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Forstwesen**Estimating Biomass partitioning in *Mytilaria laosensis* Using Additive Models****Schätzung der Biomasseverteilung in *Mytilaria laosensis* unter Verwendung additiver Modelle**Guoming Qin¹, Rongsheng Li^{*}, Wentao Zou¹, Niu Yu¹, Jinchang Yang¹, Guangtian Yin¹, Zhihai Wang¹, Zhaoli Chen¹**Keywords:** *allometric model; biomass allocation; SUR; Southeast China***Schlüsselbegriffe:** *Allometrisches Modell; Zuweisung von Biomasse; SUR; Südostchina***Abstract**

If the additivity of the biomass allometric equation is not taken into account, it can result in erroneous estimation of forest biomass. The aim of this study was to evaluate biomass allocation patterns within separate tree parts, and to develop additive allometric equations for *Mytilaria laosensis* in southeast China. For this study, 42 destructive sampled trees were used to develop allometric equations for total biomass. We estimated biomass allocation by calculating the biomass fraction of each component (stem, branches, roots and leaves). We examined the relationships between each biomass fraction and diameter at breast height, tree height and crown diameter as independent variables. The seemingly unrelated regressions method was used to fit the biomass into additive allometric equations. The stem had the largest proportion of biomass (70.44%), followed by roots (20.35%), and branches (7.17%), with the smallest proportion of biomass being in the leaves (2.04%). Stem, leaf, and branch

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biomass ratios increased with diameter at breast height, while a reverse trend was found for belowground biomass ratios. The additive biomass models showed a good model fit explaining 94–98% of variance. This study contributes to species-specific allometric equations and the knowledge of crown, aboveground, and total biomass, which is lacking for most subtropical forests. The allometric biomass model constructed in our study can be used to estimate the biomass and carbon pool of *Mytilaria laosensis* plantations in Southeast China.

Zusammenfassung

Wenn die Additivität in allometrischen Biomassefunktionen nicht berücksichtigt wird, kann dies zu fehlerhaften Schätzungen der Waldbiomasse führen. Das Ziel dieser Studie war es, die Allokationsmuster für Biomasse in einzelne Baumkompartimente zu evaluieren und additive allometrische Gleichungen für *Mytilaria laosensis* im Südosten Chinas zu entwickeln. Für diese Studie wurden 42 gefällte Bäume verwendet, um allometrische Gleichungen für die gesamte Biomasse zu entwickeln. Wir berechneten erst die Anteile von Stamm, Ästen, Wurzeln und Blättern. Wir untersuchten dann die Beziehungen zwischen Biomassefraktionen und Brusthöhendurchmesser, Baumhöhe und Kronendurchmesser als unabhängige Variablen. Die ‚seemingly unrelated regressions‘ Methode wurde verwendet, um die Biomasse mit additiven allometrischen Funktionen zu ermitteln. Der Stamm hatte den größten Anteil an Biomasse (70.44 %), gefolgt von Wurzeln (20.35 %) und Ästen (7.17 %) mit dem geringsten Anteil an Biomasse in den Blättern (2.04 %). Der Anteil von Stamm-, Blatt- und Astbiomasse nahm mit dem Durchmesser in Brusthöhe zu, wobei der Anteil der unterirdischen Biomasse mit Durchmesser abnimmt. Die additiven Biomassemodelle zeigten eine gute Modellperformance mit einer erklärten Varianz von 94–98 %. Unsere Baumart-spezifischen allometrischen Gleichungen tragen zum Wissen über Kronen-, ober- und unterirdische Biomasse subtropischer Wälder bei, die noch wenig untersucht wurde. Die in unserer Studie erstellten Funktionen können nun verwendet werden, um den Biomasse- und Kohlenstoffpool von *Mytilaria laosensis* Plantagen in China abzuschätzen.

1. Introduction

Forest biomass is an important indicator to evaluate forest ecosystem productivity (Bond-Lamberty et al. 2002), to quantify vegetation carbon pools, and to examine ecosystem structure and function (Garkoti et al. 2008; Overman et al. 1994). Forests dominate terrestrial biomes, and are in consequence important for the earth's biosphere, playing a key role in maintaining regional ecological environments, carbon balance, and mitigating global warming (Brown et al. 1999; Bayen et al. 2016).

This important role makes it imperative to estimate forest biomass accurately. Destructive biological sampling (Brown et al. 1997) involves felling of all trees within a certain area, followed by measuring the weight of each of their parts (Basuki et al.

2009). While this sampling method is most accurate, it is expensive, labor-intensive and time-consuming. Destructive sampling is thus suitable only for a small areas or with small sample sizes (Mensah et al. 2017). Combining non-destructive sampling and allometric biomass models is trade-off of accuracy and costs. The allometric equations permit estimating biomass at different scales and multiple time steps (Ter-Mikaelian and Korzukhin 1997). Allometric biomass models are essential for converting non-destructive obtained tree information, from ground-based investigation or remote sensing to biomass (Dimobe et al. 2018).

Different biomass estimation models have been established globally (Lambert et al. 2008; Jenkins et al. 2003). Several predictive variables, such as diameter at breast height (DBH), tree height, crown diameter (CD), crown area, or wood density have been considered in such models, depending on study objectives and the species of interest. DBH, irrespective which biomass is studied, is the most commonly used predictive variable in allometric equations, because its measurements are easy and accurate (Riofrío et al. 2015; Chen et al. 2017; Xiao et al. 2011). Many other allometric growth equations use tree height (Dimobe et al. 2018), CD (Kuyah et al. 2012; Schneider et al. 2011; Mäkelä and Albrektson 1992), or wood density (Basuki et al. 2009; Kalita et al. 2015) as additional predictive variables. The results from these studies show that combining different predictive variables can improve the model performance at different locations and tree species (Dimobe et al. 2018; Schneider et al. 2011; Yang et al. 2017; Sileshi 2014).

Until now, there have been a few studies based on the allometric growth equations that considered the biomass additivity of individual tree parts (Behling et al. 2019; Affleck et al. 2016). If the relationships between the individual tree parts are ignored in estimating biomass with a model, this may result in differences between the sum of the predicted values calculated from the separate biomass models for each component and the value predicted from the biomass model for the whole tree. Thus, the construction of additive biomass models has attracted the attention of many researchers (Affleck and Diéguez-Aranda 2016; Xu et al. 2015; Carvalho and Parresol 2003), in which the biomass model for each part of a tree must be an additive to satisfy the requirements for demonstrating logical relationships (Sileshi 2014). There are several methods that can ensure the additivity of such equations, including the adjusted proportion (AP) (Dong et al. 2014), generalized method of moments (GMM), and seemingly unrelated regression (SUR) (Tang et al. 2001; Parresol 2001). Of these, SUR has been widely used as it considers the correlation between the equations and ensures high efficiency of additivity (Riofrío et al. 2015; Bi et al. 2004).

