Original Research

Allometry and Biomass Production of *Phyllostachys Edulis* Across the Whole Lifespan

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Abstract

Applying the appropriate allometric equation to accurately estimate biomass is vital for the regional carbon budget. Previous studies have focused on plant biomass at a given time, and few have been conducted on biomass estimates throughout the entire lifespan of a plant. Here we used field data measured from Moso bamboo stands to validate three common allometric equations used for biomass estimates and compared their goodness of fit using Akaike's information criterion to develop the best allometric model for Moso bamboo. Then the non-stage and staged biomass were respectively estimated using the best-fitted model, and their corresponding coefficients (or scalings) were compared to examine whether the allometric equation developed for non-stage biomass estimates were suitable for staged biomass estimates. As a result, $w = aD^bH^c$ was fitted well for both total and component biomass estimates of Moso bamboo. Comparisons in allometric coefficients showed that most coefficients for staged biomass estimates exceeded the confidence interval of non-stage allometric coefficients, indicating that the staged coefficients varied as the bamboo developed. This result suggested that using a uniform allometric equation (with the same coefficients) without consideration of the variations with stage might be inadequate to accurately estimate the biomass of Moso bamboo forests throughout the entire lifespan. It can be suggested that differential allometric coefficients by stage should be applied to estimate the biomass of Moso bamboo so as to improve the accuracy of biomass estimates. These findings provide insights into the use of allometry theory for biomass estimates.

Keywords: equation, Anhui, biomass estimates, lifespan, *Phyllostachys edulis*

Introduction

Allometry is considered the most common and reliable method for estimating forest biomass and biogeochemical budgets [1, 2]. The most commonly used allometric relationship can be expressed with the bivariate model: $y = ax^b$, where y is the mass (biomass), x is an easily measured size variable (e.g., tree diameter), and a and b are the allometric coefficients [3-5]. However, the coefficients of the allometric equation vary frequently with species, site, and climatic conditions [6-8]. In addition, some studies have proposed the inclusion of tree height (H) [9] or age (A) [10, 11] as a second predictor in biomass estimates. Despite the flexibility of allometric variables and coefficients, equations tailored to estimate the biomass of a particular species can provide more accurate estimates of biomass in cases for which species-specific information is available.

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Table 1. Three candidate models, their coefficients, and the performance criteria used to develop the best-fitted equations to estimate the biomass of Moso bamboo irrespective of the development stage.

Components	Models	Expressions	Coefficients			Performance criteria	
			a	*b*	*c*	R^2	AIC
Foliage	Model 1	$w = aD^b$	0.045	1.255	-	0.350	-169.387
	Model 2	$w = aH^c$	0.044	-	1.433	0.402	-175.698
	Model 3	$w = aD^bH^c$	0.044	0.031	1.402	0.388	-173.702
Branch	Model 1	$w = aD^b$	0.082	1.373	-	0.754	-294.412
	Model 2	$w = aH^c$	0.076	-	1.437	0.746	-285.777
	Model 3	$w = aD^bH^c$	0.949	0.889	0.565	0.784	-297.815
Culm	Model 1	$w = aD^b$	0.095	2.123	-	0.954	-418.426
	Model 2	$w = aH^c$	0.063	-	2.269	0.897	-298.761
	Model 3	$w = aD^bH^c$	0.098	1.823	0.483	0.984	-439.521
Rhizome	Model 1	$w = aD^b$	0.035	1.684	-	0.757	-299.403
	Model 2	$w = aH^c$	0.019	-	2.038	0.800	-256.336
	Model 3	$w = aD^bH^c$	0.030	1.756	0.315	0.887	-299.156
Root	Model 1	$w = aD^b$	0.034	1.865	-	0.654	-242.353
	Model 2	$w = aH^c$	0.025	-	1.962	0.693	-285.777
	Model 3	$w = aD^bH^c$	0.039	1.744	0.251	0.770	-297.815
Aboveground biomass	Model 1	$w = aD^b$	1.089	0.146	-	0.907	-323.474
	Model 2	$w = aH^c$	1.056	-	0.112	0.842	-285.157
	Model 3	$w = aD^bH^c$	1.000	0.107	0.034	0.916	-331.449
Belowground biomass	Model 1	$w = aD^b$	0.345	0.142	-	0.849	-287.150
	Model 2	$w = aH^c$	0.347	-	0.108	0.764	-253.929
	Model 3	$w = aD^bH^c$	0.327	0.117	0.022	0.851	-287.544
Total biomass	Model 1	$w = aD^b$	0.243	1.870	-	0.932	-392.878
	Model 2	$w = aH^c$	0.199	-	2.001	0.893	-314.141
	Model 3	$w = aD^bH^c$	0.288	1.516	0.514	0.970	-408.892

