Allometric scaling relationships for morphology and biomass allocation are mediated by stand ages in *Cyclobalanopsis glauca*

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Abstract: Metabolic theory of ecology predicts a 'universal scaling law' of tree growth. However, this scaling law was continuously debated in both theoretical and empirical studies. It is still unclear that whether this scaling law varies with tree age. In this study, we investigated the allometric scaling relationships for morphology and biomass allocation in young, immature and mature *Cyclobalanopsis glauca*. The results showed that universal scaling law can not be applied to all the allometric scaling relationships for morphology and biomass allocation across different ages *Cyclobalanopsis glauca* communities. For morphology, the scaling lines for height vs diameter at breast height (H-D), canopy vs diameter at breast height (C-D), and canopy vs height (C-H) in young age were stepper and higher than those of mature age. While for biomass allocation, except for total biomass vs stem biomass (M_T-M_S), the scaling lines for total biomass vs leaf biomass (M_T-M_L), stem biomass vs leaf biomass (M_S-M_L), total biomass vs root biomass (M_T-M_R) in young age were flatter and lower than those of mature age. Therefore, it was implied that the allometric scaling relationships for morphology and biomass allocation are mediated by stand ages.

1. Introduction

Trees morphology and biomass allocation always or often vary with environmental variables, such as temperature, light intensity and the availability of water and essential minerals (Bloom *et al*.1985; Luo *et al*. 2005). The allometric scaling relationships for morphology and biomass allocation show fundamental similarities suggested general underlying principles (Coomes *et al*. 2003). The metabolic theory of ecology has predicted specific relationships among tree stem diameter, biomass, height, and growth (West *et al*. 1999; Brown *et al*. 2004). As demographic rates are important to estimates of carbon fluxes in forests, this theory might offer important insights into the global carbon budget, and deserves careful assessment (Phillips *et al*. 1998; Clark *et al*. 2001).

In metabolic theory of ecology, basic principles of physics, chemistry and biology were applied to explain the physiology and performance of individual organisms and the structure of populations, communities and ecosystems (West *et al*. 1997; 1999; 2001; Brown *et al*. 2004). In past decade, abundant evidences indicated that diverse fundamental characteristics of plants, including physiological, morphological and allometric attributes, scaled

universally with increasing metabolic rates (West *et al*. 1997; 1999; Gillooly *et al.* 2001; White & Seymour. 2003; Brown *et al*. 2004). However, this universal scaling law was also criticized on theoretical and empirical grounds (Dodds *et al*. 2001; Kozlowski and Konarzewski 2004; Meinzer *et al*. 2005; Deng *et al*. 2006; Zhang *et al*. 2010a). For trees, in particular, we suggest that the scaling of metabolic rates with size will depend not only on the potential for resource uptake, redistribution and availability that is central to metabolic ecology theory, but may also on life stage.

Some studies have indicated that the life stages can be important in the physiology, morphological of tree individual and pattern (Nagamatsu *et al*. 2002; Collins and Carson 2004; Tsujino *et al*. 2006). However, these studies did not investigate the relationship between life stage and the universal scaling law of trees. To understand the role of life stage in plant allometric scaling law, there is still need to compare the allometric scaling relationship for plant morphology and biomass allocation in different life stages.

Our previous studies have showed that the scaling relationship between biomass and density was influenced by gene mutation or salinity stress (Zhang

et al. 2005; 2006; 2010b). But, it is still unclear that whether this scaling law varies with tree age. In this study, we investigated the allometric scaling relationships for morphology and biomass allocation in young, immature and mature *Cyclobalanopsis glauca*. Specifically, we asked the two questions: (1) Whether the universal exponent held in these relationships; (2) How the life stage changes the allometric scaling relationships for morphology and biomass allocation? The aim of this study is to explore the linking between morphology, biomass allocation, allometric scaling relationship and life stage.