Mytilaria laosensis Lecomte is a valuable broadleaved tree species mainly distributed in South China and Southeast Asia (Guo et al. 2006). It is well known for fast-growing high-yield plantations and has a broad biological adaptability to soil type and environmental condition (Huang et al. 2009). The *M. laosensis* wood has high quality due to moderate density and not easy to crack and it is therefore widely used as raw

material for high quality furniture and covering plywood (Liang et al. 2007). In addition, it also has strong carbon sink potential (Ming et al. 2014). Zheng et al. (2014) studied the carbon storage and distribution pattern of different indigenous species plantations system in subtropical China and found that *M. laosensis* had large carbon storage capacity. Consequently, *M. laosensis* is expected to become one of the main tree species used in afforestation in the subtropical forests in China (Liu et al. 2012). However, only a few allometric growth equations are available for measuring its above- and belowground biomass (Zhang 2016; Ming et al. 2012; Wu 2005), and no additive allometric model for *M. laosensis* has been developed. The lack of accurate species-specific allometric models may lead to inaccurate estimations of carbon stocks (Van Vinh et al. 2019; Mahmood et al. 2019). In addition, different management and geographical conditions also lead to differences in above- and belowground biomass allocation (Meng et al. 2019). The objective of this study was to develop additive allometric biomass models for *M. laosensis*.

2. Materials and Methods

2.1 Study Sites

The study was conducted in Xijiang Forestry Station, Yunfu City, Guangdong Province, southeast China (23°07'N, 111°51'E) (Figure 1). The site has south subtropical monsoon climate with annual average temperature of 21.5°C. The average annual frost-free period is about 315–340 days. The average precipitation is 1600–1700 mm per year with the wet season extending from April to September and the dry season from October to March. The understory shrub layer consists of *Microstegium vagans* (Nees ex Steud.), *Mimosa bimucronata* (DC.) Kuntze, and *Ilex asprella* (Hook. Et Arne.) Champ. Ex Benth. The studied plantation was established in early 2010 by planting 1-year-old seedlings, with an average seedling height of 0.6 m. The density of the studied plantation was 1667 trees per hectare, the survival rate was 97.1%, the average DBH was 15.23 cm, the average tree height was 16.41 m, and the basal area was 22.37 m² per hectare. The plantation has not been thinned.

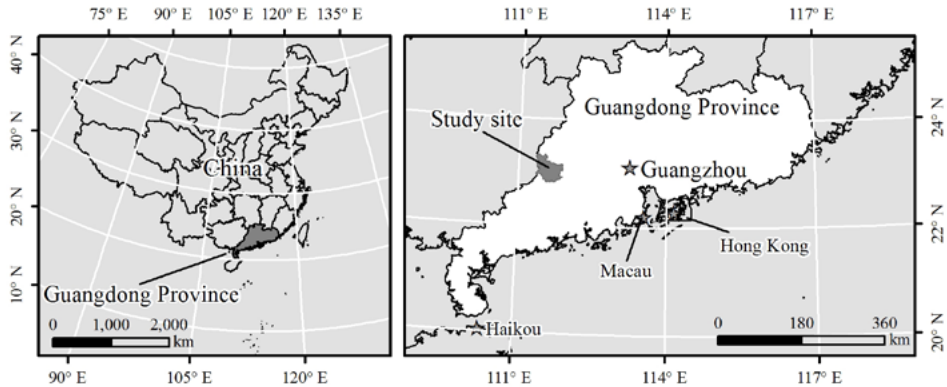


Figure 1: The Location of the study site.

Abbildung 1: Der Standort des Untersuchungsortes.

2.2 Biomass Data

In July 2018, six sampling plots (each 20 m × 30 m) were established at random locations in this *M. laosensis* plantation forest. Then we measured the diameter at breast height (DBH) using a diameter tape. We chose and excavated seven sample trees for biomass evaluation. The DBH of the sampled trees ranged from 10.5 cm to 21.5 cm, and the tree height from 14.1 m to 18.2 m (Table 1). The DBH of each tree was measured before being cutting the tree. Tree height, lowest living branch height, and crown diameter (CD) in four directions were recorded after felling.

Table 1: Range of diameter at breast height, tree height, crown diameter and biomass of sampled trees. (mean \pm standard deviation).

Tabelle 1: Durchmesserbereich in Brusthöhe, Baumhöhe, Kronendurchmesser und Biomasse der untersuchten Bäume. (Mittelwerte \pm Standardabweichung).

| Diameter at breast height range (cm) | Tree height (m) | Crown diameter (m) | Biomass (kg) | | | | Number of harvested tree |
|--|--------------------|-----------------------|-------------------|------------------|-----------------|------------------|-----------------------------|
| | | | Stem | Branch | Leaf | Root | |
| 10—12 | 14.50 \pm 0.28 | 2.45 \pm 0.06 | 29.56 \pm 3.46 | 2.70 \pm 0.32 | 0.76 \pm 0.07 | 10.84 \pm 0.74 | 4 |
| 12—14 | 15.16 \pm 0.22 | 2.97 \pm 0.33 | 45.18 \pm 2.54 | 4.49 \pm 0.61 | 1.33 \pm 0.15 | 14.47 \pm 1.04 | 7 |
| 14—16 | 15.86 \pm 0.24 | 3.54 \pm 0.31 | 61.72 \pm 7.25 | 6.18 \pm 1.26 | 1.82 \pm 0.22 | 17.77 \pm 2.31 | 6 |
| 16—18 | 16.72 \pm 0.32 | 4.13 \pm 0.15 | 80.34 \pm 7.42 | 8.02 \pm 1.03 | 2.27 \pm 0.31 | 21.53 \pm 1.83 | 11 |
| 18—20 | 17.44 \pm 0.38 | 4.68 \pm 0.18 | 101.75 \pm 9.66 | 10.82 \pm 1.73 | 2.97 \pm 0.31 | 27.04 \pm 2.78 | 11 |
| 20—22 | 18.01 \pm 0.17 | 4.74 \pm 0.09 | 126.34 \pm 12.3 | 14.55 \pm 1.18 | 3.91 \pm 0.26 | 35.46 \pm 5.45 | 3 |

To measure stem biomass, stems were cut into 2 m long pieces, and the fresh weight of each segment was measured in the field. A thin disc was then cut from each piece to determine the weight with an accuracy of 0.5 g. The samples were then transported to the laboratory and dried to a constant weight in an oven at 75°C. From stem moisture content we calculated stem biomass. The tree crown was evenly vertically divided into three layers, and all branches, including leaves, were weighted in the field with a precision of 0.5 g. We separated leaves and wood for three selected branches and weighted wood and leaves separately and the ratio between leaves and branch mass were used to estimate leaf mass of the other branches. Finally, the samples (minimum 200 g) were taken back to the laboratory and dried to a constant mass in an oven at 75°C, after which the dry weight was measured, and the moisture content of each layer was calculated to obtain the biomass of branches and leaves (Ketterings et al. 2001).