w, *D* and *H* in expressions denote biomass (kg), diameter at breast height (cm) and height (m) of Moso bamboo, respectively; *a*, *b* and *c,* are allometric coefficients.

Trees can grow over decades or centuries; thus few species are appropriate for examining changes in the biomass at different stages over a comparatively short period of time. Additionally, a long-term observation at a given site requires excessive expense, making it impossible to estimate the biomass for every stage of a tree over the entire lifespan. Consequently, essentially all of the empirical studies have focused on estimating biomass at a given time. To our knowledge, few studies have been conducted on biomass estimates throughout the lifespan of a single tree.

Phyllostachys edulis (Moso bamboo) covers 3.87 million ha in China, accounting for 70% of the bamboo forest area in China and more than 80% of the Moso bamboo area in the world [12]. Moso bamboo stands, with bamboo culms of different ages ranging from 1 to 11 years (considered to be the lifespan of a given Moso bamboo culm in this paper), present appropriate materials and experimental stands to examine the changes in an allometric equation and its coefficients over the lifespan of this species.

In this paper we employed the field data from Moso bamboo forests to validate the three most commonly used allometric equations and compared their goodness of fit to develop allometric equations for the components (e.g., foliage, branch, culm, rhizome, and root) and for the total biomass estimates of Moso bamboo forests using Akaike's information criterion (AIC) [13, 14]. Then the best-fitted allometric model was used for the four growth stages (i.e., young stage, shooting stage, maturity stage, and decline stage). Finally, the coefficients (or scalings) of allometric equations developed for non-stage and staged biomass estimates across the entire lifespan were compared to examine whether the allometric equation developed

Table 2. Comparison of allometric coefficients for each developmental stage with corresponding coefficients for non-stage equation of Moso bamboo using logarithmically transformed equations ($lgy = a+blgD+clgH$).

Allometric coefficient	Developmental stage				Non-stage confidence interval	
	Young stage (1-2 years)	Shooting stage (3-5 years)	Maturity stage (6-7 years)	Decline stage (>8 years)	Lower limit	Upper limit
a	-0.678	-0.487	-0.419	-0.638	-0.693	-0.504
b	0.590	1.488	1.540	1.654	0.998	1.452
c	1.448	0.507	0.356	0.500	0.597	1.075
n	16	30	19	16	81	81
R^2	0.96	0.96	0.97	0.97	0.97	0.97

for non-stage biomass estimates is adequate for staged biomass estimates of Moso bamboo forests.

Materials and Methods

Sampling and Biomass Estimates

From July 2012 to September 2012 a total of 20 plots (20 × 20 m) at Huangshan Forestry Station (118.10 E - 118.14 E, 30.20 N - 30.24 N) and Guangde Forestry Station (119.28 E - 119.31 E, 30.84 N - 30.85 N) were established in the main region of the pure Moso bamboo forest in southern Anhui Province, China (Fig. 1). Southern Anhui is located in a north subtropical climatic zone and has distinct seasonal changes, with an annual mean temperature and precipitation of 10ºC and 1,800 mm, respectively. Four pure Moso bamboo stands were in the Guangde Forestry Station, and 16 were in the Huangshan Forestry Station, with altitudes ranging from 80 to 120 m and from 200 to 800 m, respectively. For each plot, bamboo height (H, m), age (A, yr), and diameter at breast height (D, larger than 2 cm) of the Moso bamboo culms and other woody trees were measured and recorded.

