

POLISH JOURNAL OF ECOLOGY (Pol. J. Ecol.)	57	3	441–449	2009
--	----	---	---------	------

*Regular research paper*

Dong-Liang CHENG,<sup>1</sup> Gen-Xuan WANG<sup>2\*</sup>, Quan-Lin ZHONG<sup>1\*</sup>

<sup>1</sup> College of Geographical Sciences, Fujian Normal University, Fuzhou, Fujian Province 350007, China

<sup>2</sup> College of Life Sciences, Zhejiang University, Hangzhou, Zhejiang Province 310027, China

\*e-mails: wanggx@zju.edu.cn, qlzhong@126.com (*corresponding authors*)

## AGE-RELATED RELATIONSHIP BETWEEN ANNUAL PRODUCTIVITY AND BODY SIZE OF TREES: TESTING THE METABOLIC THEORY

**ABSTRACT:** Metabolic theory of ecology predicts a  $3/4$  power relationship between annual productivity  $P_T$  and body size  $M_T$  (i.e.,  $P \propto M^{3/4}$ ), which has important implications to estimates of carbon fluxes, ecosystem health, global carbon budgets, and a variety of other phenomena. To test this prediction, we examined a large dataset for Chinese forests. Such dataset covers six major forest biomes and a total of 17 forest types grown across a range of annual temperature ( $-6.6$  to  $25.2^\circ\text{C}$ ), mean annual rainfall (27 to 2989 mm), elevation (10 to 4240 m a.s.l.), and stand age (3 to 350 yrs.). Reduced major axis (RMA) regression analyses were used to compare the  $P_T$  versus  $M_T$  scaling exponents and normalization constants (i.e., slopes and  $Y$ -intercepts of log-log linear relationships, respectively). Comparisons were made for ten different age-sequences (stand age ranges from 20 to 200 yrs). When stand age was less than 100 yrs, relationship of  $P_T$  versus  $M_T$  had similar scaling exponents ( $\alpha_{\text{RMA}} \approx 1.0$ ), while the  $Y$ -intercepts decreased systematically. When stand age exceeded 140 yrs, scaling exponents decreased ( $\alpha_{\text{RMA}} < 0.86$ ). Both the aboveground annual productivity and aboveground body size per individual tree ( $P_A$  and  $M_A$ , respectively) showed the same behavior. We therefore conclude that the relationship of  $P_T$  versus  $M_T$  systematically declined with the stand age, and was inconsistent with the predictions of metabolic theory.

**KEY WORDS:** age-sequence, annual productivity, community resource use, metabolic theory of ecology

### 1. INTRODUCTION

Body size is recognized as an important factor which affects almost all characteristics of organisms (Brown *et al.* 2004). Most size-related variation can be described by allometric equations of the form:  $Y = Y_0 M^b$ , where  $Y$  is the dependent variable,  $M$  is body mass,  $Y_0$  is a normalization constant,  $b$  is a scaling exponent (Calder 1984, Niklas 1994, Brown *et al.* 2004, Marquet *et al.* 2005). Furthermore, many studies have demonstrated that  $b$  takes on a limited set of values, which are typically simple multiples of  $1/4$ , they include lifespan ( $b \approx 1/4$ ), heart rate ( $b \approx 1/4$ ), population density ( $b \approx -3/4$ ), or growth rate ( $b \approx -1/4$ ). The best-known of these scaling laws is Kleiber's law, which showed that metabolic rates of mammals and birds scale as the  $3/4$  power of body mass (Kleiber 1932). Subsequent research found that this  $3/4$  slope can be applied virtually all animal species (e.g. Peters 1986).

Recently, West, Brown and Enquist presented a general theoretical framework for explaining such allometric scaling laws in biology based on geometric and biophysical principles (West *et al.* 1997, 1999a, b, 2001, Brown *et al.* 2004). The model includes body size or volume which imposes the geometric constraints on biological exchange surfaces and distribution networks that transport resources from surface to the other parts of the body (Enquist 2003, Brown *et al.* 2004). Consequently, organisms tend to obey a common set of 'quarter-power' scaling relationships with body mass or volume (West *et al.* 1997, 1999a, b, 2001). An important allometric scaling relationships predicted by this general framework has been that metabolic rates of plants,  $B$ , scale with their size  $M$  as a  $3/4$  power law ( $B \propto M^{3/4}$ ) (West *et al.* 1997, 1999a, b, Enquist *et al.* 1998, Brown *et al.* 2004). Furthermore, because rates of biomass production are intimately dictated by metabolic rates  $B$ , annual productivity  $P$  are expected to be directly proportional to  $B$  ( $P \propto B$ ) such that  $P \propto M^{3/4}$  (West *et al.* 1999a, Enquist *et al.* 1998, 1999, Niklas and Enquist 2001, Ernest *et al.* 2003).