Then we excavated a hole with radius of 1 m around each tree to a depth of 0.5 m and extracted the all root components including the broken roots. All roots were separated into thick roots (≥ 5 cm diameter), medium roots (2–5 cm diameter), fine roots (≤ 2 cm diameter) and stump. Representative samples (minimum 500 g) of each root fraction were weighed in the field. Then all samples were taken to the laboratory, dried to a constant weight, and the total belowground biomass was calculated (Wang 2006).

2.3 Data Analysis

The allocation of biomass to the stems, branches, leaves, and roots was estimated by calculating the ratio of the biomass of each part to total biomass. Statistical factors, such as arithmetic mean and standard deviation of total biomass (e.g., stem, bran-

ches, roots, and leaves) were calculated. The biomass portioning was used to test significance ($p < 0.05$). Additionally, the one-way ANOVA was used to test the differences between the biomass portions. The relationship between the explanatory variables (DBH, height, and CD) and the dependent variables (biomass stem, branch, leaf, and root) was evaluated using graphs to determine the abnormal values that might affect the fitted results. The allometric equations were created for the leaves, branches, roots, stems and total components depended on three different non-linear models with DBH, height (H) and CD as independent variables: equation (1), DBH as the only predictor variable; equation (2), DBH combined with tree height; and equation (3), DBH combined with tree height and CD as additional predictor variables. Logarithmic transformation was used to correct heteroscedasticity. The allometric models for the biomass of different parts (W_i) related to DBH, H and CD were established (Brown et al. 1989; Chave et al. 2005):

$$\begin{aligned} \ln(W_i) &= \ln(\alpha_i) + \beta_i \cdot \ln(\text{DBH}) && \text{Eq.(1),} \\ \ln(W_i) &= \ln(\alpha_i) + \beta_i \cdot \ln(\text{DBH}^2 \times H) && \text{Eq.(2),} \\ \ln(W_i) &= \ln(\alpha_i) + \beta_i \cdot \ln(\text{DBH}^2 \times H) + \gamma_i \cdot \ln(\text{CD}) && \text{Eq.(3),} \end{aligned}$$

The integration of DBH and tree height as a combined variable could solve the problem of collinearity and explain the changes in DBH at different heights (Dimobe et al. 2018). The SUR (Riofrío et al. 2015) fitting biomass model realized the additivity of the equation by constraining the equation parameters. This technique explained the correlation between regression residues, resulting in a small variance of the regression coefficients (Parresol 1999). The aggregated additive allometric equation satisfied the following conditions: (1) the sum of the biomass of individual part was equal to the total biomass; (2) the sum of the biomass of stem, branches, and leaves was equal to the aboveground biomass; and (3) the sum of branches and leaves was equal to the crown biomass. Estimation of three systems of equations were conducted by the SAS procedure of PROC model (SAS Institute Inc, Cary, NC, USA). For equation (1):

$$\begin{aligned} \ln(W_s) &= \ln(\alpha_s) + \beta_s \cdot \ln(\text{DBH}) \\ \ln(W_b) &= \ln(\alpha_b) + \beta_b \cdot \ln(\text{DBH}) \\ \ln(W_l) &= \ln(\alpha_l) + \beta_l \cdot \ln(\text{DBH}) \\ \ln(W_r) &= \ln(\alpha_r) + \beta_r \cdot \ln(\text{DBH}) \\ \ln(W_c) &= \ln(\alpha_b \cdot \text{DBH}^{\beta_b} + \alpha_l \cdot \text{DBH}^{\beta_l}) \\ \ln(W_a) &= \ln(\alpha_s \cdot \text{DBH}^{\beta_s} + \alpha_b \cdot \text{DBH}^{\beta_b} + \alpha_l \cdot \text{DBH}^{\beta_l}) \\ \ln(W_t) &= \ln(\alpha_r \cdot \text{DBH}^{\beta_r} + \alpha_s \cdot \text{DBH}^{\beta_s} + \alpha_b \cdot \text{DBH}^{\beta_b} + \alpha_l \cdot \text{DBH}^{\beta_l}) \end{aligned}$$

Where W_s , W_b , W_l , W_r , W_c , W_a , W_t are stem, branch, leaf, root, crown, aboveground, and total biomass (kg), respectively; and α_i , β_i , and γ_i are the coefficients.

For equation (2):

$$\begin{aligned}
 \ln(W_s) &= \ln(\alpha_s) + \beta_s \cdot \ln(DBH^2 \times H) \\
 \ln(W_b) &= \ln(\alpha_b) + \beta_b \cdot \ln(DBH^2 \times H) \\
 \ln(W_i) &= \ln(\alpha_i) + \beta_i \cdot \ln(DBH^2 \times H) \\
 \ln(W_r) &= \ln(\alpha_r) + \beta_r \cdot \ln(DBH^2 \times H) \\
 \ln(W_c) &= \ln(\alpha_b \cdot (DBH^2 \times H)^{\beta_b} + \alpha_i \cdot (DBH^2 \times H)^{\beta_i}) \\
 \ln(W_a) &= \ln(\alpha_s \cdot (DBH^2 \times H)^{\beta_s} + \alpha_b \cdot (DBH^2 \times H)^{\beta_b} + \alpha_i \cdot (DBH^2 \times H)^{\beta_i}) \\
 \ln(W_t) &= \ln(\alpha_r \cdot (DBH^2 \times H)^{\beta_r} + \alpha_s \cdot (DBH^2 \times H)^{\beta_s} + \alpha_b \cdot (DBH^2 \times H)^{\beta_b} + \alpha_i \cdot (DBH^2 \times H)^{\beta_i})
 \end{aligned}$$

For equation (3):

$$\begin{aligned}
 \ln(W_s) &= \ln(\alpha_s) + \beta_s \cdot \ln(DBH^2 \times H) + \gamma_s \cdot \ln(CD) \\
 \ln(W_b) &= \ln(\alpha_b) + \beta_b \cdot \ln(DBH^2 \times H) + \gamma_b \cdot \ln(CD) \\
 \ln(W_i) &= \ln(\alpha_i) + \beta_i \cdot \ln(DBH^2 \times H) + \gamma_i \cdot \ln(CD) \\
 \ln(W_r) &= \ln(\alpha_r) + \beta_r \cdot \ln(DBH^2 \times H) + \gamma_r \cdot \ln(CD) \\
 \ln(W_c) &= \ln(\alpha_b \cdot (DBH^2 \times H)^{\beta_b} \cdot (CD)^{\gamma_b} + \alpha_i \cdot (DBH^2 \times H)^{\beta_i} \cdot (CD)^{\gamma_i}) \\
 \ln(W_a) &= \ln(\alpha_s \cdot (DBH^2 \times H)^{\beta_s} \cdot (CD)^{\gamma_s} + \alpha_b \cdot (DBH^2 \times H)^{\beta_b} \cdot (CD)^{\gamma_b} + \alpha_i \cdot (DBH^2 \times H)^{\beta_i} \cdot (CD)^{\gamma_i}) \\
 \ln(W_t) &= \ln(\alpha_r \cdot (DBH^2 \times H)^{\beta_r} \cdot (CD)^{\gamma_r} + \alpha_s \cdot (DBH^2 \times H)^{\beta_s} \cdot (CD)^{\gamma_s} + \alpha_b \cdot (DBH^2 \times H)^{\beta_b} \cdot (CD)^{\gamma_b} + \alpha_i \cdot (DBH^2 \times H)^{\beta_i} \cdot (CD)^{\gamma_i})
 \end{aligned}$$

