBH, b), height (c), density (d), latitude (e), longitude (f), and elevation (g). The model with the best fit among the linear, quadratic and power function models is presented. * indicates that the model is significant at $\alpha = 0.05$ level. Error bars are too small to be shown.

analyses were conducted using SAS 9.1 (SAS Inc., Cary, NC; Hui and Jiang, 1996).

3. Results

3.1. Means and variations of tree productivity and biomass in China

Tree productivity in the database varied greatly, ranging from 0.04 to 68.36 t ha^{-1} year^{-1}, with a mean value of 7.59 t ha^{-1} year^{-1} and a standard deviation of 7.13 t ha^{-1} year^{-1}. Aboveground productivity accounted for 88.27% of total productivity. Large variations in productivity were found among different age groups, tree sizes and locations. Tree productivity decreased with tree age following a power function (Fig. 1). Significant quadratic equations were developed for the relationship between tree productivity and DBH, height, and tree density. Tree productivity increased with tree size and density, reached the maximum values and then decreased for large trees and high density. Productivity showed no significant patterns with latitude and longitude, but decreased with elevation. Note that productivity monotonically declined with
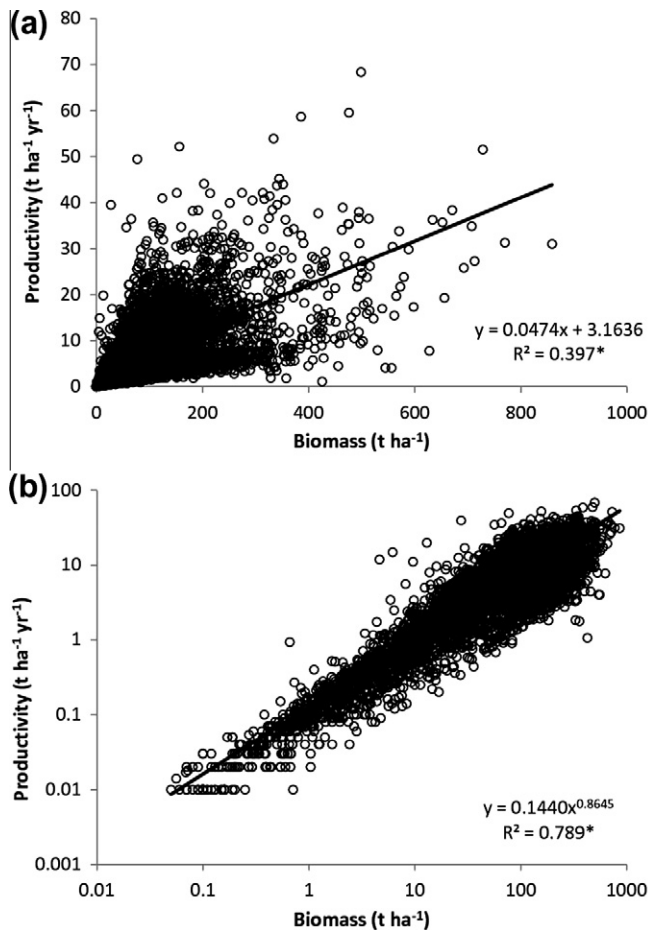
Fig. 3. Relationships between tree productivity and biomass in China. Both linear regression models (a) and allometric relationship models (power function) (b) were fitted for the data. Reduced major axis (RMA) regression analysis was applied to derive parameters for the power function. * indicates that the model is significant at $\alpha = 0.05$ level.

age, but not with size measurements (height and DBH). This apparent contradiction arises from the fact that all trees in an age group are not the same size and this lack of a close correlation between specific sizes and specific ages permits different relationships between productivity and size or age.