However, Reich *et al.* (2006a) demonstrate that plant metabolic rates (measured as the whole plant dark respiration) failed to fit the  $3/4$  slope predicted by metabolic scaling theory. Rather, they demonstrated that metabolic rates scaled isometrically with plant mass across the six orders of magnitude in mass that they tested. Interestingly, a theoretical question is brought if metabolic rates changing in direct proportion to variations in plant mass can be extend from the size of tree saplings to mature trees, i.e. the annual productivity  $P$  are expected to be directly proportional to  $B$  ( $P \propto B$ ) such that  $P \propto M$ . Furthermore, a number of authors argued that forest level aboveground production declined in ageing stands, while, the biomass increased (Ryan and Waring 1992, Gower *et al.* 1996, Berger *et al.* 2004), which may result in a systemically change for the relationship between average  $P$  and  $M$ . Thus, analyses of age-related variation in the statistical parameters governing annual productivity  $P$  and body size  $M$  patterns are highly needed.

Here, we report the relationship between annual productivity and body size in a chro-

nosequence by using a biomass dataset including 1266 plots of 17 main forest types across China. These data were divide into ten groups in terms of stand age and showed that the scaling exponent of the relationship of  $P$  vs.  $M$  was unity (i.e.  $\alpha_{\text{RMA}} \gg 1$ ) at the early stage (i.e. age less than 100 years) and systematically declined with the stand age.

## 2. MATERIAL AND METHODS

We tested our predictions by using the Luo (1996) compendium for standing community biomass and productivity. Most of these data came from inventories of the Forestry Ministry of China between 1989 and 1993. Additional data were collected and sorted from published forest reports, as well as over 60 Chinese journals (Acta Botanica Sinica, Acta Phytoecologica Sinica, Acta Ecologica Sinica, Chinese Journal of Ecology, Forestry Science of China etc.), and some unpublished literature in the past 20 yrs over China (Li *et al.* 2005).

These data covered six major forest biomes and a total of 17 forest types across China (e.g., boreal or boreal/alpine forests dominated by *Larix*, *Picea-Abies*, or *Pinus sylvestris* var. *mongolica*; temperate forests dominated by *Pinus koraiensis* or typical deciduous broadleaved species; and tropical rainforest and monsoon forests). Mean annual temperature ranges from  $-6.6$  to  $25.2^\circ\text{C}$ ; mean annual rainfall ranges from 27 to 2989.1 mm per year, elevation ranges from 10 to 4240 m a.s.l.; stand age varies from 3 to 350 yrs. The broad coverage of the data set allowed us to quantify the age-dependend relationship between annual productivity and body size.

The dataset includes stand biomass (metric tons of dry matter per hectare), density (number of plants per hectare), and annual production rate (metric tons of dry matter per hectare per yr) for trees, as well as – where available – information on the components of biomass and productivity (i.e. stem, leaf, branch and root, respectively) (Luo 1996). A more detailed description of the methodology of biomass measurement and annual production estimate for the dataset can be found in Ni *et al.* (2001). Subsequently, total forest biomass  $M_T$  (kg dry matter per plant) and total annual productivity  $P_T$  (kg dry matter per

plant per yr) were calculated as the ratio of total standing biomass or total net production to plant density, respectively (see Niklas and Enquist 2001). Given that some authors indicated that there is a systematic underestimate of root biomass with increasing plant size (e.g. Niklas 2005), we also computed the aboveground biomass  $M_A$  and productivity  $P_A$ . Leaf biomass  $M_L$  and nonphotosynthetic organs biomass  $M_N$  (stem, branch and root) were computed from the quotation of total

biomass allocated to each organs and plant density. In the present paper, the dataset were divided into ten age-sequences according to the stand age (20 yr intervals). For example, the 20 age group contains the samples age ranges from 3 to 20 (Tables 1, 2 and 3). In the last groups stand age ranges from 181 to 350 yr. because of the smaller number of samples in this age range, we sorted these data into one 200 yr group.

Table 1. Reduced major axis regression slopes and Y-intercepts ( $\alpha_{\text{RMA}}$  and  $\log \beta_{\text{RMA}}$ , respectively) for  $\log_{10}$ -transformed data of total annualized biomass production rates  $P_T$  (kg dry matter plant<sup>-1</sup> yr<sup>-1</sup>) and total biomass  $M_T$  (kg dry matter plant<sup>-1</sup>) with a age-sequences. Data taken from Luo (1996).

Stand age (yr)	Sample size	$\alpha_{\text{RMA}}$ (95% CI)	$\log \beta_{\text{RMA}}$ (95% CI)	$r^2$
20 (3–20)	112	0.949 (0.895, 1.003)	-0.751 (-0.841, -0.661)	0.908
40 (21–40)	387	0.952 (0.927, 0.977)	-0.887 (-0.934, -0.841)	0.930
60 (41–60)	356	0.937 (0.910, 0.964)	-0.967 (-1.022, -0.912)	0.924
80 (61–80)	126	0.894 (0.839, 0.948)	-0.938 (-1.061, -0.815)	0.883
100 (81–100)	75	0.955 (0.870, 1.040)	-1.214 (-1.427, -1.001)	0.854
120 (101–120)	55	0.915 (0.806, 1.024)	-1.196 (-1.482, -0.911)	0.814
140 (121–140)	50	0.923 (0.805, 1.042)	-1.305 (-1.612, -0.999)	0.804
160 (142–160)	46	0.786 (0.686, 0.887)	-0.991 (-1.260, -0.722)	0.824
180 (161–180)	30	0.802 (0.627, 0.977)	-1.048 (-1.517, -0.579)	0.682
200 (181–350)	29	0.860 (0.687, 1.032)	-1.237 (-1.733, -0.741)	0.742
All data	1266	0.715 (0.696, 0.734)	-0.534 (-0.575, -0.493)	0.766