2. Material and Methods

This study was conducted in Baise, Guangxi Province, which is located in the southwest of China (106°07'E, 23°33'N ~ 106°56'E, 23°33'N). The climate of study area belongs to subtropical monsoon climate and average annual temperature is 22.1℃. Mean precipitation is 1,155 mm/year, with most of it occurring from May to October although estimated evapotranspiration is about 1,090 mm/year. Soil types in the area include red earth soil and rendzina soil. In May 2011, we choose three sites, Xilin, Tianlin and Leye, as this study area. These sites represent the *Cyclobalanopsis glauca* with young (8-12 years), immature (25-30 years) and mature (50-55 years) stages. Each site has three plots, which projection area was 50 × 20 m. The plot was established following the standard of the Centre for Tropical Forest Science (Condit 1995), and was divided into 10 quadrats of 10 × 10 m in size. In October 2011, we collected field data along a natural life stage gradient.

In the field data collection, all trees with diameter at breast height (DBH) ≥ 5 cm were tagged, identified, measured, and georeferenced during October of 2011. Within each site, we measured the DBH (abbreviation as D) of *Cyclobalanopsis glauca L.* and height (H) with rule and holometer respectively. Canopy radius (C) was measured with rule based on the projection of canopy and calculated by the average value of maximum and minimum.

We also selected and cut some trees of different diameter represented each site in the outside of quadrat. Fresh leaf biomass (M_L), stem biomass (M_S), and root biomass (M_R) were weighed by poidometer. Total biomass (M_T) was calculated as sum of M_L, M_S, and M_R. And, small fresh sample of leaf, stem and root each tree were collected and dried at 105 ± 2℃ for 12 h to compute the plant water content. Then, the dried M_L, M_S, M_R, and M_T were computed according to the different water content.

Allometric equations derived from these harvested trees were then used to estimate leaf, stem and root biomass of other trees from easily measurable variables such as D and or H, the most commonly used equations take the form: $M = xD^y$ or $M = x(D^2H)^y$, where x and y are parameters (Luo *et al*. 1996; 2005; Zhang *et al*. 2011).

Life stage of *Cyclobalanopsis glauca* was determined by case recorder of forest farm. In order to acquire the life stage accurately, the growth ring was measured after the *Cyclobalanopsis glauca* were cut down.

To qualify physical conditions of soil near the treatments, pH,water content and available nitrogen were measured. Measurements were taken adjacent (10 cm) to the plants at depth of 30 cm in October 2011. pH was determined in a 1:5 soil-water slurry, using a combination glass electrode in the laboratory. Fresh soil were collected using a polyvinyl chloride (PVC) sampling tube and were dried at 105 ± 2℃ for 12 h to compute the soil water content. The available nitrogen was determined by firstly shaking 10 g fresh soil with 25 ml 1M KCI for 30 min on an orbital shaker. Then, resulting suspension was filtered through Whatman no. 1 paper and the concentration of nitrogen in the extracts was determined by autoanalyser procedures (Ross, 1992).

The scaling exponents (b) and intercepts (IT) of M_T-M_L, M_T-M_S, M_S-M_L, and M_T-M_R relationships were estimated by the reduced major axis (RMA) regression of log-transformed data. If one b was embraced in the 95% confidence interval of other, the difference was considered to be non-significant (Zhang *et al*. 2006). In addition, data were presented as means ±S.E. for each treatment. All data were analysed by the method of two factors ANOVA with Statistical Program for Social Sciences (SPSS) 15.0 and Microsoft excel 2003. When significant differences occurred, means were separated by the LSD (P-0.05 and P-0.01) method.

