

Improving allometry models to estimate the above- and belowground biomass of subtropical forest, China

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Abstract. Subtropical forests are important carbon sinks and have a huge potential for mitigating climate change. However, few studies have developed biomass models to give robust estimates of subtropical forest aboveground and belowground biomass. Although wood density (WD) can greatly reduce the uncertainty in aboveground biomass (AGB) estimates in tropical forest, it has never been applied in other ecosystems. In addition, crowns hold a large component of tree biomass and vary among forest types, so crown dimensions as new variables have been recommended for AGB models. To test the role of wood density and crown dimensions and to select the best AGB model in subtropical forest, we harvested and weighted dry mass of 147 trees from 41 dominant species in subtropical forest. In order to account the belowground biomass (BGB) of these forests, 23 roots systems were excavated following aboveground harvest. Models with wood density performed better than all those without wood density, and models with height performed better than those without height, indicating wood density and tree height (H) are crucial factors in AGB models of subtropical forest. Adding crown radius (CR) did not improve the model performance. The BGB models with diameter at breast (DBH) in power form were significant ($***p < 0.001$). The new AGB models presented here, with wood density and tree height, and BGB models substantially improve biomass estimates in subtropical forest.

Key words: aboveground biomass; allometry; belowground biomass; subtropical forest.

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INTRODUCTION

Accurately quantifying forest carbon stocks and flux is crucial for understanding the forest ecosystem services and the importance of forests on global climate (Watson 2000, Fang et al. 2001). The forest sink is large based on recent studies, but varies with locations (Pan et al. 2011). Previous results show that the forests in high

latitudes are carbon sinks (Myneni et al. 2001), but data on carbon circles of subtropical forest are lacking. A recent study shows that average net ecosystem productivity (NEP) of East Asian subtropical forest is $362 \pm 39 \text{ g C m}^{-2} \text{ yr}^{-1}$, higher than Asian tropical and temperate forest, and even higher than forests at the same latitudes in North America, Europe and Africa (Yu et al. 2014). So there is a pressing need to accurately

quantify and monitor carbon dynamics in subtropical regions.

Due to the uplift of the Tibetan-Himalayan Highland and moisture supplied by the East Asian monsoon (Kira 1991), the subtropical region has four distinct seasons and is characterized by two humid, warm summer and a dry, cold winter. The main forest types are evergreen broad-leaved, deciduous broad-leaved and mixed (Yu et al. 2014). China has the largest subtropical evergreen broad-leaved forest in the world, which occupies about one-fourth of the total forest area in China and covers 2.5×10^6 km² between 23° and 34° N and 102°31' and 122° E (Wu 1980). Due to human activities and forest degradation, the subtropical forests have been severely fragmented and large areas of forest changed to farmland over the last century. However, forest protection and reconverting farmland to forests have been widely applied and thus forest cover in some region is increasing rapidly. Despite the assumed critical role of subtropical forest in regulating climate change, there are only rough estimates (based on limited data) of carbon cycling.

Most biomass studies only focus on aboveground component, while other pools such as belowground biomass, coarse debris and litter have rarely been studied. Tree roots also contribute significantly to total biomass and forest carbon storage (Norby and Jackson 2000). Due to the high labor cost and limited knowledge about the distribution of root biomass (Bolte et al. 2004), it is very difficult to directly estimate belowground biomass. Unlike the aboveground component, studies of belowground biomass estimates are seldom documented, and models of belowground biomass are lacking (Lai et al. 2013). In the past few decades, due to a lack of the information about the size dimensions of root, tree species, sampling location and climatic conditions (Bolte et al. 2004). Methods using ratios of belowground to aboveground components have been suggested. These ratios vary among forest types and this may lead to extremely biased estimates of total biomass. One allometric relationship, between stem diameter and coarse root biomass, is recommended for estimating root biomass estimate.

Many studies have developed biomass models for different forest types throughout the world.

However, predicted biomass values vary greatly when applying different models, and the greatest uncertainties are the lack of a standard biomass model and sampling at different scales (Chave et al. 2004). Models with just a few sample trees, or sample trees that are poorly representative, such as those with crown damage (Chambers et al. 2001), and those with bent, askew or hollow trunks, can render very different biomass estimates. In addition, some published equations are several decades old, and specific information about the models, such as number of sample trees, species information, location and residual sum of errors (RSE, very important for calculating the correction factor when applying log-transformed models), are lacking and result in severely biased model estimates of forest biomass.

Allometric scaling laws are often expressed as a scaling exponent on mass and size and applied in forest studies (Niklas 2004, Dietze et al. 2008). For trees, this power relationship between biomass and covariates such as DBH, tree height and other variables is prevalent. Diameter is the most common factor because it is easily acquired, and because it explains most of the variance in aboveground models (Goodman et al. 2014). Thus, diameter is an essential variable in all AGB models. Although it is more difficult to measure tree height than diameter, tree height and diameter are highly correlated for each species, so we can measure height for a subset of trees and develop models to estimate all trees in the forest. Species composition (Baker et al. 2004) and forest structure across subtropical forests may differ within a region. A potential adjustment includes using wood density and crown dimensions in models. Wood density has been successively applied in one model of tropical forest (Chave et al. 2014). Likewise, Goodman et al. (2014) tested the role of crown dimensions in biomass models, and showed that models with crown dimensions improved tropical forest biomass estimates. However, wood density and crown dimensions have never been incorporated into models for tree biomass estimates of subtropical forest.