Table 2. Reduced major axis regression slopes and Y-intercepts ( $\alpha_{\text{RMA}}$  and  $\log \beta_{\text{RMA}}$ , respectively) for  $\log_{10}$ -transformed data of aboveground annualized biomass production rates  $P_A$  (kg dry matter plant<sup>-1</sup> yr<sup>-1</sup>), and aboveground biomass  $M_A$  (kg dry matter plant<sup>-1</sup>) with age-sequences. Data taken from Luo (1996).

Stand age (yr)	Sample size	$\alpha_{\text{RMA}}$ (95% CI)	$\log \beta_{\text{RMA}}$ (95% CI)	$r^2$
20 (3–20)	112	0.938 (0.886, 0.989)	-0.714 (-0.795, -0.633)	0.916
40 (21–40)	387	0.941 (0.916, 0.965)	-0.840 (-0.884, -0.797)	0.932
60 (41–60)	356	0.923 (0.894, 0.952)	-0.904 (-0.959, -0.848)	0.911
80 (61–80)	126	0.889 (0.832, 0.947)	-0.893 (-1.018, -0.767)	0.867
100 (81–100)	75	0.955 (0.866, 1.045)	-1.180 (-1.395, -0.965)	0.838
120 (101–120)	55	0.904 (0.793, 1.014)	-1.134 (-1.415, -0.854)	0.803
140 (121–140)	50	0.895 (0.773, 1.016)	-1.203 (-1.504, -0.901)	0.783
160 (142–160)	46	0.756 (0.655, 0.857)	-0.896 (-1.158, -0.634)	0.807
180 (161–180)	30	0.774 (0.604, 0.944)	-0.954 (-1.395, -0.514)	0.678
200 (181–350)	29	0.839 (0.668, 1.010)	-1.149 (-1.623, -0.675)	0.734
All data	1266	0.717 (0.699, 0.736)	-0.529 (-0.568, -0.491)	0.774

Table 3. Reduced major axis regression slopes and Y-intercepts ( $\alpha_{\text{RMA}}$  and  $\log \beta_{\text{RMA}}$ , respectively) for  $\log_{10}$ -transformed data of photosynthetic biomass  $M_L$  (kg dry matter plant<sup>-1</sup>) and nonphotosynthetic biomass  $M_N$  (kg dry matter plant<sup>-1</sup>) with a age-sequences. Data taken from Luo (1996).

Stand age (yr)	Sample size	$\alpha_{\text{RMA}}$ (95% CI)	$\log \beta_{\text{RMA}}$ (95% CI)	$r^2$
20 (3–20)	112	1.016 (0.886, 1.147)	-1.095 (-1.308, -0.883)	0.540
40 (21–40)	387	1.007 (0.950, 1.065)	-1.249 (-1.354, -1.143)	0.674
60 (41–60)	356	0.952 (0.897, 1.006)	-1.123 (-1.233, -1.013)	0.698
80 (61–80)	126	0.873 (0.785, 0.961)	-0.974 (-1.171, -0.777)	0.680
100 (81–100)	75	0.953 (0.827, 1.079)	-1.253 (-1.565, -0.941)	0.679
120 (101–120)	55	1.020 (0.894, 1.146)	-1.441 (-1.768, -1.113)	0.801
140 (121–140)	50	0.882 (0.695, 1.069)	-1.103 (-1.582, -0.625)	0.468
160 (142–160)	46	0.670 (0.547, 0.793)	-0.590 (-0.918, -0.262)	0.637
180 (161–180)	30	0.702 (0.517, 0.888)	-0.678 (-1.173, -0.183)	0.533
200 (181–350)	29	0.854 (0.682, 1.026)	-1.094 (-1.585, -0.602)	0.741
All data	1266	0.852 (0.829, 0.874)	-0.955 (-1.001, -0.908)	0.776

