



# Filling the “vertical gap” between canopy tree species and understory shrub species: biomass allometric equations for subcanopy tree species

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**Abstract** Subcanopy tree species are an important component of temperate secondary forests. However, their biomass equations are rarely reported, which forms a “vertical gap” between canopy tree species and understory shrub species. In this study, we destructively sampled six common subcanopy species (*Syringa reticulata* var. *amurensis* (Rupr.) Pringle, *Padus racemosa* (Lam.) Gilib., *Acer ginnala* Maxim., *Malus baccata* (Linn.) Borkh., *Rhamnus davurica* Pall., and *Maackia amurensis* Rupr. et Maxim.) to establish biomass equations in a temperate forest of Northeast China. The mixed-species and species-specific biomass allometric equations were well fitted against diameter at breast height (DBH). Adding tree height (H) as the second predictor increased the  $R^2$  of the models compared with the *DBH-only* models by  $-1\%$  to  $+3\%$ . The  $R^2$  of *DBH-only* and *DBH-H* equations for the total biomass of mixed-species were 0.985 and 0.986, respectively. On average, the biomass allocation

proportions for the six species were in the order of stem (45.5%) > branch (30.1%) > belowground (19.5%) > foliage (4.9%), with a mean root: shoot ratio of 0.24. Biomass allocation to each specific component differed among species, which affected the performance of the mixed-species model for particular biomass component. When estimating the biomass of subcanopy species using the equations for canopy species (e.g., *Betula platyphylla* Suk., *Ulmus davidiana* var. *japonica* (Rehd.) Nakai, and *Acer mono* Maxim.), the errors in individual biomass estimation increased with tree size (up to 68.8% at 30 cm DBH), and the errors in stand biomass estimation (up to 19.2%) increased with increasing percentage of basal area shared by subcanopy species. The errors caused by selecting such inappropriate models could be removed by multiplying adjustment factors, which were usually power functions of DBH for biomass components. These results provide methodological support for accurate biomass estimation in temperate China and useful guidelines for biomass estimation for subcanopy species in other regions, which can help to improve estimates of forest biomass and carbon stocks.

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## Introduction

Forests store about 80% of all the biomass on earth (Reichstein and Carvalhais 2019), and have a high carbon sequestration potential through regrowth and afforestation (Bastin et al. 2019; Cook-Patton et al. 2020). Increasing forest biomass is considered as the most important natural solution of mitigating global climatic change (Yao et al. 2018; Pugha et al. 2019). However, estimating forest biomass accurately

on a global scale remains a challenge (Ploton et al. 2016; Yang et al. 2020). Accurate estimation with airborne and satellite-based techniques or large-scale forest inventory needs reliable ground biomass measurements as validation (Chave et al. 2015). Biomass allometric equations, usually fitted against easily-measured variables such as diameter at breast height (DBH) and height (H) (Saint-André et al. 2005; Mosseler et al. 2014; Xu et al. 2015; Ploton et al. 2016), are the foundation for estimating forest biomass and carbon storage at the plot scale (Gonzalez-Akre et al. 2021). Therefore, model development and comparison are preconditions for accurate estimations at both local and regional scales.