To validate three common allometric equations used for biomass estimates (i.e., Models 1-3 in Table 1), a total of 81 culm ranging in age from 1 to 11 years old were randomly selected using a destructive sampling technique [15]. Each sampled bamboo culm was felled, and the fresh weights (FW) of five components, i.e., foliage, branch, culm, rhizome, and roots were determined. After the field survey, the five components were collected and immediately returned to the laboratory. The dry weight (DW) (i.e., biomass) of each component was measured after drying at 80ºC for 72 h, and thus the total and components biomass could be determined by multiplying the FW by the DW/FW ratio.

Model Development

Prior to model development, a suitable choice of the independent variables used in allometric equations, which can relate the biomass of the sample trees to D and/or H, is required. However, the rapid asexual reproduction of new culms often results in Moso bamboo stands with uneven ages [16, 17]. Thus, age may have an effect on the biomass estimates.

In this paper the effects of D, H, and A on the biomass of Moso bamboo were examined. In addition, the relationships between H and D and between A and D were analyzed. To evaluate the goodness of fit of the candidate models we used a value of AIC [14] to determine the allometric equation with the best fit. The best model is the one with the smallest value of AIC.

It is noted that the choice of the best-fitted equation by AIC was examined based on the non-stage biomass data.

Comparison of Staged Allometric Coefficients with Non-Stage Ones

The staged biomass means the estimated biomass by stage. According to the growth characteristics of Moso bamboo, we divided the lifespan of bamboo into four stages (Table 2). In the Young Stage (1-2 years old), the Moso bamboo responds to a decrease in aboveground resources with increased allocation to rhizome. During the shooting stage (3-5 years old), the bamboo begins to expand the leaf and branch. The bamboo becomes mature in the maturity stage (6-7 years old) and then begins to die after 8 years (the decline stage).

Based on the best-fitting allometric equation (i.e., Table 1; see more details below), the overall biomass at the young, shooting stage, maturity stage and decline stages were, respectively, estimated. Then the change (i.e., difference) between the staged allometry and non-stage allometry was examined by comparing their allometric coefficients. If one coefficient in any staged allometric equation is within the confidence interval of the corresponding coefficient in the non-stage equation, we assumed that the coefficients have no significant difference and the uniformity (i.e., no significant difference) in biomass estimated using the non-stage and staged allometric equations; otherwise, the two corresponding coefficients and thus allometric equations were treated significantly different. The coefficients and its confidence interval were calculated using the ordinary least square (OLS) method.