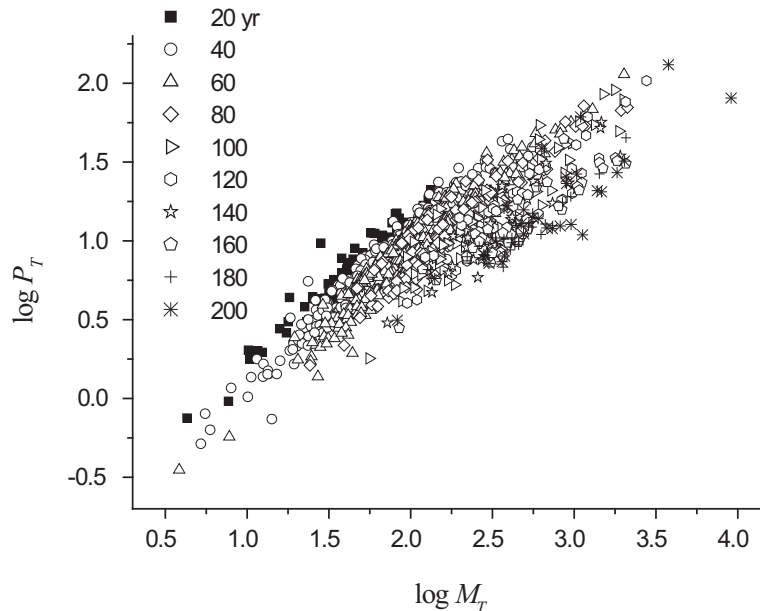


Fig. 1. Total annualized biomass production (growth) rates  $P_T$  (kg dry matter plant<sup>-1</sup> yr<sup>-1</sup>) of trees plotted against total body mass  $M_T$  (kg dry matter plant<sup>-1</sup>) with different age-sequences (see insert for symbols). RMA regression statistics reported in Table 1.

Data for biomass and annual biomass productivity were  $\log_{10}$ -transformed. Reduced major axis (RMA) regression protocols were used to determine the slope and Y-intercept of log-log linear functions (i.e.,  $\alpha_{\text{RMA}}$  and  $\log \beta_{\text{RMA}}$ , respectively) because the error variance resulting from measurement error and real biological variation was equivalent among all variables (Niklas 1994). RMA regression was performed using RMA version 1.17.

### 3. RESULTS

The results show that for forest younger than 100 yrs, the relationship between annual productivity  $P$  and body mass  $M$  had similar scaling exponents ( $\alpha_{\text{RMA}} \approx 1.0$ ), while the normalization constants ( $\log \beta_{\text{RMA}}$ ) decreased systematically. When stand age exceeds the 140 yr, scaling exponents decreased (Tables 1 and 2). The last 200 yr group had a strange higher

scaling slope than 160yr group. We attributed such variation to the fact that we combined samples which stand age ranged from 181 to 350 years into one age range (see Material and Methods), because the small sample sizes and multiple stand age will result in large re-

gression model errors. After all, age-related decline of the scaling exponents for the relationship of  $P$  vs.  $M$  for the Chinese forest were statistically verified (Figs 2 and 3). Specifically, for  $P_T$  vs.  $M_T$  the following relations were found ( $A$  denotes stand age): scaling

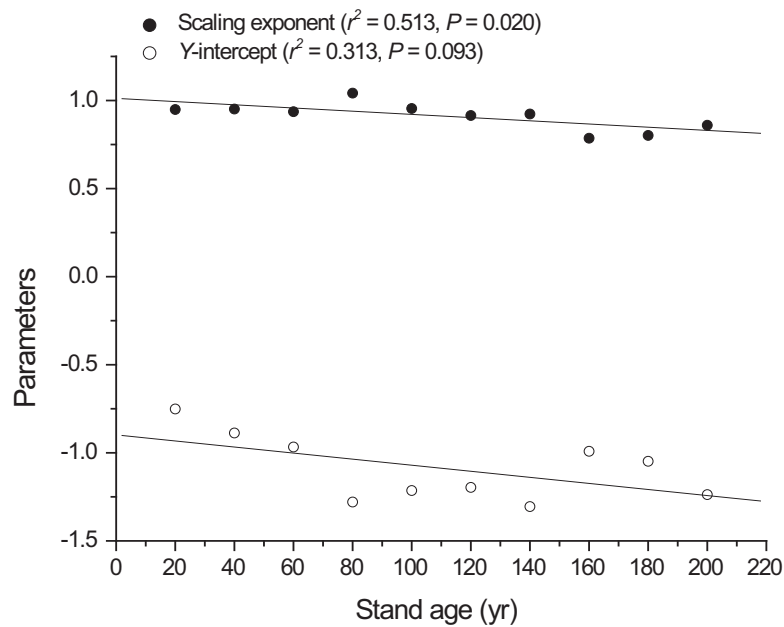


Fig. 2. RMA regression parameters for the relationship of  $\log P_T$  versus  $M_T$ , where  $P_T$  is annual biomass production and  $M_T$  is the total biomass for trees.