In this study, we aimed to (1) test the importance of wood density and crown dimensions on AGB models; (2) examine the suitability of published allometric models in subtropical

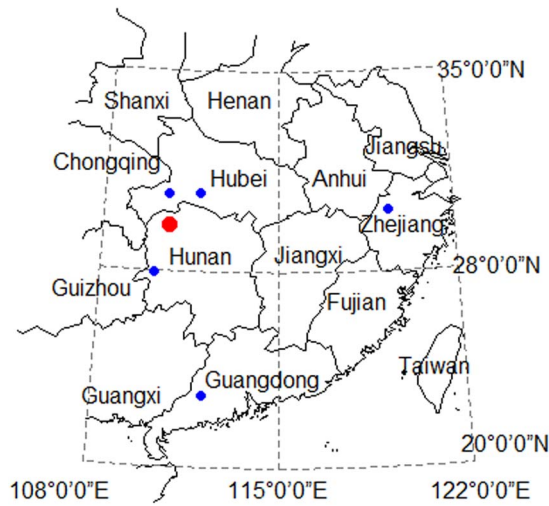


Fig. 1. Geographical location of study site compiled from published literature. The red dot is the study location, and blue dots are locations of published literature for estimating forest biomass.

forest; and (3) develop a suite of AGB and BGB models for the subtropical forest, with a focus on AGB models with wood density and crown dimensions which have practical application in AGB estimates.

MATERIALS AND METHODS

Study sites and data description

Study sites.—This study was carried out in the Badagongshan National Nature Reserve (BNNR) in Hunan province, central China (Fig. 1). The BNNR became a National Nature Reserve in 1983 and is fairly well protected. The forest vegetation type is broadly classified as evergreen and deciduous broad-leaf mixed forest (Guo et al. 2013), which covers a large part of China. The BNNR is characterized by undulating terrain and the forest is characterized by high diversity, uneven vertical structure and closed forest canopy with a canopy height greater than 15 m. Mean annual temperature is 11.5°C, mean precipitation ranges from 2105.4 mm to 2840.1 mm, and rainy days occur about 176 d a⁻¹ (Wang et al. 2014).

One 25-ha (500 × 500 m) forest permanent dynamic plot was established in 2012 in the core zone of the reserve, with elevation ranging from 1355 m to 1456 m (Lu et al. 2013). Within the plot,

all standing woody stems with diameter at breast height (DBH) ≥ 1 cm were tagged, measured, identified to species, and mapped based on geographic coordinates following standard field procedures (Condit et al. 1998). According to census data set, 238 species and 186,556 stems occurred within the plot. The dominant species include *Fagus lucida* Rehder. & E.H. Wilson, *Castanea seguinii* Dode, *Carpinus viminea* Wall. ex Lindl., and *Sassafras tzumu* (Hemsl.) Hemsl (Guo et al. 2013). These inventory data were used to calculate the most common species in the plot and to develop biomass models.

Destructive sampling.—Due to the high diversity in the plot, it is logical to develop a simple and general way to model AGB. Ideally, each species should have its own AGB model; however, it is not practical. In total, 147 trees from 41 species (based on their importance; see Wang et al. 2014) were destructively sampled from August to September in 2012. When choosing the time of harvest, we avoided the period in which leaves were not matured or had fallen. Due to the restriction of destructive sampling even for scientific purposes, we harvested all sample trees outside of the reserve and did not harvest protected species.

Before felling, selected trees were identified to species and DBH was measured. In addition, height was measured at the top of tree crown using Vertex IV (<http://www.haglofco.com>) and crown radius was measured as the length from the midpoint of the trunk to the edge of crown in four cardinal directions. Crown radius was calculated as the mean value of the four directions. Any tree with damaged, hollow trunks or crown irregularity was avoided. Selected trees were cut down at ground level and then separated into module large branches (≥ 5 cm diameter), small branches (< 5 cm diameter), bole, leaves and fruit (if present). Fresh mass of each module was weighed in the field using a portable electronic balance with a 100-kg capacity scale and 20-g precision; large boles were cut down and weighted separately.

After felling, four common species (*Cyclobalanopsis multinervis* Cheng et T. Hong, *Quercus serrata* Thunb., *Machilus ichangensis* Rehd. et Wils. and *Carpinus viminea* Wall.) were selected for root extraction. A total of 23 roots from eight species were sampled. Of these roots, there were five

deciduous and three evergreen species. We dug a round hole with radius of 1 m around the stem and a depth of 0.2 m, removing the upper soil and exposing the main roots, and then carefully pickaxed to extract all root components including minor roots. Roots were then separated into large roots (≥ 2 cm diameter), small roots (< 2 cm diameter) and stump and weighed. Samples of each were packed and taken back to the laboratory.

To calculate moisture content, samples (minimum 300 g) of each module were weighed. Wood samples were taken as a disk with 3–5 cm thickness from large branches, small branches and stems. For stems, two disks were collected, one for calculating moisture content and the other for determining wood density. Fresh mass of each sample was measured with an electronic balance with 0.1-g precision.

Laboratory work.—A cuboid (minimum 100 g) was taken across the center of the stem disk. The fresh volume of each cuboid was measured by water displacement with a 1000 ml measuring cylinder. All samples were dried at 103°C to constant weight, measured and recorded. Wood density was calculated as dry wood mass divided by fresh volume, and moisture content was calculated as fresh mass minus dry mass, divided by fresh mass (Chave et al. 2009). Tree crown mass was estimated as the sum of large and small branches, fruit and leaves.

Assessment of existing models

Based on literature search, there were 19 published equations for estimating AGB in subtropical forest of China. Of those, 18 estimated subtropical forests AGB, and one was a global AGB model (Table 1). For equations published in 1990s, important information was missing, such as the harvest method, sample size and RSE values (for calculating the correction factor (CF) value when models back-transformed). Ten models contained separate sub-models for leaf, branch and stem, so we calculated biomass for each module and summed for total AGB.