Tree biomass also showed large variation similar to tree productivity. The mean value of tree biomass was 95.32 t ha^{-1} with a standard deviation of 96.72 t ha^{-1}. Biomass ranged from 0.02 to 858.95 t ha^{-1}. Aboveground biomass contributed most to total biomass (80.91%). But the responses of tree biomass to age, size and location were quite different from tree productivity. Tree biomass linearly increased with tree age, DBH and height (Fig. 2). There was no significant relationship between biomass with tree density. The influence of geographical location on biomass was not quite clear. Biomass tended to decline with latitude and increased with longitude, but increased significantly with elevation.

3.2. Relationships between tree productivity and biomass in China

Both the linear regression and the allometric model (power function) were fitted to the relationship between tree productivity and biomass (Fig. 3). Both equations were statistically significant, but the power function explained more of the total variation. As in many data synthesis studies, there was significant variation in the data. Based on the linear regression model, tree productivity linearly increased with tree biomass, on average, by 0.0474 t ha^{-1} year^{-1}

as tree biomass increased by 1 t ha^{-1}. About 40% of the total variation of tree productivity could be explained by the biomass alone.

When converted into logarithm scales, a better linear regression equation ($\log P = \log a + b \times \log M$) was found for tree productivity and biomass (Fig. 3). The scaling exponent of the allometric equation was 0.8645 ± 0.010.

3.3. Influences of tree age, size and geographical location on the relationship between productivity and biomass in China

To detect the influences of the biotic (i.e., tree age, size and density) and abiotic factors (i.e. latitude, longitude, and elevation) on the relationships between tree productivity and biomass, we developed both linear equations and power functions for each age, DBH, height, density, latitude, longitude, and elevation groups. All 112 equations were significant. The mean value of the coefficient of determination (r^2) for the linear regression model was 0.590 with a range of 0.224–0.918. Forty-one equations of the 56 equations had r^2 values larger than 0.5. The mean value of r^2 for the power functions was 0.625 with a range of 0.298–0.920. Forty-five of the 56 equations had r^2 values larger than 0.5.

Since the slope of the linear regression model and the scaling exponent of the power function model reflect the direct influence of biomass on tree productivity, we focused on how these two parameters were influenced by biotic and abiotic factors. The linear regression slope showed significant relationships with all factors except latitude (Fig. 4). Slope decreased with tree age following a power function, but linearly decreased with tree size (i.e. DBH and height) and tree density. A significant quadratic equation was developed between slope and longitude. The slope also decreased with elevation following a power function.

The scaling exponent showed slightly different relationships with the biotic and abiotic factors, compared to the slope of the linear regression (Fig. 5). Significant quadratic equations were developed for the scaling exponent with age, height, and density, but not DBH. There was also no significant relationship between the scaling exponent and latitude. The scaling exponent linearly increased with longitude, but decreased with elevation.

4. Discussion

Based on a large database of tree productivity and biomass in China, we derived the relationship between tree productivity and biomass using both linear regression and allometric equations. We found both the linear regression model and the power function provided statistically significant fits, confirming the results of previous studies (Whittaker and Likens, 1973; Cheng et al., 2009). The most interesting finding was that, when splitting the whole database into different tree age, size, density, latitude, longitude, and elevation groups, the slope of the linear regressions and the scaling component of allometric equations varied with most biotic (i.e., tree age, size, and density) and abiotic factors (i.e. longitude and elevation). These results demonstrate, for the first time to our knowledge, that the scaling exponent and slope of the relationship between tree productivity and biomass are not constants but vary with biotic and abiotic factors. Tree size and location matter in terms of their influences on the relationship between tree productivity and biomass.