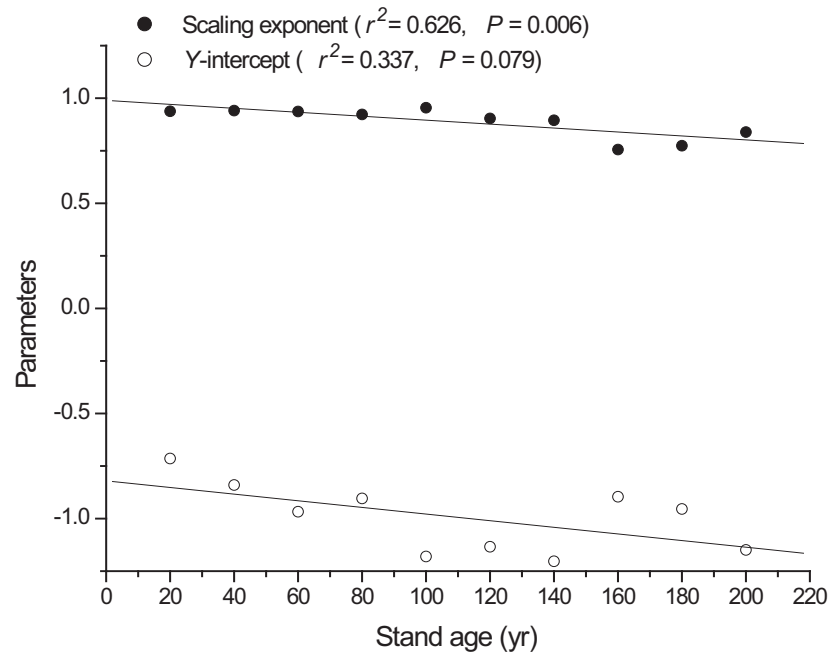


Fig. 3. RMA regression parameters for the relationship of  $\log P_A$  versus  $\log M_A$ , where  $P_A$  is annual biomass production and  $M_A$  is the total biomass for trees.

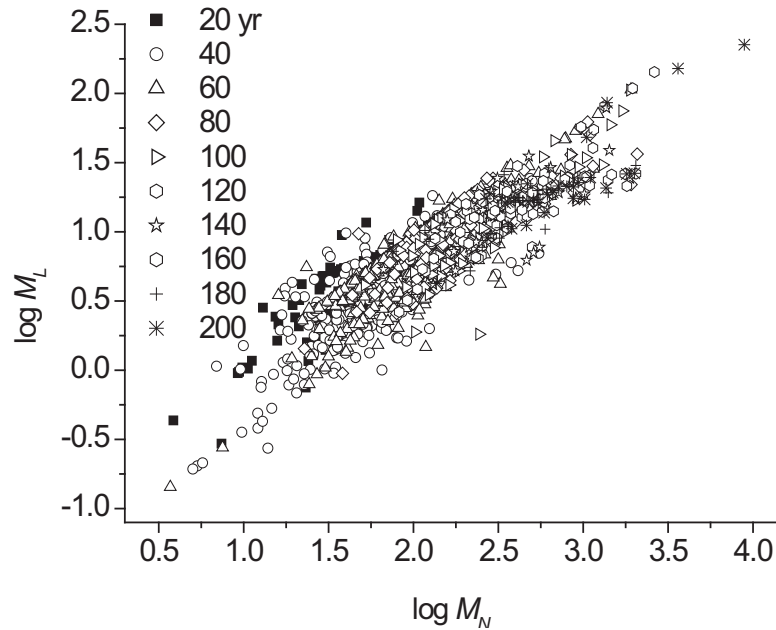


Fig. 4. Log-log bivariate plots of photosynthetic biomass and nonphotosynthetic biomass ( $M_L$  and  $M_N$ , respectively) relationships for data compiled by Luo (1996) sorted into 10 age-sequences (see insert for symbols). RMA regression statistics reported in Table 3.

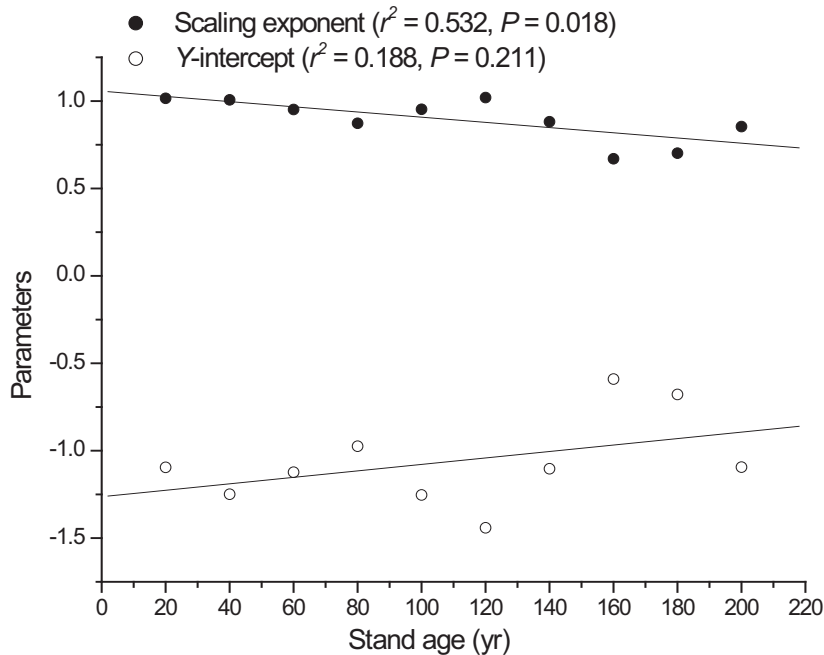


Fig. 5. RMA regression statistics for the relationship of  $\log M_L$  versus  $M_N$ , where  $M_L$  is leaf biomass and  $M_N$  is the nonphotosynthetic biomass for trees.

exponents  $\alpha_{\text{RMA}} = -0.001 A + 0.982$  ( $r^2 = 0.576$ ,  $P = 0.011$ ) and Y-intercept  $\log \beta_{\text{RMA}} = -0.002A - 0.898$  ( $r^2 = 0.313$ ,  $P = 0.093$ ) (Fig. 2); For  $P_A$  vs.  $M_A$ ,  $\alpha_{\text{RMA}} = -0.001A + 0.979$  ( $r^2 = 0.594$ ,  $P = 0.009$ ) and  $\log \beta_{\text{RMA}} = -0.002A - 0.801$  ( $r^2 = 0.370$ ,  $P = 0.062$ ) (Fig. 3).