The use of logarithmic allometric equation may produce the systematic deviations of the response variable when converting back to the original scale (Ledermann and Neumann 2006; Eckmüllner 2006). To correct this bias, the correction factors (CF) of these equations were computed (Baskerville 1972; Sprugel 1983).

$$CF = \exp\left(\frac{SEE^2}{2}\right) \quad \text{Eq.(4)}$$

SEE is the standard error of the estimates. The model was evaluated by the following three goodness-of-fit statistical methods: root mean square error (RMSE), Akaike information criterion (AIC), and the adjusted coefficient of determination (Adj. R²) (Cai et al. 2013). The most suitable model was that with the lowest RMSE and AIC, and the highest Adj. R². A t-test was used to examine significant deviations between the observed and estimated values of the crown, aboveground, and total biomass, and graphical analyses between the predicted vs. observed values were carried out using the best additive allometric models.

$$RMSE = \sqrt{\frac{\sum_{i=1}^N (Y_i - \hat{Y}_i)^2}{n}} \quad \text{Eq.(5),}$$

$$AIC = n \ln(SSR) + 2(k+1) - n \ln(n) \quad \text{Eq.(6),}$$

$$Adj.R^2 = 1 - \left(1 - \frac{\sum_{i=1}^n (Y_i - \hat{Y}_i)^2}{\sum_{i=1}^n (Y_i - \bar{Y})^2}\right) \frac{n-1}{n-k} \quad \text{Eq.(7).}$$

Where Y_i is the observed value, \hat{Y}_i is the estimated biomass values based on models, \bar{Y}_i is the mean value of the biomass, n is the number of samples, and k is the number of parameters.

3. Results

3.1 Biomass Partitioning

The biomass of the different *M. laosensis* tree parts (stems, roots, branches, and leaves) were significantly different ($p < 0.001$). The stem accounted for the largest contribution to the total biomass at $70.44\% \pm 2.33$ (mean \pm SD), while the contributions of the belowground, branch, and leaf biomass were $20.35\% \pm 2.80$, $7.17\% \pm 0.84$, and $2.04\% \pm 0.18$, respectively. The proportion of stems, branches, and leaves biomass exhibited similar incremental trends with DBH (Figure 2). With increasing DBH from 10.5 to 21.5 cm, the proportion contributed by the stem to the total biomass increased from 65.85% to 75.60%, while that of the branches and leaves increased from 5.05% to 9.27% and 1.59% to 2.41%, respectively. In contrast, the proportion attributed to belowground biomass decreased from 26.39% to 18.15%.

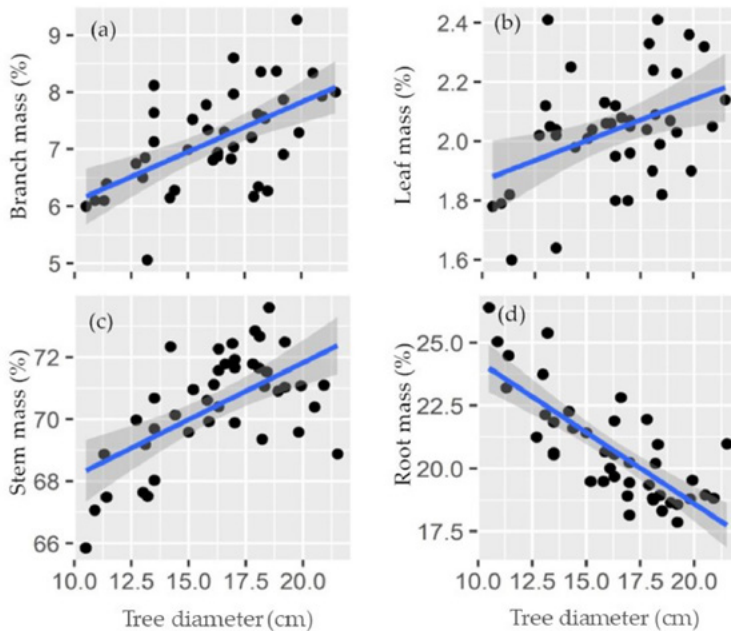


Figure 2: Partitioning of total biomass in relation to diameter of *M. laosensis*, percentage of (a) stem biomass, (b) leaf biomass, (c) branch biomass, (d) belowground biomass.

Abbildung 2: Verteilung der Gesamtbiomasse in Bezug auf den Durchmesser von *M. laosensis*, Prozentsatz von (a) Stammbiomasse, (b) Blattbiomasse, (c) Zweigbiomasse, (d) unterirdische Biomasse.

3.2 Biomass Allometric Equations

The non-linearity trend in the observed values for tree height, crown, aboveground, and total biomass as a function of DBH is displayed in Figure 3. Our results showed model 1 with DBH as the only predictor, could effectively explain the biomass of individual part, with $R^2 > 94\%$ and $RMSE < 0.1$ (Table 2). The addition of tree height into the biomass model significantly improved the fit of some models, while the addition of CD only significantly improved the fit of the root biomass model. For leaf biomass, model 2 had a larger R^2 and smaller RMSE and AIC, and the addition of CD did not improve the fit of the model. For branch biomass, model 1 was a better fit. For stem biomass, each model had a similar fit, but model 2 showed a better fit with respect to R^2 , RMSE, and AIC. For root biomass, the addition of height and CD improved the overall fit of the model, and model 3 had a larger R^2 , and smaller RMSE and AIC.