We compared the predicted value (pred) of each model to the observed value (obs) in this study. Error (kg) was calculated as $AGB_{pred} - AGB_{obs}$, and relative error was calculated as $(AGB_{pred} - AGB_{obs}) / AGB_{obs} \times 100\%$. Positive values mean that the model overestimates AGB and

negative values indicate underestimates (Goodman et al. 2014). Models were compared and the best existing model selected based on these criteria sum, mean and standard deviation of true error, mean and standard deviation of relative error.

Biomass modeling

Based on comparing a large number of regression models for estimating forest biomass in published papers, a subset of these model shapes were chosen for their simplicity and applied relevance. Allometry relationships between mass and measure factors DBH, H (total tree height), WD (wood density) and CR (crown radius), is often expressed as a power law:

$$y = ax^b + \varepsilon, \varepsilon \sim N(0, \sigma^2) \quad (1)$$

or in a logarithmic form:

$$\log y = \log a + b \log x + \varepsilon, \varepsilon \sim N(0, \sigma^2) \quad (2)$$

y represents biomass and x represents variables, a is the model constant and b is the scaling exponent of the law (Huxley 1932).

Biomass models in this study were separated into AGB models and BGB models. For AGB models, we tested the importance of H , WD and CR , respectively. Tree height was not always available from the forest inventory, so we considered this practical restriction in model fitting procedure. MCMC methods are primarily used for calculating the parameter value as we state in Bayesian rules description later.

Testing the importance of wood density (model I).—Wood density is an essential explanatory variable but a new variable for subtropical forest allometric models. Thus, it is necessary to test its importance in models. Five candidate models (as follows) were put forward to test the importance of wood density in model fitting. Wood density as a single variable or joint with other variables existed in all five models, given here in decreasing complexity.

$$\ln(AGB) = a + b \ln(D) + c \ln(H) + d \ln(WD) \quad (I.1)$$

$$\ln(AGB) = a + b \ln(D^2 H) + c \ln(WD) \quad (I.2)$$

$$\ln(AGB) = a + b \ln(D^2 H \times WD) \quad (I.3)$$

$$\ln(AGB) = a + b \ln(D) + c \ln(WD). \quad (I.4)$$

Table 1. Summary of errors and relative error s of various models for estimating aboveground biomass in subtropical forests.

Model	Forest type and location	n	Variables	Form	Error (kg)			Rel. err (%)	
					Sum	Mean	SD	Mean	SD
QC I	EBF, Zhejiang	20	D	W ¹	-929.52	-6.32	45.54	-413	2057
ZH I	EBF, Guangdong	15	D	C	447.76	3.05	29.91	-0.76	29
WFI	EBF, Hubei	...	D	W	2239	15.23	35.39	32.6	30.5
TX II	EBF, Hunan	...	D	C	2213	15.06	27.51	131	163
ZI I	EBF, Global	...	D	W	712.89	4.84	28.37	14.4	25.9
JLI	DBF, Fujian	7	D	C	326.2	2.22	38.81	-13.7	26.1
LZI	EBF, Guangxi	6	D	C	-1442	-9.81	27.73	-9.63	20.3
FJI	EBF, Guizhou	21	D	C	-1352	-9.20	27.47	-11.59	19.63
ZHII	EBF, Guangdong	45	D	W	-9106	-61.95	85.65	-88.16	2.91
YCI	EBF, Fujian	13	D	W	1891	12.87	48.16	2.70	28.72
QC II	EBF, Zhejiang	20	D ² H	W	26.69	0.18	81.45	79.3	72.96
SJ I	EBF, Hunan	...	D ² H	C	24026	163.5	150.8	464	303
HKI	DBF, Subtropical	...	D ² H	W	3367	22.9	41.99	39.13	29.31
XYI	EBF, Guangdong	...	D ² H	C	92763	631	833	996	236
J I	EBF, Zhejiang	52	D ² H	W	162.95	1.11	25.98	23.4	32.6
TX I	EBF, Hunan	...	D ² H	C	-1613.8	-10.98	39.81	32.2	61.9
LZII	EBF, Guangxi	6	D ² H	C	-2483	-16.89	34.92	-14.61	19.63
XYI	DBF, Hubei	6-12	D ² H	C	-1356	-9.23	29.48	-27.82	22.01
YCI	EBF, Fujian	13	D ² H	W	-1426	-9.7	27.53	-18.64	18.70

Notes: In the model column, the author name and number together represent the name of model; in the forest type column, EBF = evergreen broad leaved and DBF = deciduous broad-leaved forest; the location is the province name; n = the number of sampled trees; see text for variable abbreviations. Ellipses in row of TX I and TX II indicates missing data. For XYI, 6-12 indicates that the exact number of sampled trees was not known. "W" represents a whole tree model and C represents combined sub-models. The "1" in the first row means that the model is a linear model. The data sources and references are listed in Appendix: Table A1.

Model I.1 is the full model with three variables and four parameters in which variables were independently fit. D^2H as a compound variable combined with wood density was incorporated in model I.2. Model I.3 is a simplification of model I.1, but assumes that $\beta_1 = 2$, $\beta_2 = 1$ and $\beta_3 = 1$ in model I.1. Model I.3 for its simplicity was widely applied in tropical forest biomass estimates (Chave et al. 2005, 2014); it was worth testing its power in subtropical forest. Model I.4 has diameter and wood density only and assumes height data are unavailable.