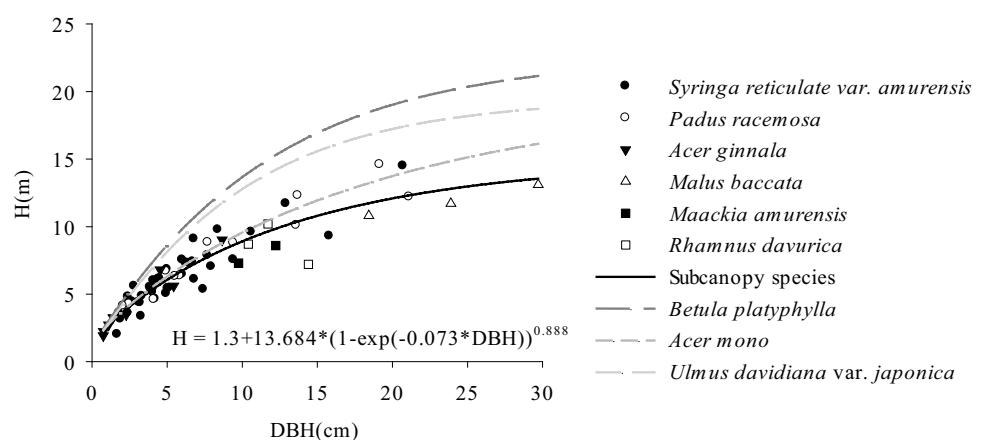
Model selection can substantially influence the accuracy of local and even regional biomass estimations (Vorster et al. 2020). Most of the allometric equations used to estimate forest biomass focus on canopy species, and some on shrub species (Zeng et al. 2010; Ali et al. 2015), while subcanopy species have largely been neglected. For example, in temperate forests of northeast China, biomass equations have been developed for major canopy species (Wang 2006; Dong et al. 2011, 2015) and shrub species (Li et al. 2010), but rarely for subcanopy species (c.f., He et al. 2018), resulting in a “vertical gap” in the biomass equations between canopy species and understory species.

The gap in forest biomass equations cannot be simply solved by using tree or shrub equations instead of equations for subcanopy species for two reasons. First, canopy species are often significantly higher than subcanopy species for the same DBH due to their contrasting H curves, and the maximum heights of subcanopy tree species are usually within 15 m in Chinese temperate forests (Fig. 1), roughly half the maximum H of the canopy species (25–35 m) (Wang et al. 2013; Liu et al. 2016). Therefore, using biomass equations for canopy species to estimate the biomass of subcanopy species is likely to produce a positive bias. Second, the biomass equations for shrub

species are generally fitted against ground diameter, which cannot be directly used to calculate the biomass of subcanopy species because in practice the ground diameters of subcanopy species are usually not measured. Even if the ground diameters are estimated according to the relationship between DBH and ground diameter, and then substitute the modeled ground diameter of subcanopy species into the ground diameter-based shrub equations, the bias in biomass (systematic overestimation or underestimation of the true value) caused by the extrapolation of the diameter range may be large (van Breugel et al. 2011; Ploton et al. 2016).

Secondary forests are a large carbon sink in global terrestrial ecosystem (Suzuki 2021), and reliable estimates of their carbon stocks are critical to understand the global carbon balance and initiatives to reduce CO<sub>2</sub> emissions (van Breugel et al. 2011; Cook-Patton et al. 2020). Temperate secondary forests, created from logged primary forests, are the major forest ecosystems in northeast China (Wang 2006). Subcanopy tree species are commonly seen in secondary forests because of increased sunlight during early stages of succession after logging. Lack of appropriate biomass models for subcanopy species will introduce errors to biomass estimations of natural secondary forests. This study was carried out to: (1) develop mixed-species and species-specific biomass equations for subcanopy species in Northeast China; (2) quantify errors in biomass estimations at both individual and stand scales when estimating biomass of subcanopy species with canopy species equations; and, (3) calculate the adjustment factors (Zhou et al. 2015) against DBH to convert biomass equations for canopy species into those for subcanopy species. The results will provide models for more accurate estimation of biomass of the temperate forest ecosystems in Northeast China, and guidelines for bridging the gap in biomass equations between canopy species and shrubs in global forests.

**Fig. 1** Comparison of height curves between canopy species (*Betula platyphylla*, *Ulmus davidiana* var. *japonica*, *Acer mono*) and subcanopy species. The height curves of *B. platyphylla* and *A. mono* were reported by Wang (2006)



## Materials and methods

### Study site

This study was carried out at the Maershan Forest Ecosystem Research Station of Northeast Forestry University, Harbin, Northeast China (45°24'N, 127°40'E, 400 m a. s. l.). The climate is continental monsoon, with warm-wet summers and cold-dry winters. The mean annual temperature is  $2.1 \pm 0.8$  °C, and mean annual precipitation  $726 \pm 261$  mm from 2008 to 2019 (Sun et al. 2021). The major forest type is a natural secondary forest (approximately 70-years old), which developed from industrial logged broad-leaved and *Pinus koraiensis* Siebold & Zucc. mixed forest, with embedded plantation islands.