The fact that  $P_T$  vs.  $M_T$  and  $P_A$  vs.  $M_A$  had a similar transition with the stand age showed that annual growth rates systematically declined from isometric, although the total dataset yield a near 3/4 scaling slope (0.715 for  $P_T$  vs.  $M_T$ , 95% confident intervals (CI)

$= 0.696 \leq \alpha_{\text{RMA}} \leq 0.734$ , 0.717 for  $P_A$  vs.  $M_A$ , 95% confident intervals (CI) =  $0.699 \leq \alpha_{\text{RMA}} \leq 0.736$ , respectively) without considering the effects of stand age (Tables 1 and 2). Thus the observed patterns for the relationship between  $P$  and  $M$  were inconsistent with the prediction of metabolic ecology.

An age-dependent systemic variation of the scaling exponents for the relationship between photosynthetic (leaf) mass  $M_L$  and non-photosynthetic  $M_N$  was also statistically verified (Figs 4, 5 and Table 3).  $\alpha_{\text{RMA}} = -0.001A + 1.057$  ( $r^2 = 0.523$ ,  $P = 0.018$ ) and  $\log \beta_{\text{RMA}} = 0.002A - 1.263$  ( $r^2 = 0.188$ ,  $P = 0.211$ ) (Fig. 3).

#### 4. DISCUSSION

The relationship between annual productivity  $P$  and biomass  $M$  was examined by several researchers because  $P$  was considered as a reasonable surrogate measure for the metabolic rates  $B$  (West *et al.* 1999a, Enquist *et al.* 1998, Niklas and Enquist 2001, Ernest *et al.* 2003), thus allowing to indirectly assessing the metabolism-biomass relationship for terrestrial plants (e.g. Niklas and Enquist 2001, Ernest *et al.* 2003, Li *et al.* 2005). Using the stand-level data of Cannell (1982) for the average productivity and average mass of individuals per stand, Niklas and Enquist (2001) reported that annual rates of growth  $P$  scaled as the 3/4-power of body mass  $M$  over 20 orders of magnitude of  $M$ .

However, Li *et al.* (2005) used data previously compiled by Luo (1996) for Chinese forested communities and reported that the scaling exponents between  $P$  and  $M$  for trees varies within different forest types, and that there is no sufficient evidence to support the existence of a single constant scaling exponent for the metabolism-biomass relationship for terrestrial plants. Unfortunately, such studies did not take into consideration the effects of stand age, although a number of researches showed that aboveground annual productivity  $P$  decreased with the stand age (e.g. Gower *et al.* 1996).

Therefore, in this study we tested the stand age-sequence patterns for the relationship between  $P$  and  $M$  and found that the scaling exponents systemically changed with stand age from nearly isometric ( $\alpha_{\text{RMA}} \gg 1.0$ )

to less than 0.86 (Table 1). This result is consistent with the observation made by other authors that growth rates of forests decline with age.

The significance of our findings might be limited by two methodological constraints. First, the increased error in sampling the smallest roots from large trees, which may induce a decreasing of the scaling slopes for  $P$  vs.  $M$  with the stand age, and, second, Luo's (1996) dataset covers only four orders of magnitude in standing tree mass and each forest group used in the present paper consisted the weight of plants of a relatively wide age range (ten years or more), which can yield regression curves with low correlation coefficients, large regression model errors, and thus numerically ambiguous scaling exponents. These limitations may, however, of minor relevance for two reasons. First, the result deriving from the aboveground dataset (i.e.  $P_A$  vs.  $M_A$ ), is consistent with the result performed by using that total one (i.e.  $P_T$  vs.  $M_T$ ) (Figs 2 and 3). Second, for each age-sequence, relationship of  $P$  vs.  $M$  has high  $r^2$  values, especially for those stand age are less than 100 years (Tables 1 and 2). Therefore, our results show that in forests  $P$  scales with respect to  $M$  in a different manner than previously described for animals (i.e. Kleiber's 3/4-power law). Rather, in some sense, these results show that tree metabolic rates scale approximately isometrically (scaling exponent  $\gg 1$ ) with biomass, which is consistent with the results of Reich *et al.* (2006a).