3. Results

Allometric scaling relationship for morphology characteristics was changed with different life stages in *Cyclobalanopsis glauca* (Figure 1). The scaling lines for height vs diameter at breast height (H-D), canopy vs diameter at breast height (C-D), and canopy vs height (C-H) in young age were stepper and higher than those of mature age (Figure 1; Table 1). Specifically, the lines of H–D scaling relationship of young stage and that of mature stage were defined by logH=0.490+0.443logD (RMA=0.443±0.014) and logH=0.808+0.342logD (RMA=0.342±0.018), respectively, while the H–D scaling relationships trajectory of immature stage was defined by logH=0.740+0.326logD (RMA=0.326±0.013). Similarly, the lines of C–D scaling relationship of young stage and that of mature stage were defined by logC=0.490+0.444logD

(RMA=0.444±0.015) and logC=0.739+0.328logD (RMA=0.328±0.016), respectively. While, the lines of C–H scaling relationship of young stage and that of mature stage were defined by logC=0.267+0.698logH (RMA=0.698±0.015) and logC=0.535+0.562logH (RMA=0.562±0.012), respectively. The 95% confidence interval (CI) of slopes indicated that three exponents along three life stages were statistically different (Table 1).
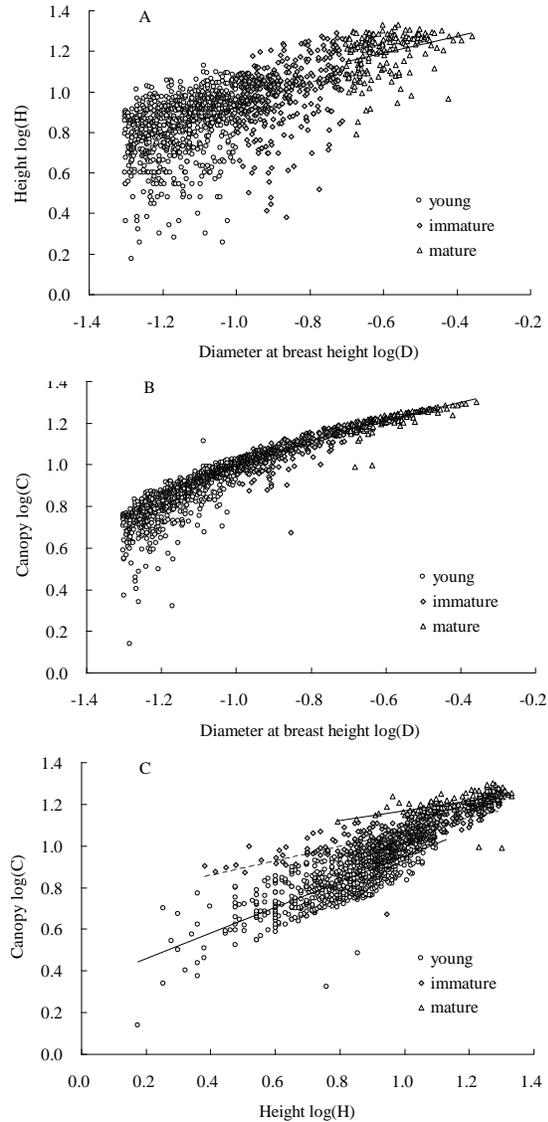