Testing the importance of crown dimensions (model II).—In addition to wood density, the importance of crown dimensions for predicting AGB was tested using the following four models. Model II.1 is the most robust model using four independent explanatory variables. Model II.2 assumes that height data are unavailable. Model II.3 is like model II.1, but the three variables (D , H , WD) are compounded.

$$\ln(\text{AGB}) = a + b\ln(D) + c\ln(H) + d\ln(WD) + e\ln(\text{CR}) \quad (\text{II.1})$$

$$\ln(\text{AGB}) = a + b\ln(D) + c\ln(WD) + d\ln(\text{CR}) \quad (\text{II.2})$$

$$\ln(\text{AGB}) = a + b\ln(D^2H \times WD) + c\ln(\text{CR}). \quad (\text{II.3})$$

AGB and diameter relationship (model III).—

$$\ln(\text{AGB}) = a + b\ln(D^2H) \quad (\text{III.1})$$

$$\ln(\text{AGB}) = a + b\ln(D) + c(\ln(D))^2 + d(\ln(D))^3. \quad (\text{III.2})$$

Model III.1 is the most popular model type in previous forest biomass studies, because species identification can be difficult and other variables are relatively difficult to acquire. As previously mentioned, total tree height data are not always available from field inventories. However, the relationship between diameter and total tree height can be described by a power law (Niklas 2004), so we can use a polynomial model with a single variable (model III.2) to solve the problem of missing tree height data.

BGB models with diameter (model IV).—It is very difficult to measure the architecture of roots as is done with trees even when roots are extracted, but the aboveground part and belowground part

of trees are highly correlated. Thus, we can develop a relationship between root biomass and DBH using the following simple model

$$\ln(\text{BGB}) = a + b\ln(D). \quad (\text{IV.1})$$

Bayesian rules description

MCMCregress function in “MCMCpack” was used to update the parameters in R version 3.1.1 (R Development Core Team 2014). This function simulates from the posterior distribution by standard Gibbs sampling, the prior for beta vector using a multivariate Gaussian prior, and the conditional error variance for inverse Gamma prior.

The model used in this study was

$$y_i = x_i'\beta + \varepsilon_i$$

where error term ε_i is assumed to be Gaussian distribution $\varepsilon_i \sim N(0, \sigma^2)$. In this study, y_i is mass for tree with $\text{DBH} \geq 1$ cm, and variables of the model included diameter at breast (D), height (H), wood density (WD) and tree crown radius (CR).

The β vector is assumed to be of standard, semi-conjugate priors $\sigma^{-2} \sim \text{gamma}(\frac{c_0}{2}, \frac{d_0}{2})$

$$\beta \sim N(b_0, B_0^{-1})$$

and

$$\sigma^{-2} \sim \text{gamma}(\frac{c_0}{2}, \frac{d_0}{2})$$

where β and σ^2 are assumed to be independent; only starting values for β are allowed because simulation is done using Gibbs sampling with the conditional error variance as the first block in the sampler.

For each model in this study, 1000 iterations were burned in and 10000 iterations were retained for each parameter. In order to guarantee that each Markov chain converged to a unique stationary state, Gelman-Rubin diagnostic method was used to ensure that the within-chain variation was roughly equal to the between-chain variation (Gelman and Rubin 1992, Liang et al. 2015). The “chi95” was chosen to calculate marginal likelihood of each model.

Selection of candidate models

To ensure accuracy and efficiency, several evaluation criteria were considered when select-

ing the best model to estimate tree biomass: (1) statistical significance of each parameter and the model itself; (2) minimum residual standard error; (3) homogeneity of variance and normal distribution of residuals; (4) non-biasness; and (5) parsimony (de-Miguel et al. 2014). We used six kinds of criteria to evaluate all candidate models. These criteria are (1) R^2 , (2) residual standard error (RSE), (3) F value, (4) Deviance Information Criterion (DIC); (5) Bayes Factor (BF), and (6) model prediction. The DIC value is similar to Akaike information criterion (AIC) and commonly used for model selection in Bayesian methods; the model with the lower DIC score is better (Spiegelhalter et al. 2002). WinBUGS software was used to calculate DIC values for each model in this study. The BF also provides a way of comparing pairs of competing models, a likelihood ratio for candidate models. For example, the Bayes factor $\text{BF}_{i,j}$ quantitatively measures the strength of model i against model j . The larger the value of $\text{BF}_{i,j}$, the greater weight of the data supported by model i to model j (Link and Barker 2009). We used the same methods for evaluating the existing models.

RESULTS

Wood density information

In this study, all sample trees ($n = 147$) were identified to species and a total of 41 species were harvested. Most harvested individuals were of the 25 most dominant species (>5 individuals of each) in the BNNR subtropical forest plot. Large differences in wood density values among species were found, ranging from 0.43 to 0.699 g/m^3 with a mean value of 0.569 g/m^3 . Only eight species were in the wood density global database (Chave et al. 2009). We compared the relative bias of the measured data and the database; seven species had estimates of wood density 2–10% lower than the database. In all sample trees, wood density increased as $\text{DBH} (\leq 25 \text{ cm})$ increased to 25 cm, but decreased with $\text{DBH} \geq 30 \text{ cm}$ (Fig. 2).

Evaluating existing models

We found that most published equations were poor predictors of AGB for our tree samples (Table 1), primarily due to using combined sub-models. Only nine models were whole-tree

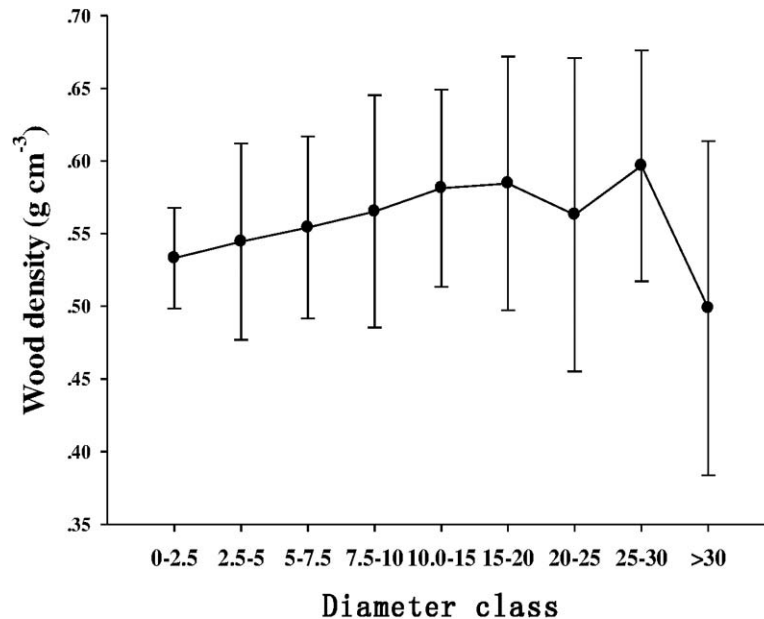


Fig. 2. Wood density for different diameter classes from 147 sampled trees in BNNR, China.