We attribute the fact that scaling exponents decrease with the stand age at least in part to the following two features. First, there is an altered balance between photosynthetic  $M_L$  and nonphotosynthetic  $M_N$  biomass.  $M_L$  represented the light-harvesting capability which intimately dictated the annual productivity (i.e.  $P \propto M_L$ ). Thus, growth rates for trees can vary as the function of shifts in the relative amount of photosynthetic biomass  $M_L$  and nonphotosynthetic biomass  $M_N$  (Niklas and Enquist 2001). Scaling exponents for the relationship of  $M_L$  vs.  $M_N$  systematically changed from 1 to 3/4 in the ageing stands, which is consistent with the pattern of  $P$  vs.  $M$  (Figs 2, 3 and 5 and Tables 1, 2 and 3). Second, there is the decreasing nutrient availability during forest stand development, particular

nitrogen N (Gower *et al.* 1996). Declined supply of N could limit the plants leaf area and the capacity of photosynthesis, which resulting in the decreasing light interception and rates of plant biomass production (McMurtrie *et al.* 1994, Peterson *et al.* 1999). In addition, previous research shows that limitations to productivity resulting from the insufficient availability of N are widespread in both unmanaged and managed vegetation (Oren *et al.* 2001, Reich *et al.* 2006b). Thus, one alternative and more desirable theory to explain the scaling law in relationship between  $P$  and  $M$  might be the association of nitrogen stoichiometry with body mass (e.g. Niklas *et al.* 2005, Niklas 2006).

In addition, a subsequently more interesting question is brought about community resource use  $R_{\text{Tot}}$ . In particular, metabolic theory predicts that the number of individuals  $N$  within a plant community scale as  $-3/4$ -power of body mass (i.e.  $N \propto M^{-3/4}$ ) (Enquist *et al.* 1998, Belgrano *et al.* 2002), whereas annual productivity scale as  $3/4$ -power of body mass (i.e.  $P \propto M^{3/4}$ ) (Enquist *et al.* 1999, Niklas and Enquist 2001, Ernest *et al.* 2003). Assuming that  $P$  is a reasonable surrogate measure of the rate of resource use per individual  $Q$ , we note that the rate of community metabolic production  $Q_{\text{Tot}}$  (which is proportional to the rate of community biomass production  $P_{\text{Tot}}$ ) is the product of the number of individuals  $N$  and  $Q$ . Thus, community resource use  $R_{\text{Tot}}$  is predicted to be proportional to  $Q \times N$  and, because  $Q \propto P \propto M^{3/4}$ , it follows that  $R_{\text{Tot}} \propto Q \times N \propto P \times N \propto P \times M^{-3/4}$  (Enquist *et al.* 1998, Enquist and Niklas 2001, Niklas and Enquist 2001, Enquist *et al.* 2003). However, based on our results, relationship between  $P$  and  $M$  decreases systemically with stand age (Figs 2 and 3). These results might imply that  $R_{\text{Tot}}$  decreases with stand age. This prediction is consistent with the fact that forest-level net primary production declines with stand age at least partly due to the declining nitrogen availability during stand development (e.g. Gower *et al.* 1996) or neighborhood competition among trees (Weiner and Thomas 2001, Berger *et al.* 2004).

In general, the results of our study provide no support for the prediction of the theory of  $3/4$ -power scaling of annual productivity to body mass for tree. However, it is premature

to reject such hypothesis because the total data might obey this prediction by ignoring the age effects. Future progress toward understanding such relationship requires theoretical explications for how and why the numerical values of scaling exponents and their associated  $Y$ -intercepts decline with stand age. It also requires additional data sets with which to estimate the predictions empirically. From the results of the present paper, we might expect that an age-related relationship between annual productivity and body mass could be established, which are relevant to forest management and carbon budget issues.

**ACKNOWLEDGMENTS:** We sincerely thank Prof. Tian-Xiang Luo for providing helpful information for this manuscript. We also thank Tao Li for reviewing and improving early drafts of the manuscript and Dr. Yan-Jiang Luo for helping to develop many of the ideas. We acknowledge the support of the natural science foundation of china (30730020) and hi-tech research and development program of China (863 program, 2006AA100202).

## 5. REFERENCES

- Belgrano A., Allen A.P., Enquist B.J., Gillooly J.F. 2002 – Allometric scaling of maximum population density: a common rule for marine phytoplankton and terrestrial plants – *Ecol. Lett.* 5: 611–613.
- Berger U., Hildenbrandt H., Grimm V. 2004 – Age-related decline in forest production: modeling the effects of growth limitation, neighborhood competition and self-thinning – *J. Ecol.* 92: 846–853.
- Brown J.H., Gillooly J.F., Allen A.P., Savage V.M., West G.B. 2004 – Towards a metabolic theory of ecology – *Ecology*, 85: 1771–1789.
- Calder W.A. 1984 – *Size, Function and Life History* – Harvard University Press, Cambridge, Mass, 431 pp.
- Cannell M.G.R. 1982 – *World Forest Biomass and Primary Production Data* – Academic Press, London, 391pp.
- Enquist B.J. 2003 – Scaling the macroecological and evolutionary implications of size and metabolism within and across plant taxa (In: *Macroecology: Pattern and Process*, Eds. T. Blackburn, K. Gaston) – Oxford University Press, Oxford, pp. 321–341.
- Enquist B.J., Niklas K.J. 2001 – Invariant scaling relations across tree-dominated communities – *Nature*, 415: 655–660.