Figure1 Allometric scaling relationship for morphology characteristics in young, immature and mature *Cyclobalanopsis glauca*. (A) Height vs Diameter at breast height (H-D); (B) Canopy vs Diameter at breast height (C-D); (C) Canopy vs Height (C-H).
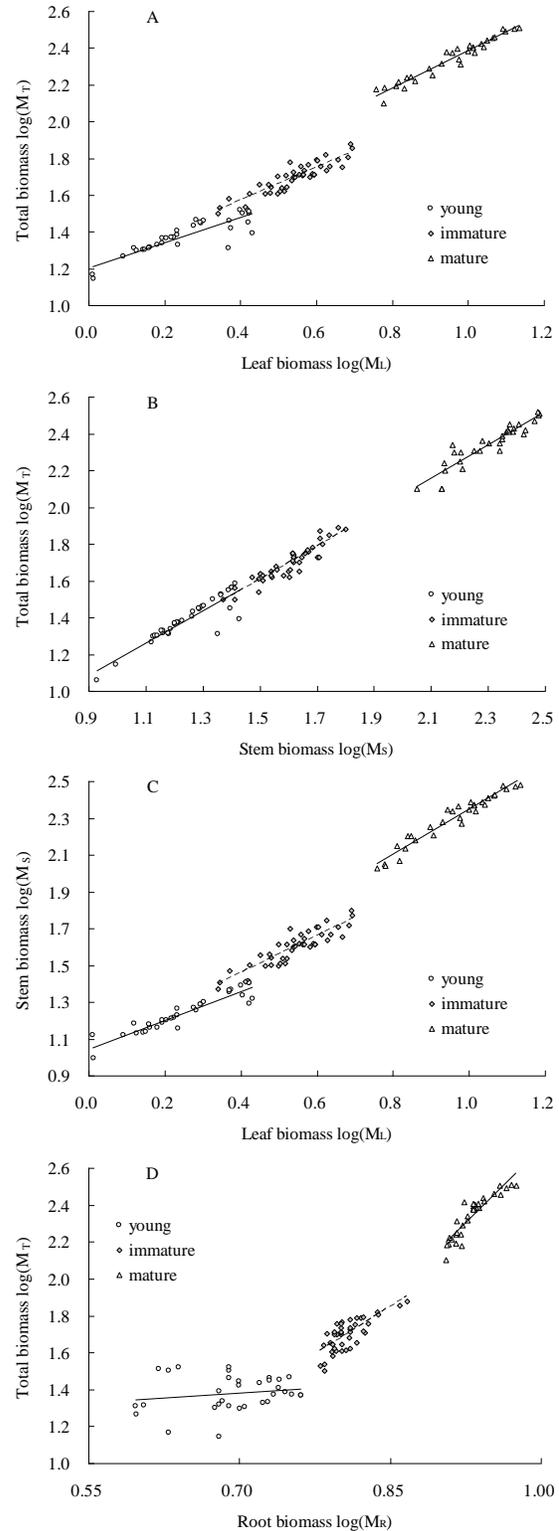

Figure 2 Allometric scaling relationship for biomass allocation in young, immature and mature *Cyclobalanopsis glauca*. (A) Total biomass vs Leaf biomass (M_T-M_L); (B) Total biomass vs Stem biomass (M_T-M_S); (C) Stem biomass vs Leaf biomass

(M_S-M_L); (D) Total biomass vs Root biomass (M_T-M_R).

For biomass allocation, the scaling lines for total biomass vs leaf biomass (M_T-M_L), stem biomass vs leaf biomass (M_S-M_L), total biomass vs root biomass (M_T-M_R) in young age were flatter and lower than those of mature age, while that of total biomass vs stem biomass (M_T-M_S) was inverse (Figure 2; Table 2). Specifically, the lines of M_T-M_L scaling relationship of young stage and that of mature stage were defined by $\log M_T=1.183+0.773\log M_L$ (RMA=0.773±0.066) and $\log M_T=1.341+1.048\log M_L$ (RMA=1.048±0.045), respectively. Similarly, the lines of MT-MS scaling relationship of young stage and that of mature stage were defined by $\log M_T=0.232+0.923\log M_S$ (RMA=0.923±0.079) and $\log M_T=0.407+0.843\log M_S$ (RMA=0.843±0.032), respectively. At the same time, the lines of M_S-M_L scaling relationship of young stage and that of mature stage were defined by $\log M_S=1.030+0.838\log M_L$ (RMA=0.838±0.050) and $\log M_S=1.108+1.243\log M_L$ (RMA=1.243±0.053), respectively. Besides, the lines of M_T-M_R scaling relationship of young stage and that of mature stage were defined by $\log M_T=0.188+1.960\log M_R$ (RMA=1.960±0.346)and $\log M_T=-3.197+5.944\log M_R$ (RMA=5.944±0.464), respectively. Finally, The 95% CI of slopes also indicated that exponents of biomass allocation were statistically different with life stages (Table 2).