models, but QC I was a linear model which was uncommon in estimating forest biomass. AGB estimates were better with whole-tree models than combined sub-models (branch, leaf, stem sub-models) based on our criteria. True errors and relative errors (mean and standard error values) showed large differences between whole-tree and combined sub-models, but the values were smaller and ranges were narrower in whole-tree models.

We show here that models developed from the same data but using different variables resulted in very different predictions (e.g., QCI and QCII, ZHI and ZHII). All models with diameter as the single variable poorly predicted AGB; both

severe underestimation and overestimation occurred. Models with tree height improved the estimate in QCII and TXI, but also led to greater bias.

New models with diameter, height and wood density

Within our data set (Tables 2 and 3), models with wood density performed better than all those without wood density (III.1 and I.3; III.2 and I.4), and models with height performed better than those without height (III.2 and III.1; I.4 and I.1). In addition, the variation explained by wood density was slightly lower than height (Fig. 3). All nine models and variable parameters

Table 2. Model parameters for above-ground biomass (AGB; kg dry mass) estimate using diameter (D ; centimeter), total tree height (H ; meters), wood density (WD ; g cm⁻³) and crown radius (CR ; meters) developed from 147 trees and 41 species.

Code	Model type	a	b	c	d	e
I.1	$\ln(\text{AGB}) = a + b\ln(D) + c\ln(H) + d\ln(WD)$	-2.334	2.118	0.544	0.595	
I.2	$\ln(\text{AGB}) = a + b\ln(D^2H) + c\ln(WD)$	-2.672	0.944	0.615		
I.3	$\ln(\text{AGB}) = a + b\ln(D^2H \times WD)$	-2.456	0.939			
I.4	$\ln(\text{AGB}) = a + b\ln(D) + c\ln(WD)$	-1.823	2.411	0.578		
II.1	$\ln(\text{AGB}) = a + b\ln(D) + c\ln(H) + d\ln(WD) + e\ln(CR)$	-2.296	2.07	0.555	0.603	0.088
II.2	$\ln(\text{AGB}) = a + b\ln(D) + c\ln(WD) + d\ln(CR)$	-1.793	2.385	0.583	0.055	
II.3	$\ln(\text{AGB}) = a + b\ln(D^2H \times WD) + c\ln(CR)$	-2.373	0.911	0.155		
III.1	$\ln(\text{AGB}) = a + b\ln(D^2H)$	-3.062	0.949			
III.2	$\ln(\text{AGB}) = a + b\ln(D) + c(\ln(D))^2 + d(\ln(D))^3$	-1.959	1.906	0.315	-0.056	

Table 3. Results of model comparison among nine candidate models.

Code	R^2	RSE	F	DIC	BF	df
I.1	0.950	0.173	913.1	-340.8	32.16	3, 143
I.2	0.939	0.193	1113	-310.8	-92.6	2, 144
I.3	0.987	0.197	2128	-302.5	19.08	1, 145
I.4	0.932	0.207	988.2	-266.6	9.62	2, 144
II.1	0.949	0.173	640.4	-336	29.76	4, 142
II.2	0.929	0.207	614.6	-285.7	6.08	3, 143
II.3	0.997	0.193	1047	-309.8	19.59	2, 144
III.1	0.924	0.209	1723	-285	9.92	1, 145
III.2	0.911	0.220	485.9	-269	-4.86	3, 143

were significant. Among all models, model I.1 (with D , H and WD) performed the best; five of six criteria for model I.1 were better than model I.3, but the R^2 of model I.3 was higher than model I.1, and model I.3 was the reduced model of model I.1 with three coefficients given fixed value ($D = 2$, $H = 1$, $WD = 1$). The results of trace plot and Gelman-Rubin diagnostic method for parameters in model I.1 also showed that model I.1 was stable in MCMC simulation (Appendix: Figs. A1, A2). For those models without height, model I.4 was best.

New models with crown radius incorporated

On the basis of the former seven models (Tables 2 and 3), we added crown dimensions to the models and results are shown in Table 4 and Fig. 4. The three models (models II.1–II.3) with crown radius were significant ($***p < 0.001$), but did not greatly improve AGB estimates. All model criteria with CR (model II.1) were slightly

lower in CR models than models without CR (model I.1), and the coefficients of the three variables were very close. However, the relationship was reversed when comparing model II.1 and model I.3. In general, models with four variables (D , H , WD and CR) performed better than models with three variables (D , H and WD), but the difference was minimal.

Evaluation of all AGB models

Finally, we evaluated the performance of the nine new equations of this study to estimate tree AGB on the log-transformed scale (Table 4). Despite the old models also incorporating variables D or D^2H , our new models performed better, and the new models were more stable in predictions of AGB than the older models. Moreover, the performances of models with height were more stable than models without height, but the values may be overestimates. In addition, models with CR just slightly improved model performance (Fig. 4). Taken together, with little improvement to models, crown dimensions variables do not seem worth the effort for estimating AGB after tradeoff with measure error. We will discuss this more in the *Discussion*.