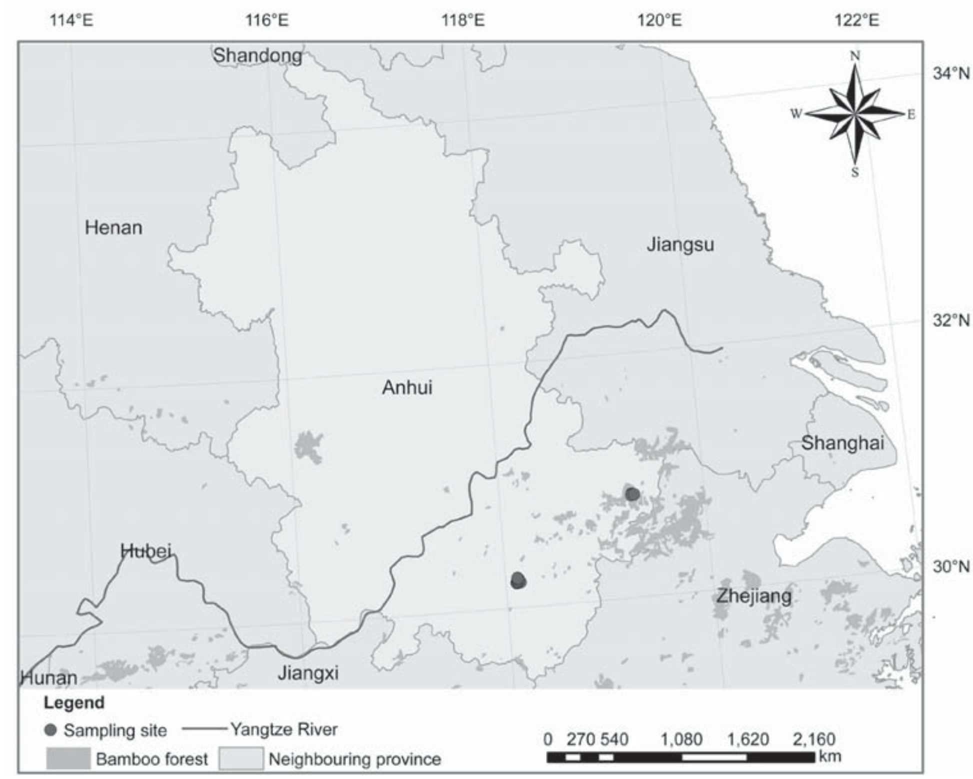

Fig. 1. Sampling sites of Moso bamboo stands in south Anhui Province, China. A total of 20 plots were randomly established in these two sites and are depicted as solid circles.

Results

Interrelationships between *D*, *H*, and *A*

To validate and explore the best-fitting model used for the biomass estimates, the effects of *D* and *H* on the total measured biomass of Moso bamboo were examined. The relationship between *A* and *D* was examined in this study, and no significant correlation was found (Fig. 2A). In other words, *A* had no significant effect on the *D* of Moso bamboo. However, a strong linear relationship was found between *H* and *D* (Fig. 2B).

Fitting the Relationship between the Measured Biomass and *D* and/or *H*

Three commonly used allometric equations that included *D* and/or *H* as independent variables (Models

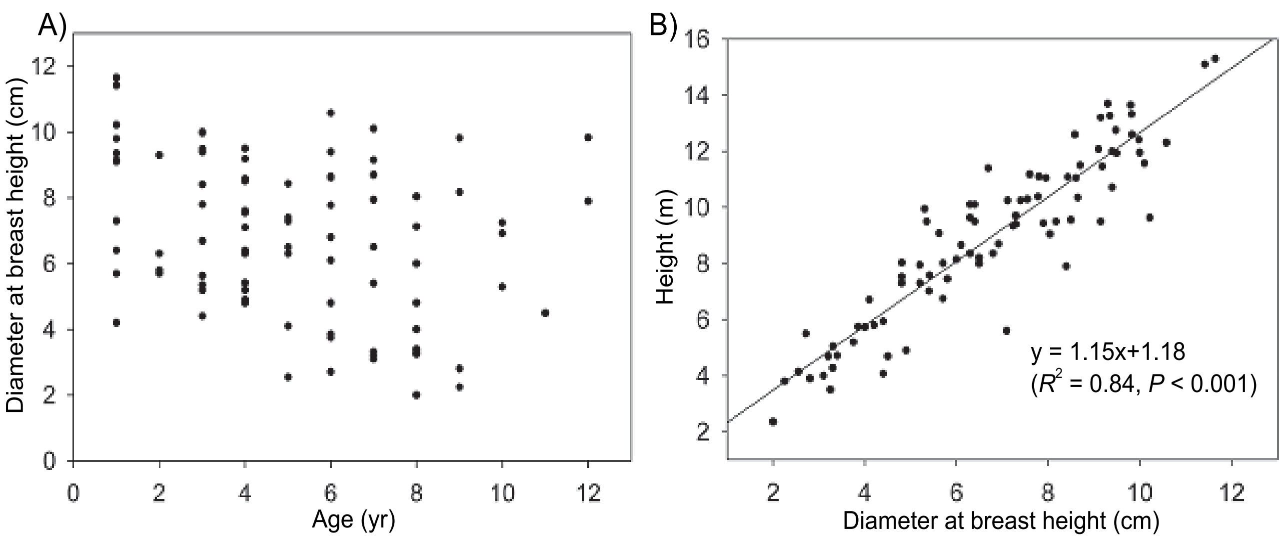

Fig. 2. Interrelationships between diameter at breast height (*D*, cm), height (*H*, m) and age (*A*, year) of Moso bamboo. A: *D* versus *A*; B: *H* versus *D*.