Table 1 Slopes (b) and intercepts (IT) of H–D, C-D and C–H relationships in young, immature and mature *Cyclobalanopsis glauca*, as estimated by RMA regression of log-transformed data. s.e. is standard error.

	Life stages	b (s.e.)	95% CI of b	IT (s.e.)	n	R^2	Location
H-D	Young	0.443(0.014)	0.416, 0.470	0.490(0.012)	855	0.175	Xinlin
	Immature	0.326(0.013)	0.300, 0.352	0.740(0.013)	403	0.333	Tianlin
	Mature	0.342(0.018)	0.308, 0.378	0.808(0.021)	177	0.535	Leye
C-D	Young	0.444(0.015)	0.415, 0.473	0.490(0.013)	855	0.156	Xinlin
	Immature	0.422(0.031)	0.361, 0.484	0.712(0.041)	403	0.242	Tianlin
	Mature	0.328(0.016)	0.296, 0.359	0.739(0.013)	177	0.377	Leye
C-H	Young	0.698(0.015)	0.652, 0.734	0.267(0.008)	855	0.470	Xinlin
	Immature	0.610(0.015)	0.569, 0.651	0.413(0.010)	403	0.376	Tianlin
	Mature	0.562(0.012)	0.533,0.601	0.535(0.013)	177	0.478	Leye

H is height; C is canopy; D is diameter at breast height.

Table 2 Slopes (b) and intercepts (IT) of M_T-M_L, M_T-M_S, M_S-M_L, and M_T-M_R relationships in young, immature and mature *Cyclobalanopsis glauca*, as estimated by RMA regression of log-transformed data. s.e. is standard error

	sites	b (s.e.)	95% CI of b	IT (s.e.)	n	R^2
M_T-M_L	Young	0.773(0.066)	0.638, 0.909	1.183(0.019)	32	0.772
	Immature	0.974(0.063)	0.847, 1.100	1.171(0.034)	43	0.831
	Mature	1.048(0.045)	0.956, 1.139	1.341(0.043)	30	0.747
M_T-M_S	Young	0.923(0.079)	0.762, 1.083	0.232(0.098)	32	0.775
	Immature	0.872(0.025)	0.861, 0.882	0.303(0.038)	43	0.899
	Mature	0.843(0.032)	0.777, 0.909	0.407(0.075)	30	0.857
M_S-M_L	Young	0.838(0.050)	0.735, 0.941	1.030(0.014)	32	0.888
	Immature	1.117(0.046)	0.963, 1,271	0.996(0.042)	43	0.810
	Mature	1.243(0.053)	1.134, 1.352	1.108(0.051)	30	0.847
M_T-M_R	Young	1.960(0.346)	1.254, 2.667	0.188(0.024)	32	0.542
	Immature	4.511(0.458)	3.586, 5.436	-1.941(0.369)	43	0.778
	Mature	5.944(0.464)	4.995, 6.893	-3.197(0.432)	30	0.823

M_L is leaf biomass; M_S is stem biomass; M_R is root biomass; M_T is total biomass.

Table 3 Results of one-way ANOVA for the effect of life stage on the variance of height, diameter at breast height, canopy, leaf biomass, stem biomass, root biomass, and total biomass. For each variable, the Mean Square (MS), F-value (F) are shown.