The database used in this study is the largest database reported so far from China. This type of database is very helpful, as it provides an opportunity to develop relationships among different variables and validate modeling approaches. For example, a database of metabolic rate and body mass of mammals has been used to both validate and refute the allometry scaling law, and to parameterize ecological models (Savage et al., 2004; White and
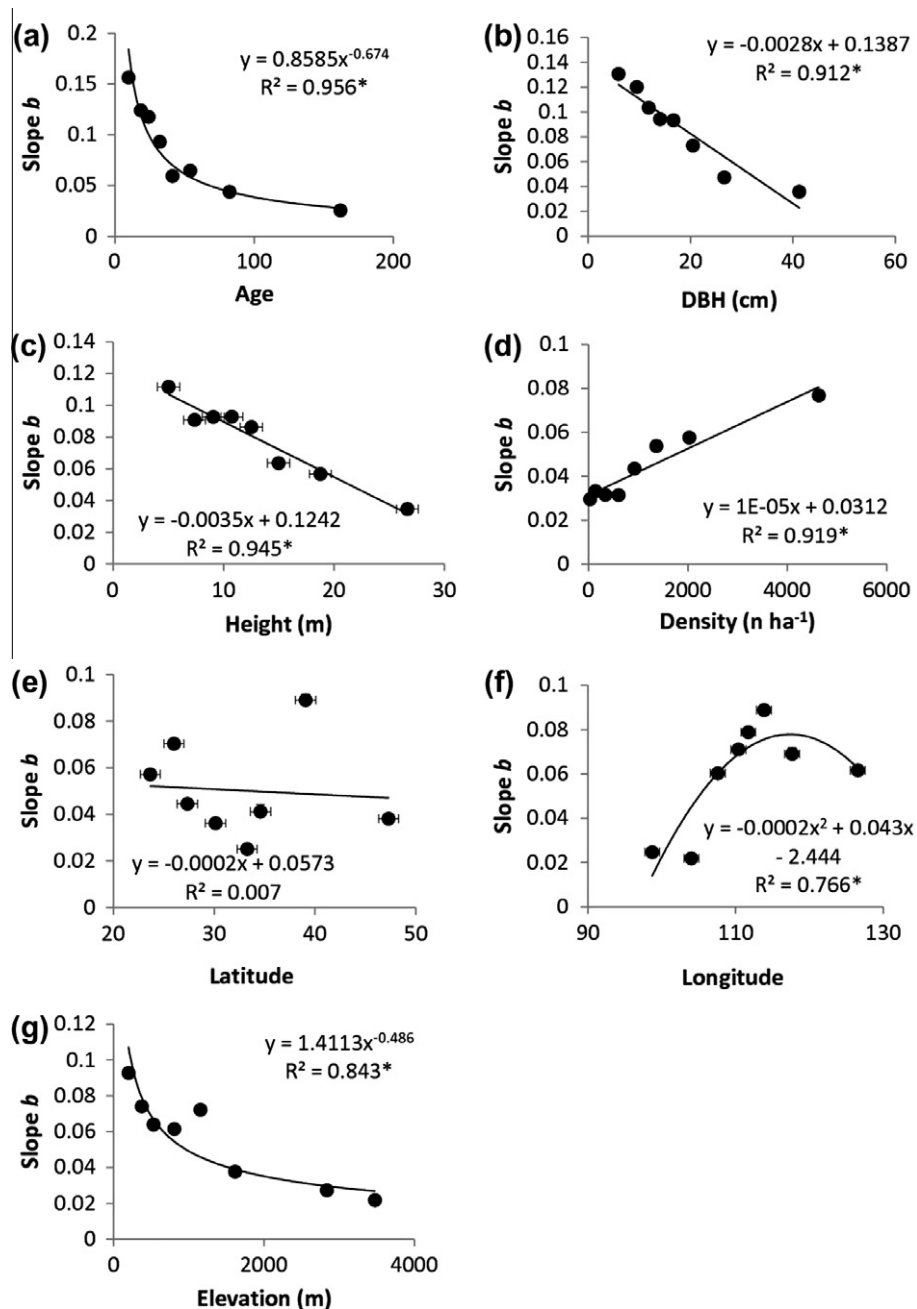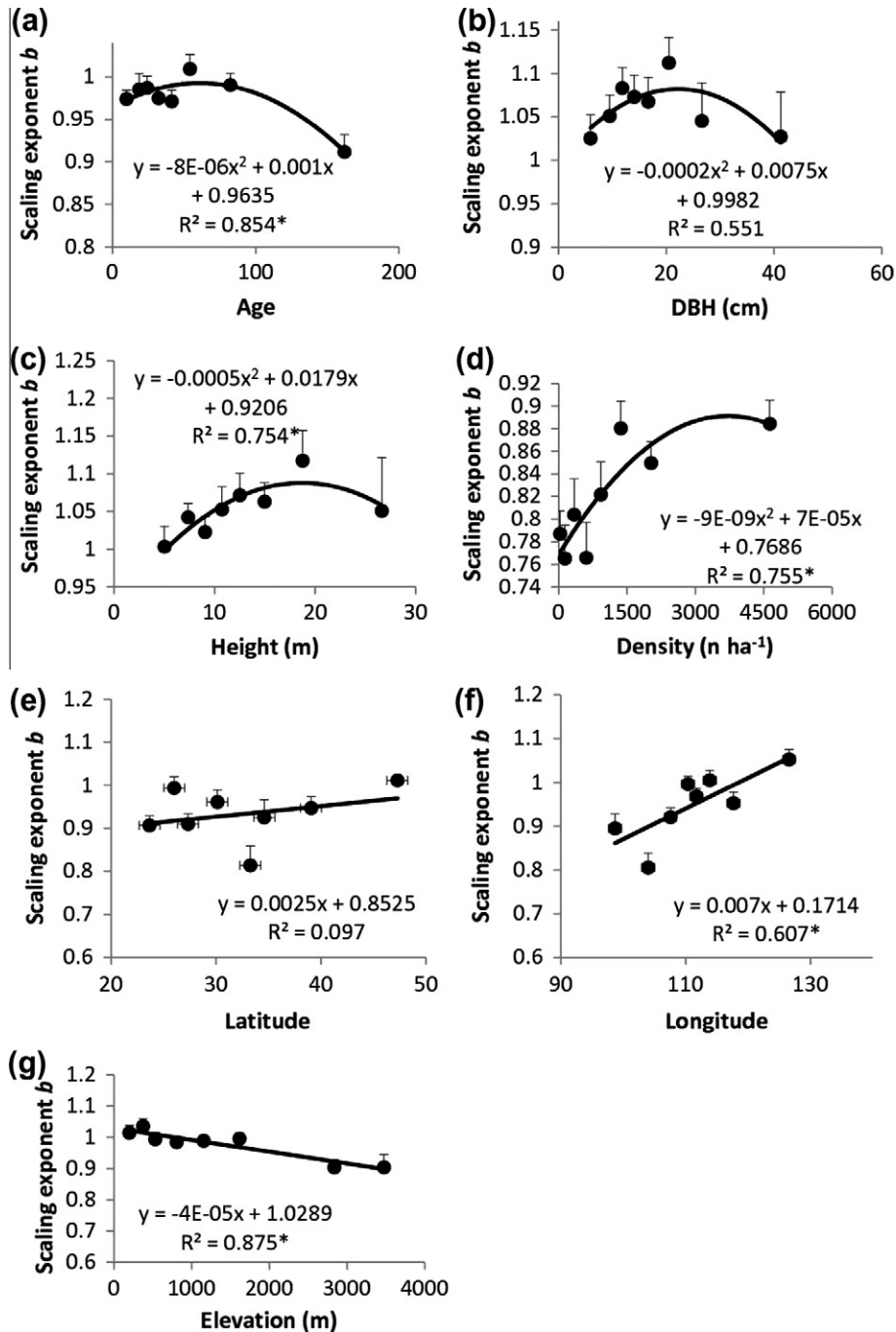
Fig. 4. Relationships between regression slope and tree age (a), diameter at breast height (DBH, b), height (c), density (d), latitude (e), longitude (f), and elevation (g). The slope of each age, DBH, height, density, latitude, longitude, and elevated group was estimated using linear regression method. The model with the best fit among the linear, quadratic and power function models is presented. * indicates that the model is significant at $\alpha = 0.05$ level. Error bars are standard errors of the slopes.