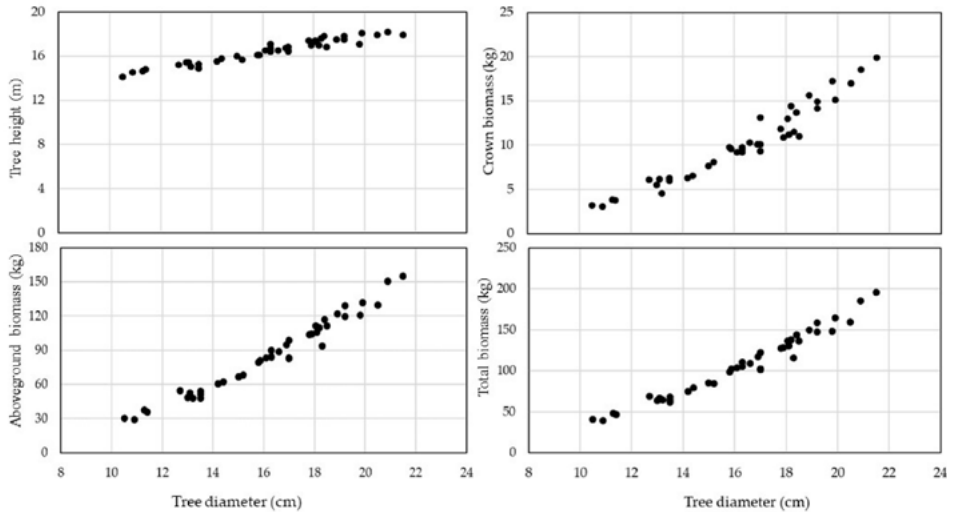


Figure 3: Relationships between DBH and (a) tree height, (b) crown biomass, (c) aboveground biomass, and (d) total biomass of *M. laosensis*.

Abbildung 3: Beziehungen zwischen DBH und (a) Baumhöhe, (b) Kronenbiomasse, (c) oberirdischer Biomasse und (d) Gesamtbiomasse von *M. laosensis*.

To estimate the biomass of *M. laosensis* more accurately, the optimal biomass model for an individual part was used to construct the multivariate additive biomass model (Table 2). The R^2 values for total biomass and the biomass of individual parts in the optimal additive biomass models were more than 95%, and the RMSE was relatively small (Table 3). The correction factors for the optimal equations were also listed (Table 3). The fit of the stem, aboveground, and whole plant biomass models was better (R^2 was relatively large and RMSE was relatively small) than that of the biomass models of leaves, branches, roots, and crowns (smaller R^2 and larger RMSE values). Figure 4 shows the linear 1:1 trend for the scatter plot of the observed and predicted crown, aboveground, and total biomass.

Table 2: Regression equations for estimation of leaf, branch, stem, and root biomass through seemingly unrelated regression in *M. laosensis*. α , β , and γ are the coefficients used in the model. DBH, diameter at breast height; H, tree height; CD, crown diameter; RMSE, root mean square error; AIC, Akaike information criterion; Adj. R^2 , adjusted coefficient of determination.

Tabelle 2: Regressionsgleichungen zur Schätzung der Biomasse von Blättern, Ästen, Stamm und Wurzeln durch seemingly unrelated regressions bei *M. laosensis*. α , β und γ sind die im Modell verwendeten Koeffizienten. DBH, Brusthöhendurchmesser; H, Baumhöhe; CD, Kronendurchmesser; RMSE, quadratischer Mittelwertfehler; AIC, Akaike-Informationskriterium; Adj. R^2 , angepasster Bestimmungskoeffizient.

| Model | Predictors | Components | Regression coefficients | | | Performance criteria | | |
|-------|------------|------------|--------------------------------------|-------------------------------------|--------------------------------------|----------------------|-----------------|--------------|
| | | | ln(α) | β | γ | RMSE | AIC | Adj. R^2 |
| 1 | DBH | Leaf | -6.02*** \pm 0.22 | 2.43*** \pm 0.08 | | 0.093 | -76.148 | 0.959 |
| 2 | DBH**H | Leaf | -7.86***\pm 0.28 | 1.03***\pm 0.03 | | 0.092 | -76.614 | 0.959 |
| 3 | DBH**H;CD | Leaf | -8.81*** \pm 0.71 | 1.20*** \pm 0.12 | -0.36** \pm 0.25 | 0.093 | -76.56 | 0.955 |
| 1 | DBH | Branch | -5.19***\pm 0.25 | 2.58***\pm 0.09 | | 0.107 | -64.913 | 0.952 |
| 2 | DBH**H | Branch | -7.14*** \pm 0.33 | 1.09*** \pm 0.04 | | 0.110 | -62.408 | 0.950 |
| 3 | DBH**H;CD | Branch | -6.69*** \pm 0.86 | 1.01*** \pm 0.15 | 0.17** \pm 0.30 | 0.111 | -60.754 | 0.948 |
| 1 | DBH | Stem | -2.09*** \pm 0.15 | 2.29*** \pm 0.05 | | 0.064 | -108.021 | 0.978 |
| 2 | DBH**H | Stem | -3.84***\pm 0.18 | 0.97***\pm 0.02 | | 0.061 | -111.397 | 0.980 |
| 3 | DBH**H;CD | Stem | -3.77*** \pm 0.48 | 0.96*** \pm 0.08 | 0.02** \pm 0.17 | 0.065 | -109.418 | 0.977 |
| 1 | DBH | Root | -1.91*** \pm 0.19 | 1.77*** \pm 0.07 | | 0.083 | -86.291 | 0.940 |
| 2 | DBH**H | Root | -3.26*** \pm 0.24 | 0.75*** \pm 0.03 | | 0.081 | -88.372 | 0.943 |
| 3 | DBH**H;CD | Root | -4.77***\pm 0.58 | 1.02***\pm 0.09 | -0.57***\pm 0.20 | 0.074 | -94.167 | 0.952 |

*** Significance level: $p < 0.001$. ** Significance level: $p < 0.01$. The final selected models of each biomass part are in bold.

Table 3: Selected biomass equations simultaneously fitted through seemingly unrelated regression in *M. laosensis*. AGB, aboveground biomass; TGB, total biomass; DBH, diameter at breast height; H, height; CD, crown diameter; RMSE, root mean square error; AIC, Akaike information criterion; Adj. R^2 , adjusted coefficient of determination; CF, logarithmic correction factor.

Tabelle 3: Ausgewählte Biomassegleichungen, die gleichzeitig durch scheinbar nicht verwandte Regression bei *M. laosensis* angepasst wurden. AGB, oberirdische Biomasse; TGB, Gesamtbiomasse; DBH, Durchmesser in Brusthöhe; H, Höhe; CD, Kronendurchmesser; RMSE, quadratischer Mittelwertfehler; AIC, Akaike-Informationskriterium; Adj. R^2 , angepasster Bestimmungskoeffizient; CF, logarithmischer Korrekturfaktor.