Source	Height			Diameter at breast height			Canopy		
	df	MS	F	df	MS	F	df	MS	F
Life stage	2	3913	514.9**	2	3517	395.2**	2	2653	384.5**
Error	528	7.6		528	8.5		528	6.9	
Source	Leaf biomass			Stem biomass			Root biomass		
	df	MS	F	df	MS	F	df	MS	F
Life stage	2	458.5	147.9**	2	375.3	312.8**	2	155.7	81.9**
Error	87	3.1		87	1.2		87	1.9	

* $P<0.05$, ** $P<0.01$

4. Discussions

There is considerable debate about the validity and consistency of the underlying assumptions of metabolic ecology (e.g. Dodds *et al.* 2001; Kozlowski & Konarzewski 2004; Meinzer *et al.* 2005). Some recent literature indicates that the allometric scaling exponent varies with soil fertility (Morris 2003), soil water availability (Deng *et al.* 2006), soil salinity (Zhang *et al.* 2010a) and gene. The mutations (Zhang *et al.* 2005; 2006; 2010b). results of the present study do not support the existence of a unique scaling exponent for the metabolism and biomass of forest plants. Our results showed that allometric scaling relationships for morphology and biomass allocation vary with life stages in *Cyclobalanopsis glauca* (Figure 1 and Figure 2). Thus, the validity of the fractal volume-filling theory of West, Brown, and Enquist (the WBE model) and its predictions is unwarranted. Because the relationships among height vs diameter at breast height (H-D), canopy vs diameter at breast height (C-D), canopy vs height (C-H), total biomass vs leaf biomass (M_T-M_L), total biomass vs stem biomass (M_T-M_S), stem biomass vs leaf biomass (M_S-M_L), and total biomass vs root biomass (M_T-M_R) change significantly across different life stages, the scaling exponent for the metabolism-biomass relationship does not seem to converge to a single constant value.

Figure 1 and Table 1 indicated that the scaling lines for H-D, C-D, and C-H in young age were stepper and higher than those of mature age. This is consistent with the case in *Cunnirtghamia Lanceolata* and *Pious Massonzana* (Zhang *et al.* 2005). From young to mature stage, H, D and C became bigger asymmetrically. In mature stage, the forest plants compete primarily for light, water or nutrition and self-thinning usually occurred. So, plants in this stage should have smaller H-D scaling exponent (i.e. as plants diameter at breast height grow larger, they tend to have smaller height growth). Small C-D scaling exponent demonstrated that plants diameter at breast height grow larger, they tend to have smaller canopy growth. Additionally, it was indicated that plants height grow larger, they tend to have smaller canopy growth (Xu *et al.* 2013a; 2013b).

Previous researches have showed that the total plant grew slowly in young stage because dry matter was allocated to root, stem and leaf. At immature stage, the total plant grew quickly for rapid growth of stem and leaf. At the mature stage, the dry matter reduced than that of immature stage for stable leaf biomass (Wen *et al.* 1995; Zhang *et al.* 2004). In this study, the scaling lines for M_T-M_L, M_S-M_L, M_T-M_S, and M_T-M_R was also variant with different life stages (Figure 2, Table 2). Figure 2 and Table 2 showed that the scaling exponents of M_T-M_L and M_S-M_L in mature stage were higher than those of young stage. That was indicated that leaf biomass grew slower than stem biomass and total plant biomass. On the contrary, the scaling exponent of M_T-M_S in mature stage was smaller than that of young stage (Figure 2, Table 2). It was implied that the stem biomass grew bigger than total plant biomass. Moreover, ratio of root biomass and above ground biomass was reflected the strategy of biomass allocation. The scaling exponent of M_T-M_R in mature stage was bigger than that of young stage (Figure 2, Table 2). That was meaning that the accumulation rate of above biomass was higher than that of root biomass in mature stage.

Briefly, our data showed that the *Cyclobalanopsis glauca* morphology and biomass allocation are mediated by stand ages (Table 3). In fact, *Cyclobalanopsis glauca* biomass allocation in different areas also may be affected by comprehensive factors, such as altitude, soil, climates, human disturb, etc. In past decades, the increase forest in young stage and reducing of mature stage made the plantation forest structure of China complex. Because the forest at mature stage has fewer leaf than that of other stages, the forest carbon of China may be underestimated if the regression equation of forest biomass deduced from the young or immature forest was used. Therefore, influence of the life stage on forest biomass should be considered fully to estimate accurately vegetation carbon at regional scale in the further research.

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