1-3 in Table 1) were validated for overall and component biomass. Based on Table 1, Model 3 of three allometric equations for biomass had the smallest value of AIC., which conclude that Model 3 containing both *D* and *H* as predictors exhibited the greatest predictive power for most components (except Rhizome).

We also present the three allometric equations between the measured biomasses of the aboveground (foliage, branch, and culm) and belowground components (rhizome and root), and *D* and/or *H* so that the allometric equations can be employed to estimate rhizome-based biomass and carbon sequestration in related study areas.

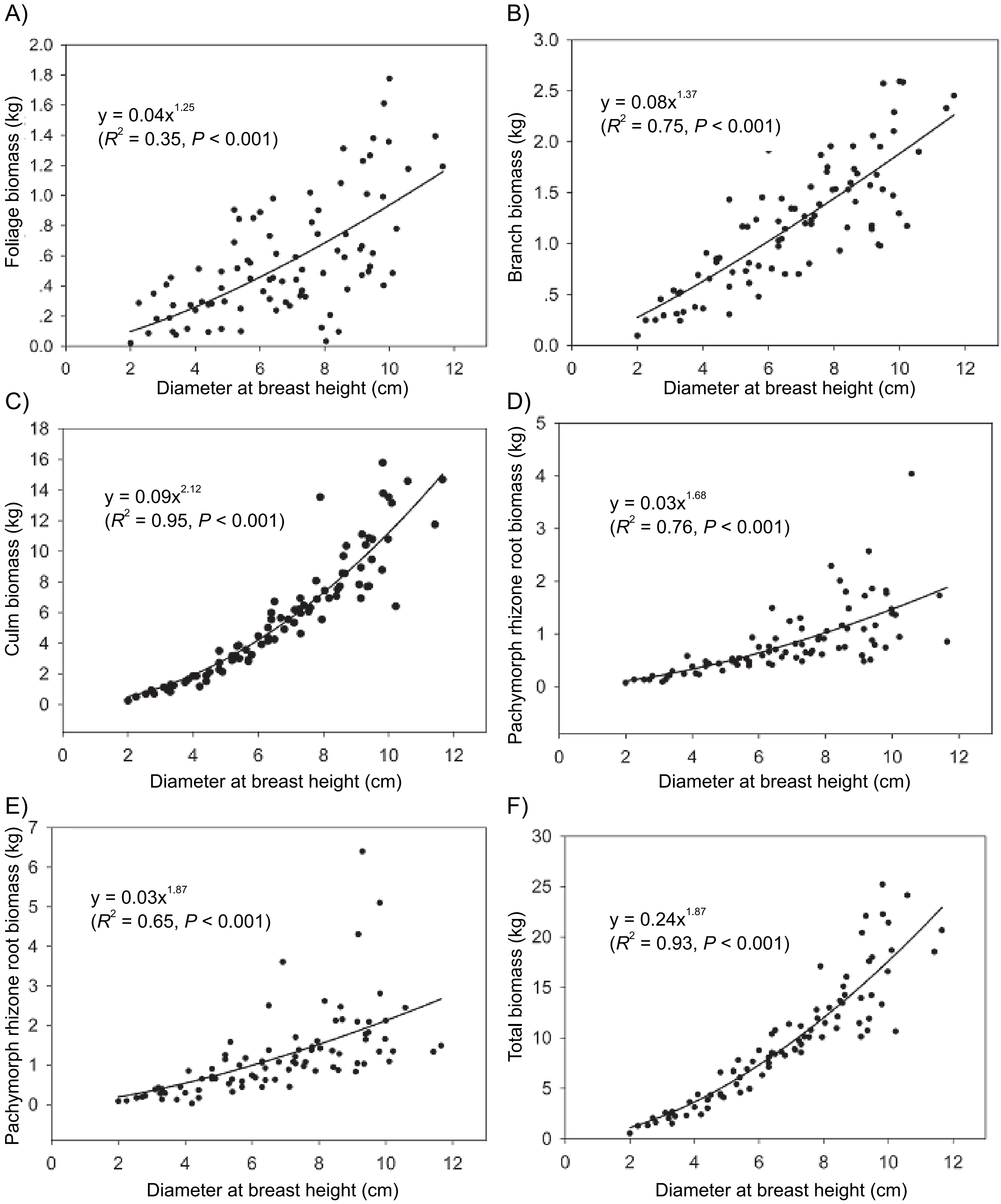

Fig. 3. The fitted allometric equations developed for the foliage (A, kg), branch (B, kg), culm (C, kg), pachymorph rhizome (D, kg), pachymorph rhizome root (E, kg), and total biomass (F, kg).