| Components | Biomass equations | RMSE | Adj. R^2 | CF |
|------------|---|-------|------------|-------|
| Leaf | $\ln W_L = -7.86 + 1.03 \ln(\text{DBH}^2 H)$ | 0.092 | 0.959 | 1.110 |
| Branch | $\ln W_B = -5.19 + 2.58 \ln(\text{DBH})$ | 0.107 | 0.952 | 1.124 |
| Stem | $\ln W_S = -3.84 + 0.97 \ln(\text{DBH}^2 H)$ | 0.061 | 0.98 | 1.096 |
| Root | $\ln W_R = -4.77 + 1.02 \ln(\text{DBH}^2 H) - 0.52 \ln(\text{CD})$ | 0.074 | 0.952 | 1.061 |
| Crown | $\ln W_{\text{CD}} = \ln(e^{-7.86}(\text{DBH}^2 H)^{1.03} + e^{-5.19}(\text{DBH})^{2.58})$ | 0.087 | 0.972 | |
| AGB | $\ln W_{\text{AG}} = \ln(e^{-3.84}(\text{DBH}^2 H)^{0.97} + e^{-7.86}(\text{DBH}^2 H)^{1.03} + e^{-5.19}(\text{DBH})^{2.58})$ | 0.058 | 0.981 | |
| TGB | $\ln W_T = \ln(e^{-4.77}(\text{DBH}^2 H)^{1.02}(\text{CD})^{-0.52} + e^{-3.84}(\text{DBH}^2 H)^{0.97} + e^{-7.86}(\text{DBH}^2 H)^{1.03} + e^{-5.19}(\text{DBH})^{2.58})$ | 0.055 | 0.979 | |

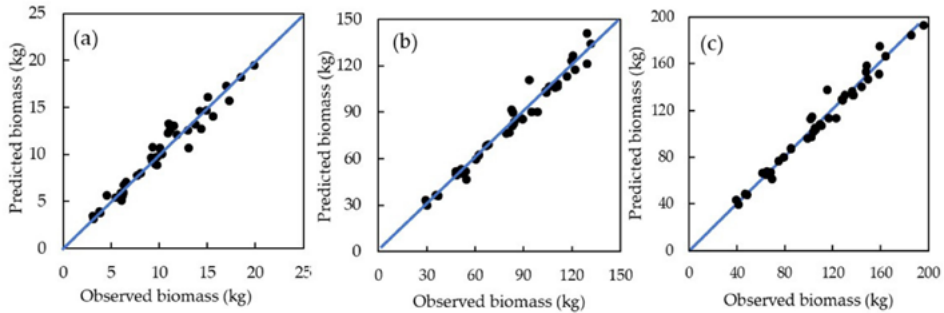


Figure 4: Scatterplots for the observed biomass and the predicted biomass of (a) crown, (b) aboveground, (c) total biomass of additive equations. Lines are 1:1 equivalence.

Abbildung 4: Streudiagramme für die beobachtete Biomasse und die vorhergesagte Biomasse von (a) Krone, (b) oberirdisch, (c) Gesamtbiomasse der additiven Gleichungen. Linien entsprechen 1:1.

4. Discussion

Biomass is a form of energy accumulated in the process of plant growth and development (Mensah et al. 2017; Dong et al. 2014). Plant species, age, and the external environment can change biomass distribution patterns in various parts of forest trees. Our results demonstrated that the stem accounted for the largest proportion of the total biomass (nearly 72%), followed by the roots (19.5%). Leaf biomass contributed the smallest amount to the total biomass, about 2%; this is similar to the proportion determined in other studies (Zhang 2016; Wu 2005). Our biomass results suggest that photosynthetic products in *M. laosensis* are primarily concentrated in the stem and roots. Biomass accumulation in the stem promotes large diameter wood in the tree species, while the well-developed root system promotes the absorption of water and nutrients, thereby supporting tree growth. In our study, the biomass proportion of the stem, branches, and leaves increased, and root biomass decreased with increasing diameter class. These results contradict those of previous studies on *M. laosensis*, and we speculated that this might be owing to the difference in growth periods of the studied tree species or the strategies. As a shade-intolerant tree species, *M. laosensis* competes in the initial growth stages for limited terrestrial resources, such as light. In forests, trees with more branch biomass have a competitive advantage, mainly through advantage in tree height and expansion of the crown resulting in shading of neighboring trees (Dimobe et al. 2018). Similar growth trends have also been found in a previous study with fast-growing *Eucalyptus* spp., which allocate more biomass in the stem compared with leaves and branches (Kuyah et al. 2012).

When constructing the biomass model, the sum of the biomass of individual part was equal to the total biomass (Dimobe et al. 2018; Behling et al. 2019; Meng et al. 2019).

When the correlation between the total biomass and that of individual part was taken into account, the fitting equations were required to be additive. Some of the published biomass equations are not-additive because they were estimated by ordinary least-squares regression (OLS) (Cai et al. 2013; Blujdea et al. 2012). The use of SUR to construct an additive allometric growth equation can however account for the correlation between the biomasses of individual part, resulting in more effective parameter estimation (Parresol 2011); SUR is not only able to determine the additivity of the equation, but also reduces the predicted interval of biomass estimation (Bi et al. 2004; Parresol 2001; Dong et al. 2015).

In the current study, a logarithmic transformation equation was used to estimate the relationship between biomass and explainable variables. When an estimated value was converted back to the original untransformed value, the expected biomass will still be underestimated. To correct this deviation, Baskerville (1972) and Sprugel (1983) proposed a correction factor (CF) method, which is often used to correct system errors. Consequently, the results of this study indicated that a few deviation were produced on the process of using logarithmic transformation to fit the biomass allometric equations. Some researchers believe that the correction is unnecessary, since the difference in biomass estimation can be considered negligible (Malimbwi et al. 1994). However, it is suggested to analyze each case individually to make sure the necessity of CF in biomass estimation.

Most studies on allometric models have been based on DBH to predict tree biomass (Xiang et al. 2016; Kusmana et al. 2018). In our study, the model containing DBH as the variable had an explanation rate of over 90% for stem, branch, leaf, and below-ground biomass variability. Consistent with previous studies (Dimobe et al. 2018; Van Vinh 2019; Xiang et al. 2016), the addition of tree height as an independent variable to the equation improved the fit of the equation. It has also been suggested that the estimation of biomass could be improved by combining wood density and CD as predictors (Chave et al. 2005; Ploton et al. 2016). In our study, however, the addition of CD as a predictor variable into the equation reduced root RMSE from 0.083 to 0.074, and slightly increased the fitting degree from 0.94 to 0.952, indicating a close relationship between the crown and belowground part (Kuyah et al. 2012; Harrington et al. 2003). Additionally, the crown height, a potential and efficient input variable in other studies (Ledermann and Neumann 2006; Repola 2009) can be studied in further research on this species.