Seymour, 2005; Hui and Jackson, 2006). Li et al. (2005) used a Chinese forest biomass dataset of 1266 records and developed the relationship between productivity and biomass using a power function. They reported that the scaling exponent varies among 17 different forest types. The overall scaling exponent for all data was 0.715. The slope varied from 0.430 in a boreal pine forest ($n = 10$) to 1.104 in a sclerophyllous evergreen forest ($n = 9$), but the confidence intervals are large due to the small sample sizes that resulted when the whole dataset was split into different forest types. Cheng and Niklas (2007) developed allometric relationship between biomass and its components (i.e. leaf, stem, branch) using the same database. Genet et al. (2011) recently used a large database of 670 trees to study the allometric relationship among biomass components and found that allometric parameters vary

with stand age. The database used in this study was more comprehensive. The large number of records in the database also allowed us to split the whole database into different groups and still have a large sample size for each group, thus enabling us to test if the relationships vary among them.

We found that tree productivity and biomass were significantly influenced by most of the biotic and abiotic factors investigated, but in different patterns. For example, productivity decreased with age, but the biomass increased with age. A similar result of primary productivity was reported by Ni et al. (2001) who found a weak negative relationship between productivity and age. The relationship was much stronger in this study as the data were binned according to age groups. The increase of biomass with age has been reported in many studies (e.g. Cienciala et al., 2008; Cheng et al.,

Fig. 5. Relationships between scaling exponent and tree age (a), diameter at breast height (DBH, b), height (c), density (d), latitude (e), longitude (f), and elevation (g). The scaling exponent of each age, DBH, height, density, latitude, longitude, and elevated group was estimated using reduce major axis (RMA) regression analysis. The model with the best fit among the linear, quadratic and power function models is presented. * indicates that the model is significant at α = 0.05 level. Error bars are standard errors of the scaling exponents.

2010), as biomass accumulates as trees grow. Both productivity and biomass initially increased with tree DBH and height. However, productivity declined when the trees became too large, while biomass linearly increased with tree size. Productivity and biomass showed no or a weak relationship with geographical factors (latitude, longitude and elevation). Productivity decreased with elevation, probably due to tree species difference. Biomass increased with elevation for reasons which are not quite clear. We also found that aboveground productivity and biomass accounted for high percentages (88.27% and 80.91%, respectively) of the total productivity and biomass. These values could be overestimated, as

belowground root biomass was difficult to measure accurately. The mean values of tree productivity and biomass were also reasonable compared to the ranges of forest productivity and biomass in the world (Lieth and Whittaker, 1975), and those in China (Ni et al., 2001).

The overall slope of the linear regression equation found in this study was 0.0471. This value was larger than that estimated by Whittaker and Likens (1973) who reported a slope of 0.016 (calculated as 1/0.625/100), but much smaller than the value estimated by Keeling and Phillips (2007) which ranged from 0.1277 to 0.1597 based on data selection (excluding outliers or not) using

global above-ground net primary productivity and above-ground biomass. It should be noted that the coefficient of determination in Keeling and Phillips (2007) ranged from 0.02 to 0.24. Using a quadratic model improved model fit, due to the inclusion of tropical rain forests. In this study, as there was no rain forest data included, we found that a linear regression model was adequate. Using a quadratic model did not significantly improve our model fit. Our overall result was more comparable with Ni et al. (2001) who reported a slope of 0.024 using 670 stands from 17 forest types in China. The slope increased to 0.045 when comparison was made over 17 forest types. When separated into different groups, we found that the slope decreased with age following a power function, and linearly decreased with tree height and DBH. The results were consistent with the observation that growth rates of forests decline with age (Cheng et al., 2009). As trees grow older and larger, the relative contributions of photosynthetic biomass to nonphotosynthetic biomass also decline. Nutrient availability may not satisfy growth demand and may also limit growth (Gower et al., 1996; Peterson et al., 1999; Raich et al., 2006; Cheng et al., 2009). Slope increased with tree density, as density was usually negative related to plant size and biomass. There was no significant relationship between slope and latitude, but slope increased with longitude. Slope also decreased with elevation similar to age, probably due to slow growth of trees at high elevation.