Above all, model I.1 with three variables (D , H , WD) performed the best of all new models, and model I.1 with brevity and convenience sometimes performed well. Model I.4 performed best when height data were not available from forest inventories. The recommended models, depending on whether tree height is available, are as

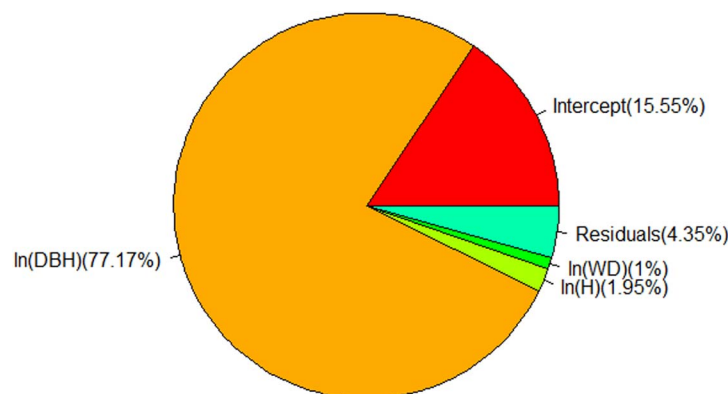


Fig. 3. Partial variations explained by each of the three variables in the log-transformed AGB models $\ln(\text{AGB}) = a + b\ln(D) + c\ln(H) + d\ln(WD) + \varepsilon$; the area in pie represented by (type III sum of squares)/(total sum of squares) $\times 100\%$.

Table 4. Errors for each model developed in this study.

Model	Form	Error (kg)			Rel. err (%)	
		Sum	Mean	SD	Mean	SD
I1	$D + H + WD$	-233.989	-1.592	21.06	1.41	17.01
I2	$D^2H + WD$	-354.058	-2.409	23.247	1.76	18.88
I3	$D^2H \times WD$	-385.235	-2.621	23.80	1.84	19.10
I4	$D + WD$	-97.971	-0.667	24.70	2.11	21.31
II1	$D + H + WD + CR$	-187.839	-1.278	21.41	1.39	16.79
II2	$D + WD + CR$	-63.925	-0.435	25.015	2.1	21.2
II3	$D^2H \times WD + CR$	-299.906	-2.040	23.521	1.71	18.68
III1	D^2H	-281.504	-1.915	26.00	2.17	21.56
III2	$D + D^2 + D^3$	-212.714	-1.447	25.222	2.36	22.34

follows.

When the height data was available, model I.1 was suggested:

$$AGB = \exp(-2.334 + 2.118\ln(D) + 0.5436\ln(H) + 0.5953\ln(WD)).$$

When the height data was not available, model I.4 was suggested:

$$AGB = \exp(-1.8226 + 2.4105\ln(D) + 0.5781\ln(WD)).$$

BGB models with diameter

The model between the BGB and diameter was

$$BGB = \exp(-2.80346 + 2.0441\ln(D)).$$

Both parameters in the model were significant ($***p < 0.001$), the residual sum of error (RSE) was 0.3437, and the R^2 value was 0.9241. The relationship between log-transformed diameters

and BGB was clear (Fig. 5).

DISCUSSION

Evaluating existing models for subtropical forest

We used 19 published equations mainly from subtropical forest to estimate AGB of 147 sample trees and test model performance in estimating AGB. As assumed, most of the models produced large bias in estimating AGB of these sample trees. Estimates were particularly poor for summed sub-models, and these models were more prone to bias than whole-tree models. Using sub-models to estimate each module (stem, branch, leaf and fruit) of tree biomass was common for subtropical forest, but these sub-models lacked a theoretical basis to develop a relationship between each module and measured variables. The amounts of error propagated in a suite of sub-models were larger than one single whole-tree model (Chave et al. 2005). We

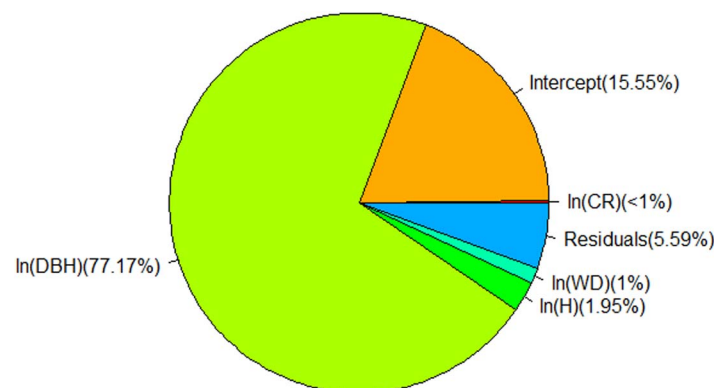


Fig. 4. Partial variations explained by each of the four variables in the log-transformed AGB models $\ln(AGB) = a + b\ln(D) + c\ln(H) + d\ln(WD) + f\ln(CR) + \varepsilon$; the area in pie represented by (type III sum of squares)/(total sum of squares) $\times 100\%$.

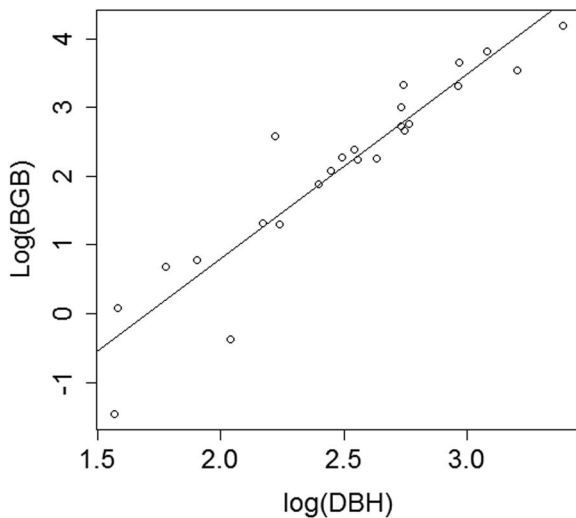


Fig. 5. Linear relationship between the CR (crown radius) and DBH (diameter at breast); $R^2 = 0.556$, $***p < 0.001$.

also tested models with different variables (D , D^2H). Models with just a single variable (D) were always biased, but models with total tree height improved AGB prediction.