To date, there have been few studies on the allometric growth equation regarding the biomass of *M. laosensis*, and only a few researchers (Zhang 2016; Ming et al. 2012; Wu 2005) from Guangxi and Fujian in China have studied *M. laosensis*. The published allometric growth equation for *M. laosensis* only uses DBH as predictor variables (Zhang 2016; Ming et al. 2012; Wu 2005). In our study, we added CD into the predictive variables of biomass for this species, but the fitting effect was not improved. We also compared the equations of this paper with other biomass allometric equations for

M. laosensis (Figure 5). For the same DBH, the models construct by Ming et al. (2012) and Wu (2005) gave higher total biomass values than our study. Ming et al. (2012) established an allometric growth equation for the biomass of 28-year-old *M. laosensis* in Guangxi using DBH and tree height as explanatory variables, with a sample size of 13 trees (DBH range of 17 cm to 31 cm, compared with the range in our study of only 10.5 cm to 21.5 cm). Paul et al. (2018) stated that a sample of fewer than 15 independent samples may give inaccurate results; however, Ming et al. (2012) used a sample size smaller 15. Therefore, the accuracy of equation previously published needs to be improved. Zhang (2016) studied the biomass of a 22-year-old *M. laosensis* plantation in the Fujian area of China, with a sample size of 15, but their sampling DBH range was not reported. However, it can be inferred from the comparison with the equations in this paper that the range of the DBH of the equation should be close to our paper. Wu et al. (2005) established biomass models for the branches, bark, leaves, and stems of 15-year-old *M. laosensis*, but they had a small sample size (only four), this may also result in the low accuracy. In their study, the individual branch and leaf biomass were estimated based on the basal diameter of the branches, and then the branch and leaf biomass of the whole tree was calculated. Compared with the method used in our study, the method used by Wu et al. (2005) was complex, the sample size was small, additivity was not taken into account, and the accuracy of model fit was low. In addition, the root sampling method may also cause a few discrepancies for biomass estimation in those studies. Excavation was used to determine the belowground biomass in this paper, which was the same way as Ming et al. (2012). Zhang (2016) studied the roots by collecting along a 1.2 m deep soil profile, which was divided into 6 layers of 20 cm sampling depth each. Wu (2005) estimated the root biomass by the root-shoot ratio of the forest communities. Currently, few studies have considered the correction for the loss of the roots on *M. laosensis* for instance using Goff's approach (2001). Furthermore, the discrepancies between the current studies of total biomass by comparing the biomass of single compartments (Supplementary Figure S1) were further explored and the results indicated that the discrepancy by Wu (2005) is mostly caused by branches and roots, while for Ming (2012) it is stem and roots, especially for larger diameters. For Zhang (2016), the discrepancy was mainly attributable to branches. In all, the differences in the estimated biomass between this study and other studies may be due to differences in sampling sites, the DBH ranges, sampling approach, number of samples, and management. The accuracy of the model increases with increasing sample size (Kusmama et al. 2018). There should be already enough material available to make a robust widely applicable biomass model for *M. laosensis*, at least for certain regions.

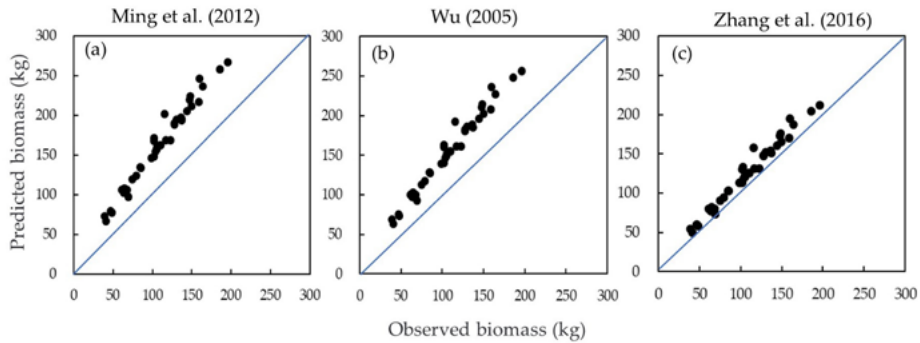


Figure 5: Scatterplots for the observed biomass and the predicted biomass of total biomass of (a) Ming et al (2012), (b) Zhang (2016), (c) Wu et al (2005). Lines are 1:1 equivalence.

Abbildung 5: Streudiagramme für die beobachtete Biomasse und die vorhergesagte Biomasse der Gesamtbiomasse von (a) Ming et al. (2012), (b) Zhang (2016), (c) Wu et al. (2005). Linien entsprechen 1: 1.

5. Conclusions

Mytilaria laosensis allocates more biomass in the woody parts, especially in stem, probably to confer a competitive advantage over its surrounding competitors. DBH is effective in estimating branch biomass; the introduction of the independent variable of tree height can improve the accuracy of determining leaf and stem biomass, while the addition of CD as a variable can improve the prediction of belowground biomass. The biomass model constructed in our study can be used to estimate the biomass and carbon pool of *M. laosensis* plantations from the same region and exhibiting similar stand properties (DBH, height, CD) as the studied stands. However, this newly constructed allometric model must be used cautiously in estimating the biomass of trees in other locations with different tree growth patterns and sizes.

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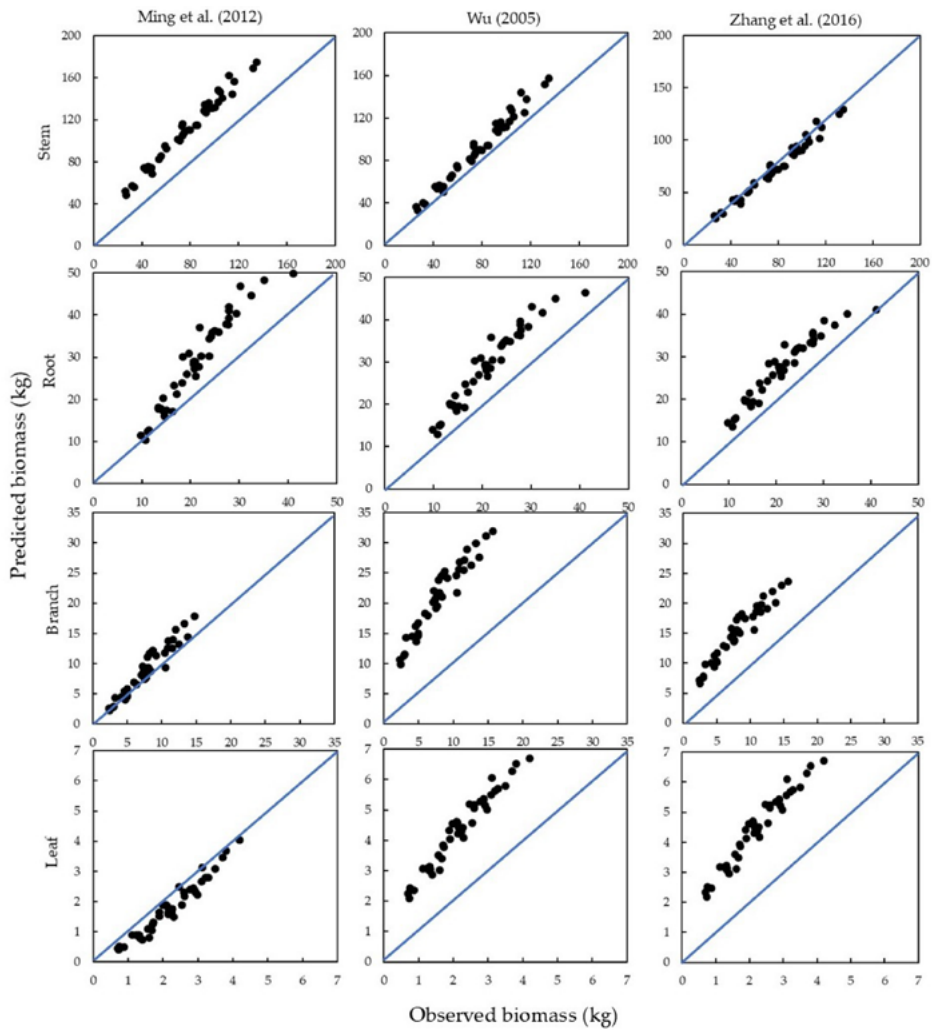
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Supplementary Material



Appendix: Supplementary Figure S1.