The estimation of the scaling exponent of productivity and biomass in previous studies also varied remarkably. We estimated the overall scaling exponent as 0.8645. Li et al. (2005) reported an overall scaling exponent for all data is 0.715. Niklas and Enquist (2001) found a scaling exponent of 0.791 for productivity and biomass in terrestrial plants. Brown et al. (2004) and Savage et al. (2004) reported a scaling exponent of 0.759 for biomass production versus mass in plants. The scaling exponents also varied at individual and community levels. Using data from 46 sites including tropical, temperate forests and grasslands, and arctic tundra, Kerkhoff and Enquist (2006) derived the scaling component of nutrient stocks and primary productivity. They found that productivity varied allometrically with total biomass, with a scaling exponent of 0.46, which is much smaller than that from the individual level. These results indicated that the regression slope or scaling exponent may vary with different samplings, regions and vegetation types.

The scaling exponent of the scaling relationship has often been considered to be the result of universal physical constraints, whereas intercepts of these relationships, and individual species deviations from them, have been attributed to various taxon-specific or ecological factors (Daan and Tinbergen, 1997; Kizlowski et al., 2003; Glazier, 2010). According to this view, ecological factors would have little influence on the exponent of metabolic scaling. For example, Cermeňo et al. (2006) found that the scaling exponent of population abundance and cell volume in marine pelagic ecosystems does not change between two locations and among resource environments (different oceanographic regions indicated by different latitude ranges); only the regression intercept varies among regions with different productivities. But great diversity in metabolic scaling exponents may exist, and little of which has already been linked to ecological differences (Glazier, 2005; Killen et al., 2008; McNab, 2008, 2009; Mulder et al., 2011). Cheng et al. (2009) reported both scaling exponent and intercept decrease with stand age ($b = -0.001$ age + 0.982, $r^2 = 0.576$ and $a = -0.002$ age – 0.898, $r^2 = 0.313$). This study provided a more systematic analysis of both biotic and abiotic factors. Our results showed that the scaling exponent increased with age, height, and tree density, reached maximum values and declined later, following quadratic patterns. One of the potential reasons might be that when trees were very young and small, productivity increased fast as tree biomass grew. Productivity declined as trees grow older and larger. The decline

of productivity with age has been attributed to changes in photosynthesis with stand development, nutrient supply, respiration, carbon allocation, and hydrological function (Gower et al., 1996; Ryan et al., 1997, 2004; Wang et al., 2011).

5. Conclusions

Using a massive forest database with 6153 records collected in China, we developed the relationships between forest productivity and biomass with both a linear regression model and an allometric equation. Either the linear regression model or the allometric equation could be used to estimate tree productivity based on biomass in Chinese forests. For the first time, to the best of our knowledge, we demonstrated that the slope of the linear regression varied with tree age, size, density, longitude and elevation. The scaling component also varied with tree size and elevation. These results indicated that the scaling exponent and slope of tree productivity and biomass are not constant, but vary with certain biotic and abiotic factors. Fitting a single line through the overall dataset may yield a misleading value for the slope (Martin et al., 2005; Marañón, 2008). While the whole dataset showed a significant relationship between productivity and biomass, size-specific relationships should be considered in order to better predict productivity based on tree biomass. Including tree age or size into the regression models will help improve the prediction of productivity.

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