### Sampling and measurements

Six common subcanopy tree species were destructively sampled from the end of July to the middle of August when foliage biomass was maximum. Trees with severe defects or near forest edges were avoided. The data included 68 trees, *Syringa reticulata* var. *amurensis* (1.7–20.7 cm, 40 individuals), *Padus racemosa* (2.1–21.1 cm, 12 individuals), *Acer ginnala* (0.7–8.7 cm, 8 individuals), *Malus baccata* (18.4–29.7 cm, 3 individuals), *Rhamnus davurica* (10.4–14.4 cm, 3 individuals) and *Maackia amurensis* (9.7–12.2 cm, 2 individuals), including 52 published tree individuals (Li et al. 2010).

After DBH was measured, stems were cut at the soil surface, and then H (m) measured. The aboveground part was divided into foliage, branches, and stems. Branches were divided into new and older branches. Stems were cut into 1 m sections, and at the end of each section, a 5 cm thick disc was removed. The belowground portion was the sum of the stumps and coarse roots (diameter > 5 mm), and excavated using a pulley system and dug manually. Root systems were cleaned, and small diameter (< 5 mm) roots cut off. The fresh mass of each component was weighed to the nearest of 100 g if greater than 1000 g, otherwise it was weighed to 1 g and recorded. A 500–1000 g specimen was randomly sampled and taken to the lab for water content determination.

The specimens for each component were placed in forced-air ovens at 105 °C for 30 min and dried at 75 °C to a constant mass and weighed to the nearest gram. Water content of each component was determined in order to calculate the dry mass (biomass) of each component and individual tree (Table 1).

### Forest plot inventory

Any errors due to biomass model selection were evaluated using the data (DBH ≥ 2 cm) of 100 20 m diameter circle plots

**Table 1** Method of calculation for components

Component	Calculation method
Stem (ST)	direct measurement
Foliage (FOL)	direct measurement
Belowground biomass (BG)	direct measurement
Branch (BR)	new branch (NBR) + older branch (OBR)
Total biomass (TOT)	ST + FOL + BR
Aboveground biomass (AG)	ST + BR + FOL
Total woody tissues (TW)	ST + BR + BG
Aboveground woody tissues (AW)	ST + BR

**Table 2** Characteristics of the 100 plots

Variable	Range	Mean	SD	CV (%)
Diameter at breast height (cm)	4.2–22.2	10.8	2.9	27.1
Stand density (N ha <sup>-1</sup> )	828–9754	2889	1339	46.4
Basal area (m <sup>2</sup> ha <sup>-1</sup> )	4.8–46.4	24.2	8.3	34.5
Dominant height (m)	10.0–31.8	22.6	3.9	17.2
Biomass density I (Mg/hm <sup>2</sup> )	22.7–304.9	155.6	59.0	37.9
Basal area percentage shared by subcanopy species (%)	0–68.1	14.9	15.2	102.1

in the secondary forest around the flux tower (Liu et al. 2016). The characteristics of the sample plots were shown in Table 2. The major tree species included *Betula platyphylla*, *Fraxinus mandshurica* Rupr., *Ulmus davidiana* var. *japonica*, *Juglans mandshurica* Maxim., *Populus ussuriensis* Kom., *Betula costata* Trautv., *Populus davidiana* Dode, *Acer mono* and *Tilia amurensis* Rupr., etc. A few *P. koraiensis* and *Larix gmelinii* (Rupr.) Kuzen. were also included. Subcanopy and understory layers were dominated by *S. reticulata* var. *amurensis*, *P. racemosa*, *A. ginnala*, and *Corylus mandshurica* Maxim et Rupr.. The herb layer was dominated by *Equisetum hyemale* Linn., *Brachybotrys paridiformis* Maxim., and *Cardamine leucantha* (Tausch) O. E. Schulz.