Our results suggest that AGB predictions from published models were poor also because there was not a standard sampling procedure to fit models for subtropical forest. Some equations were published several decades ago; they always chose one or two sample trees with diameters near the mean value of each plot, resulting in too few replicates with too little range of size to produce unrepresentative models. Moreover, all published models did not provide an RSE value, so it was difficult to correct the underestimates when models were back log-transformed. Although significant models can be produced by these data, models were not suitable for estimating biomass in other forests. In addition, most previous models were fit with just a few species, but the dominant species may change radically in different subtropical forests within the same climate zone, so lack of species-specific parameters in models may also lead to biased estimates when models are applied to new areas. These biases limit the usability of these models across the subtropical forest.

In this study, we adopted the method of sampling trees throughout climate zones of a

forest type as has been successfully done (good AGB predictions) in tropical forest (Chave et al. 2004). This new data set includes 147 samples from 41 species to estimate forest AGB from a previously unstudied geographic region, and these species are common species dominating subtropical forest throughout China. The BGB model was developed from eight common species, so these models should provide a better prediction of subtropical forest biomass.

Variables in AGB models

Wood density is a crucial variable in carbon cycle studies (Chave et al. 2009) and has been successively applied to estimate tropical forest biomass. Wood density can greatly improve model predictions and produce pool estimate without it. Ketterings et al. (2001) added wood density to Brown equations and found that wood density can reduce 12–18% of total variance and 7–10% of absolute uncertainty. The important role of wood density in AGB models also was certified by Chave et al. (2005). Furthermore, many studies suggest that wood density is more important as a variable in mixed-species AGB models than species-specific models because species differ in functional traits (e.g., wood density) and tree architecture. In this study, the coefficient of wood density was about 0.6 and the value of models with a single compound variable was as high as 0.94, comparable to Chave (2005). What's more, models with wood density can greatly reduce the RSE and DIC and increase the R^2 , and the explanation of variance by wood density was just less than total tree height (Figs. 3, 4). Wood density also improved predictions of AGB in this study (Table 4). We can thus infer that wood density plays an important role in AGB models, and models with wood density perform better than those without.

Wood density varies strongly among different geographical regions. Significant decreases were found in wood density as altitude increased in a geographical analysis, and there were additional differences among regions (Baker et al. 2004, Chave et al. 2009). Wood densities also correlated to tree architecture and functional traits; for example, wood density was positively and significantly correlated to crown radius (Goodman et al. 2014). In our regression analysis, wood density was little correlated to crown radius but

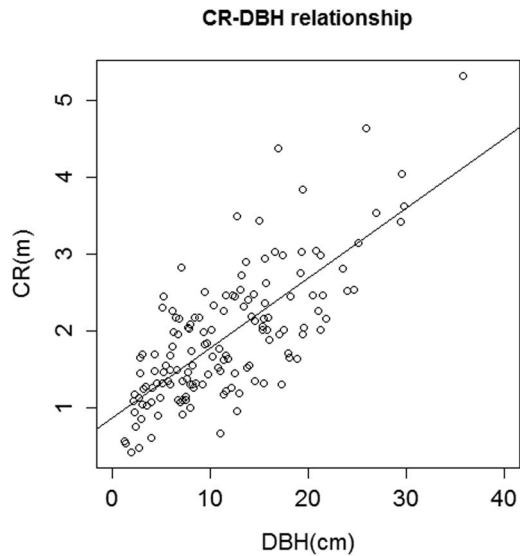


Fig. 6. Linear relationship between the CR (crown radius) and H (total tree height); $R^2 = 0.329$, $***p < 0.001$.

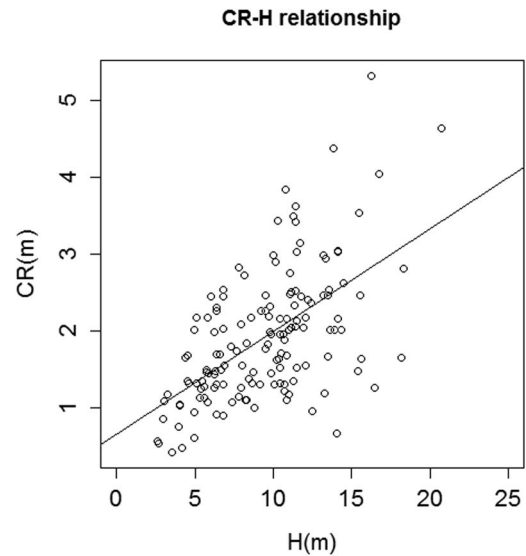


Fig. 7. Log-transformed relationship between belowground biomass and diameter at breast height; $R^2 = 0.924$, $***p < 0.001$.

showed a significant and positive relationship to diameter. This is supported by the decrease in the coefficient of diameter when wood density was included in models. So again, models with wood density can improve AGB predictions.

Tree crown dimensions measures species competition in communities (Gill et al. 2000), but is seldom adopted as a variable in AGB models (but see Goodman et al. 2014). Goodman et al. (2014) found crown radius was an important predictor of AGB, explained more variation than any other single predictor, and could replace total tree height if crown radius existed in models. In this study, we found that crown radius generally did not improve model performance in models with single variables (Tables 2 and 3); a little improvement was seen in models in which D , H , WD and CR were together as a single variable. Variance explained by crown radius was also limited and less than other variables (Fig. 4).