Table 3. Allometric coefficients and adjusted R2 of logarithmically transformed equations (lgy = a + blgD+ clgH) developed to estimate foliage biomass for each stage.

Development stage	Time span (yr)	*a*	*b*	*c*	R^2
Young stage	1 – 2	-0.74	1.19	-0.10	0.51
Shooting stage	3 – 5	-1.50	0.71	1.05	0.37
Maturity stage	6 – 7	-0.94	0.16	0.80	0.38
Decline stage	> 8	-1.24	-1.84	2.53	0.06

Comparison of Staged Allometric Coefficients with Non-Stage Ones

Following the stage divided on the changing trends in biomass with *A* (see material and methods for more details), we used Model 3 (Table 1) to fit the total biomass for each stage. As shown in Table 2, coefficient *b* increased gradually while *c* exhibited a decreasing trend, implying that there was a large variation of allometric coefficients across the developmental stages. The significant differences of the corresponding allometric coefficients in non-stage equations and staged equations were also indicated clearly; for example, coefficient *b* in the four stages are all large and exceed the upper limit of the confidence interval of the corresponding non-stage coefficient, except in the young stage. On the contrary, the staged coefficient *c* possessed a relatively small value, less than the non-stage lower limit of the confidence interval. The constant *a* in the shooting and maturity stages exceeds the upper limit of the confidence interval of the corresponding non-stage coefficient. These comparisons indicated that most coefficients or constants in the staged allometric equations are without the ranges of the confidence interval of the non-stage coefficients, suggesting that a uniform equation to estimate the biomass of Moso bamboo at the staged and non-stage levels is inadequate.

Discussion

Allometric equations have often been developed and applied to estimate tree biomass [18, 19]. In this study, three common allometric equations were validated and compared using AIC (Table 1). Our results indicated that the allometric equation can be used for biomass estimates of Moso bamboo and that the best-fitting equation is Model 3, consistent with many studies [20, 21]. As *A* is less informative than *D* and *H*, we speculate that there is good potential for using *D* and *H* in biomass estimates for Moso bamboo.

Although the allometric equations developed in this paper are very appropriate for total biomass estimates, these equations may not be applicable to any of the Moso bamboo components (Fig. 3). For instance, the allometric equation developed for the rhizome and root had weak R^2 values of 0.76 and 0.65, respectively (Figs. 3D and 3E), while the biomass of the culms was fitted with a high R^2 value (0.95) (Fig. 3C). Compared with the other components, the biomasses of the foliage (Fig. 3A) and branch (Fig. 3B) had higher variability than that of the bamboo culms (Fig. 3C).

The adjusted R^2 of the allometric equations developed based on the stage for estimating the foliage biomass decreased from 0.51 to 0.06 (Table 3), implying that using the Model 3 allometric equation was not suitable for estimating foliage biomass. However, the accuracy of the estimated foliage biomass appeared to be relatively unimportant to the total biomass because foliage accounted for less than 7% of the total biomass. Previous studies have concluded that the foliage biomass was also determined by the light level and stand density [22, 23]; thus, other independent variables should be incorporated into the allometric equation.

The Moso bamboo stands were often unevenly aged and quite different from other forest species. In this paper, we divided the entire lifespan of Moso bamboo into four stages and modeled the biomass for both the stage and non-stage levels of bamboo growth and development. In general, the staged coefficients in allometric equation were not within the confidence interval of non-stage coefficients, and thus uncertainty may happen if we employed uniform equations (with the same coefficients) to estimate the biomass of Moso bamboo. It is concluded that age structure and the suited allometric equations should be explored to accurately estimate biomass of Moso bamboo stands.

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