- Enquist B.J., Brown J.H., West G.B. 1998 – Allometric scaling of plants energetics and population density – *Nature*, 395: 163–165.
- 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.
- Enquist B.J., Economo E.P., Huxman T.E., Allen A.P., Ignace D.D., Gillooly J.F. 2003 – Scaling metabolism from organism to ecosystems – *Nature*, 423: 639–642.
- Ernest S.K.M., Enquist B.J., Brown J.H., Charnov E.L., Gillooly J.F., Savage V.M. *et al.* 2003 – Thermodynamic and Metabolic Effects on the Scaling of Production and Population Energy Use – *Ecol. Lett.* 6: 990–995.
- Gower S.T., McMurtrie R., Murty D. 1996 – Aboveground net primary production decline with stand age: potential causes – *Trends Ecol. Evol.* 11: 378–382.
- Kleiber M. 1932 – Body size and metabolism – *Hilgardia*, 6: 315–353.
- Li H.T., Han X.G., Wu J.G. 2005 – Lack of evidence for 3/4 scaling of metabolism in terrestrial plants – *J. Integ. Plant Biol.* 47: 1173–1183.
- Luo T.X. 1996 – Patterns of biological production and its mathematical models for main forest types of China – Committee of Synthesis Investigation of Natural Resources, the Chinese Academy of Sciences, Beijing.
- Marquet P.A., Quiñones R.A., Abades S., Labra F., Tognelli M., Arim M., Rivadeneira M. 2005 – Scaling and power-laws in ecological systems – *J. Exp. Biol.* 208: 1749–1769.
- McMurtrie R.E., Gholz H.L., Linder S., Gower S.T. 1994 – Climatic factors controlling the productivity of pine stands: a model-based analysis – *Ecol. Bull.* 43: 173–188.
- Ni J., Zhang X.S., Scurlock J.M. O. 2001 – Synthesis and analysis of biomass and net productivity in Chinese forests – *Ann. For. Sci.* 58: 351–384.
- Niklas K.J. 1994 – *Plant Allometry: The Scaling of Form and Process* – University of Chicago Press, Chicago, IL. 395 pp.
- Niklas K.J. 2005 – Modeling below- and above-ground biomass for woody and woody plants – *Ann. Bot.* 95: 315–321.
- Niklas K.J. 2006 – Plant Allometry, Leaf Nitrogen and Phosphorus Stoichiometry, and Interspecific Trends in Annual Growth Rates – *Ann. Bot.* 97: 155–163.
- Niklas K.J., Enquist B.J. 2001 – Invariant scaling relationships for interspecific plant biomass production rates and body size – *Proc. Nat. Acad. Sci. USA*, 98: 2922–2927.
- Niklas K.J., Owens T., Reich P.B., Cobb E.D. 2005 – Nitrogen/phosphorus leaf stoichiometry and the scaling of plant growth – *Ecol. Lett.* 8: 636–642.
- Oren R., Ellsworth D.S., Johnsen K.H., Phillips N., Ewers B.E., Maier C. *et al.* 2001 – Soil fertility limits carbon sequestration by forest ecosystems in a CO<sub>2</sub> enriched world – *Nature*, 411: 469–472.
- Peters R.H. 1986 – *The Ecological Implications of Body Size* – Cambridge University Press, Cambridge, 329 pp.
- Reich P.B., Tjoelker M.G., Machado J.L., Oleksyn J. 2006a – Universal scaling of respiratory metabolism, size and nitrogen in plants – *Nature*, 439: 457–461.
- Reich P.B., Hobbie S.E., Lee T., Ellsworth D.S., West J.B., Tilman D., Knops J.M.H., Naeem S., Trost J. 2006b – Nitrogen limitation constrains sustainability of ecosystem response to CO<sub>2</sub> – *Nature*, 440: 922–925.
- Peterson A.G., Ball J.T., Luo Y., Field C.B., Curtis P.S., Griffin K. L. *et al.* 1999 – The photosynthesis-leaf nitrogen relationship at ambient and elevated atmospheric carbon dioxide: A meta-analysis – *Glob. Change Biol.* 5: 331–346.
- Ryan M.G., Waring R.H. 1992 – Maintenance respiration and stand development in a subalpine lodgepole pine forest – *Ecology*, 73: 2100–2108.
- Weiner J., Thomas S.C. 2001 – The nature of tree growth and the “age-related decline in forest productivity” – *Oikos*, 94: 374–376.
- West G.B., Brown J.H., Enquist B.J. 1997 – A general model for the origin of allometric scaling laws in biology – *Science*, 276: 122–126.
- West G.B., Brown J.H., Enquist B.J. 1999a – The fourth dimension of life: Fractal geometry and allometric scaling of organisms – *Science*, 284: 1677–1679.
- West G.B., Brown J.H., Enquist B.J. 1999b – A general model for the structure and allometry of plant vascular systems – *Nature*, 400: 664–667.
- West G.B., Brown J.H., Enquist B.J. 2001 – A general model for ontogenetic growth – *Nature*, 413: 628–631.

*Received after revision November 2008*