Trees always exhibit a positive relationship between CR and D , and this relationship has been tested in tropical and temperate broad-leaved and coniferous forest with a high goodness of fit (Hemery et al. 2005). However, the coefficient of CR is relatively small to other variables in this study. We assume that the

collinearity between crown radius and other variables may exist in regression models. We have tested the linear relationship between CR and diameter and total tree height, and found that the R^2 for each model was 0.556 and 0.329, respectively (Figs. 6, 7), so the collinearity of these two variables may be minimal. What's more, the relationship between CR and D is strongly stand-independent (Bartelink 1996) and dependent on life-history stages. Small trees may have thinner stems with narrow crowns, whereas large trees may have wider crowns (Iida et al. 2011). However, trees show large plasticity to the environment especially in different light environments, altering the relationship between tree architecture and AGB (King 1996). Thus, the importance of crown radius as a variable in AGB models needs further study.

Another important aspect to consider is the measurement error when applying AGB models with crown dimensions. Measurement error for crown dimensions may be larger than error for diameter, total tree height and wood density. For example, crown radius should measure the distance from tree midpoint to edge of crown in four directions, but on steep slopes, this error may increase biasing AGB estimates. The error may be larger than 16%, which is stated in Chave

et al. (2004) and sometimes even exceed the range of confidence intervals. Thus, caution should be taken when incorporating crown dimensions into AGB models.

Besides wood density and crown dimensions, total tree height may be a critical variable in AGB models. Previous studies have shown that AGB models with total tree height, compared to models without, improved the accuracy of AGB estimates. Hunter et al. (2013) found that AGB values predicted by model with height were 21% and 25% lower in two sites. In this study, we also found height improved AGB models based on our evaluation criteria, and the proportion of variance explained by height was only a little lower than that explained by diameter and higher than variance explained by two other variables (D and CR).

However, tree height data are difficult to acquire, especially in dense forest. Treetops may hide in the forest canopy, and hence height data are lacking in most previous forest inventories. Based on this constraint in many studies, we provided two kinds of models, one model with height and the other without.

Belowground biomass

In previous studies, diameter at breast (DBH) was a reliable predictor for estimating coarse root biomass, and has been tested on many species (Drexhage and Colin 2001, Bolte et al. 2004). The relation of root systems to DBH is remarkably consistent (Santantonio et al. 1977); coarse root biomass exponentially increases with DBH (Omdal et al. 2001). In this study, based on allometry theory, the relationship between DBH and root biomass was significant ($R^2 = 0.9241$, $***p < 0.001$) and supported our hypothesis.

However, the relationship between root biomass and DBH also shows regional variance. Drexhage and Colin (2001) compared 11 BGB models from different tree species in different sites and found scale constants of the models ranged from 1.81 to 2.7. Four factors can influence the relationship. First, it is very difficult to accurately estimate coarse root mass. Some fine roots are lost in spite of careful extraction and the proportion of missing roots increases as diameter increases. Moreover, a considerable number of roots suffer from infections by fungi or pathogens. Omdal et al. (2001) found 42 of 89

roots with less than 5% of root cross-sectional area were affected by disease. Some scientists have assigned a small proportion of biomass to correct for missing portions, e.g., by 13% (Le Goff and Ottorini 2001) or 10.8–15.1% (Santantonio et al. 1977), but these are guesses. In this study, we carefully extracted the fine roots, and hope that this reduced ‘missing’ root biomass to an insignificant quantity.

Second, the relationship between root biomass and DBH is species-specific. Root structure and biomass are species-dependent (Vennetier et al. 2014), and large trees may need large coarse roots to provide structural support. In a recent study, BGB models from three canopy tree species were studied in subtropical forest, and results showed that the scale parameter varied greatly among species, ranging from 2.15 to 2.69 (Lai et al. 2013). In this study, the root/shoot of 23 roots from eight species ranged from 0.12 to 0.208 kg kg^{-1} . So the species factor may play an important role in root biomass estimates for forests in different climate zones, but this influence is not clear and needs further study.

Third, the choice of linear regression on log-transformed data or nonlinear regression also influences root biomass estimates (Lai et al. 2013). The most common allometry relationship uses a simple linear regression on log-transformed data, but nonlinear regression has also been recommended (Packard et al. 2011). Lai et al. (2013) evaluated both methods using a large data set and analyzed the distribution of statistical error; linear regression provided a better estimate of BGB than nonlinear regression for all three species. However, the reverse transformation always underestimates biomass and correction factors should be multiplied (Thies and Cunningham 1996).

CONCLUSIONS AND IMPLICATIONS

Studies of forest biomass are not distributed evenly throughout the globe, and models with large datasets have only been developed for tropical forests (Chave et al. 2014). However, subtropical forests deserve more attention because of their large carbon sink and dynamic carbon cycle. There is an urgent need to develop a suite of robust allometric models to estimate forest aboveground and belowground biomass.

This study shows that allometric models with wood density included can improve model performance over those without wood density. Crown dimension was tested as a new variable which further improved model estimates (Goodman et al. 2014). A model for estimating belowground biomass of subtropical forest was also developed in this study.

By testing the published models on new data, we found that most of the existing equations rendered poor estimates for AGB for our 147 trees, primarily due to using combined sub-models. Models developed from the same data set but using the different variables showed major differences in model predictions. Models with height data did not consistently improve model performance. The new models, which combine diameter, total tree height and wood density, performed better than models without. Although substantial differences in species composition and forest structure occur geographically, AGB and BGB models developed in this study contained most of the dominant species in subtropical forest and showed promise for improving subtropical forest biomass estimates.

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SUPPLEMENTAL MATERIAL

ECOLOGICAL ARCHIVES

The Appendix and the Supplement are available online: <http://dx.doi.org/10.1890/ES15-00198.1.sm>