Anhang: Supplementary Figure S1.

| Diameter at breast height (cm) | Tree height (m) | Crown diameter (m) | Biomass (kg) | | | |
|-----------------------------------|--------------------|-----------------------|--------------|--------|--------|-------|
| | | | Leaf | Branch | Stem | Root |
| 10.5 | 14.1 | 2.4 | 0.73 | 2.46 | 27 | 10.82 |
| 10.9 | 14.5 | 2.5 | 0.7 | 2.39 | 26.26 | 9.81 |
| 11.3 | 14.6 | 2.38 | 0.88 | 2.95 | 33.29 | 11.22 |
| 11.4 | 14.8 | 2.5 | 0.75 | 3.01 | 31.72 | 11.51 |
| 12.7 | 15.2 | 2.8 | 1.4 | 4.67 | 48.45 | 14.71 |
| 13 | 15.8 | 2.45 | 1.35 | 4.14 | 43.1 | 15.13 |
| 13.1 | 15.4 | 2.95 | 1.61 | 4.57 | 46.15 | 14.37 |
| 13.2 | 15 | 2.8 | 1.32 | 3.26 | 43.49 | 16.35 |
| 13.5 | 14.9 | 3.2 | 1.24 | 4.99 | 41.81 | 13.42 |
| 13.5 | 15.28 | 3.5 | 1.32 | 4.95 | 45.15 | 13.37 |
| 13.5 | 14.9 | 3.1 | 1.12 | 4.86 | 48.15 | 13.99 |
| 14.2 | 15.5 | 3.15 | 1.68 | 4.61 | 54.11 | 14.41 |
| 14.4 | 15.8 | 3.2 | 1.57 | 4.98 | 55.63 | 17.12 |
| 15 | 16.6 | 3.51 | 1.71 | 5.95 | 59.19 | 18.22 |
| 15.2 | 15.7 | 3.69 | 1.73 | 6.38 | 60.24 | 16.54 |
| 15.8 | 16.3 | 3.96 | 2.3 | 7.68 | 69.75 | 19.25 |
| 15.9 | 15.8 | 3.74 | 1.9 | 7.52 | 71.44 | 21.12 |
| 16.1 | 16.5 | 4.03 | 2.14 | 7.07 | 73.84 | 20.78 |
| 16.3 | 16.4 | 3.98 | 2.24 | 7.33 | 74.28 | 21.69 |
| 16.3 | 16.7 | 4.12 | 1.89 | 7.37 | 75.27 | 20.69 |
| 16.3 | 17.1 | 4.3 | 2.15 | 7.62 | 79.87 | 20.89 |
| 16.6 | 16.5 | 4.03 | 2.27 | 8.41 | 78.52 | 20.58 |
| 16.9 | 16.7 | 4.12 | 2.11 | 7.99 | 84.76 | 22.13 |
| 17 | 16.5 | 4.03 | 2.54 | 10.55 | 85.74 | 23.85 |
| 17 | 16.8 | 4.16 | 2.1 | 7.21 | 73.43 | 19.71 |
| 17 | 16.4 | 3.98 | 1.99 | 8.11 | 73.21 | 18.47 |
| 17.8 | 17.5 | 4.44 | 2.61 | 9.2 | 91.66 | 24.21 |
| 17.9 | 17 | 4.25 | 2.98 | 7.9 | 93.27 | 23.88 |
| 18.1 | 17.4 | 4.44 | 2.6 | 10.42 | 98.03 | 25.74 |
| 18.1 | 17.3 | 4.4 | 2.92 | 8.26 | 94.63 | 24.4 |
| 18.3 | 17.9 | 4.25 | 2.88 | 11.5 | 95.42 | 27.79 |
| 18.3 | 17.6 | 4.54 | 2.78 | 8.73 | 91.95 | 21.86 |
| 18.4 | 17.8 | 4.64 | 2.87 | 10.86 | 103.06 | 27.28 |
| 18.5 | 16.8 | 4.16 | 2.47 | 8.53 | 100.15 | 24.93 |
| 18.9 | 17.5 | 4.49 | 3.1 | 12.53 | 106.22 | 27.94 |
| 19.2 | 17.8 | 4.64 | 3.29 | 11.61 | 104.79 | 27.84 |
| 19.2 | 17.5 | 4.49 | 3.22 | 10.96 | 115.05 | 29.46 |
| 19.8 | 17.1 | 4.3 | 3.5 | 13.75 | 103.21 | 27.87 |
| 19.9 | 18.1 | 4.8 | 3.12 | 11.97 | 116.74 | 32.4 |
| 20.5 | 17.9 | 4.8 | 3.7 | 13.3 | 112.25 | 30.21 |
| 20.9 | 18.2 | 4.85 | 3.81 | 14.71 | 131.87 | 35.07 |
| 21.5 | 17.9 | 4.6 | 4.2 | 15.66 | 134.9 | 41.1 |

Appendix: Supplementary Figure S2.

Anhang: Supplementary Figure S2.

| Other studies | Allometric Equations | | | |
|------------------------|-------------------------------|-------------------------------|----------------------------------|----------------------------------|
| | Stem | Root | Branch | Leaf |
| Ming et al. (2012) | $W_s = 0.1740(D^2H)^{0.7661}$ | $W_R = 0.0094(D^2H)^{0.9538}$ | $W_{Br} = 0.0002(D^2H)^{1.2696}$ | $W_{lf} = 0.0002D^{3.2304}$ |
| Wu (2005) | $W_s = 0.0344(D^2H)^{0.9340}$ | $W_R = 0.0479(D^2H)^{0.7624}$ | $W_{Br} = 0.0586(D^2H)^{0.6985}$ | $W_{lf} = 0.0123(D^2H)^{0.6984}$ |
| Zhang et al. (2016) | $W_s = 0.0171(D^2H)^{0.9901}$ | $W_R = 0.1017(D^2H)^{0.6653}$ | $W_{Br} = 0.0252(D^2H)^{0.7587}$ | $W_{lf} = 0.0155(D^2H)^{0.6733}$ |

Appendix: Supplementary Figure S3.

Anhang: Supplementary Figure S3.