### Data analysis

Allometric equations, with the form of the power function (Zianis and Mencuccini 2004; Sileshi 2014), are commonly used to determine tree biomass (e.g., Wang 2006). The following forms were selected:

$$\log_{10} B = a + b(\log_{10} \text{DBH}) \quad (1)$$

$$\log_{10} B = a + b(\log_{10} \text{DBH}) + c(\log_{10} H) \quad (2)$$

$$\log_{10} B = a + b(\log_{10} \text{DBH}) + c(\log_{10} \text{WD}) \quad (3)$$

where  $B$  is biomass (g),  $a$ ,  $b$  and  $c$  parameters,  $\text{DBH}$  the diameter at breast height (cm),  $H$  the tree height (m), and  $\text{WD}$  the wood density ( $\text{g cm}^{-3}$ ). Equation (3) is only fitted for the mixed-species equation.

The mean square error ( $MSE$ ) and the adjusted determination coefficient ( $R^2$ ) were used to evaluate the performance of the model. The  $MSE$  was calculated from:

$$MSE = \sum_{i=1}^n \frac{(X_i - Y_i)^2}{n} \quad (4)$$

where  $X_i$  and  $Y_i$  are the observed and predicted biomass values of the  $i$ th sample tree, and  $n$  the number of sample trees.

A correction factor ( $CF$ ) was used to correct the deviation of logarithmic transformation (Gower et al. 1999):

$$CF = \exp(2.303 \times MSE^{0.5})/2 \quad (5)$$

It was also noted that, if site-specific biomass equations were unavailable, the adjustment factor ( $AF$ ) could be used to convert forest-derived equations to open-grown equations to obtain the equivalent biomass estimate (Zhou et al. 2015). A similar method for adjusting biomass equations for canopy-species to that for subcanopy species was tested. The  $DBH$ -only equation, Eq. (1), can be rewritten as:

$$B = CF \times \left(10^{a+b(\log_{10}^{DBH})}\right) = CF \times (10^a \times \log_{10} \text{DBH}^b) \quad (6)$$

Therefore,  $AF$  is the ratio of the estimated biomass by subcanopy and canopy equations, which can be expressed as:

$$AF = B/B' = (CF/CF') \times 10^{(a-a')} \times \text{DBH}^{(b-b')} = m \text{DBH}^n \quad (7)$$

where  $m$  and  $n$  are the parameters. If  $n$  is equal to zero, the  $AF$  is a constant,  $m$ .

In this study, it was assumed that, if the biomass equations of subcanopy species were unavailable, biomass equations of three canopy tree species could be used to quantify the errors in biomass estimation at the individual and stand scales: *B. platyphylla*, a dominant pioneer species in this forest; *U. davidiana* var. *japonica* and *A. mono* of middle and late successional stage, are the two species with the most abundant saplings. The species-specific biomass equations for canopy species were obtained from Wang (2006) or from unpublished sources (Table S1). Considering that interspecific differences in biomass allocation for particular components may influence developing mixed species equations, biomass allocation was also compared among species by an analysis of covariance with  $\text{DBH}$  as the covariable. Duncan's multiple comparison was used to determine significance in biomass allocation between species and components. The

data were analyzed with R and figures made with Sigmaplot 12.5.

## Results

### Mixed-species and species-specific $DBH$ -only component biomass equations

The mixed-species biomass equations were well fitted against  $\text{DBH}$  (Fig. 2). Among all components, total biomass, and total woody tissue biomass were the best among the biomass components ( $R^2 = 0.985$ ), followed by above-ground biomass and aboveground woody tissue components ( $R^2 = 0.980$ ). The new branch was the poorest ( $R^2 = 0.824$ ).

For specific species, the  $R^2$  of total biomass equations for *S. reticulata* var. *amurensis*, *P. racemosa*, and *A. ginnala* were 0.971, 0.985, and 0.984, respectively (Table 3). Among the three subcanopy species, the *S. reticulata* var. *amurensis* biomass equation was the poorest, of which the  $R^2$  of the new branches was only 0.722. Contrary to expectations, the mixed-species equations explained more variations in some components, such as all components of *S. reticulata* var. *amurensis*, stems of *P. racemosa*, and total woody tissues of *A. ginnala*.

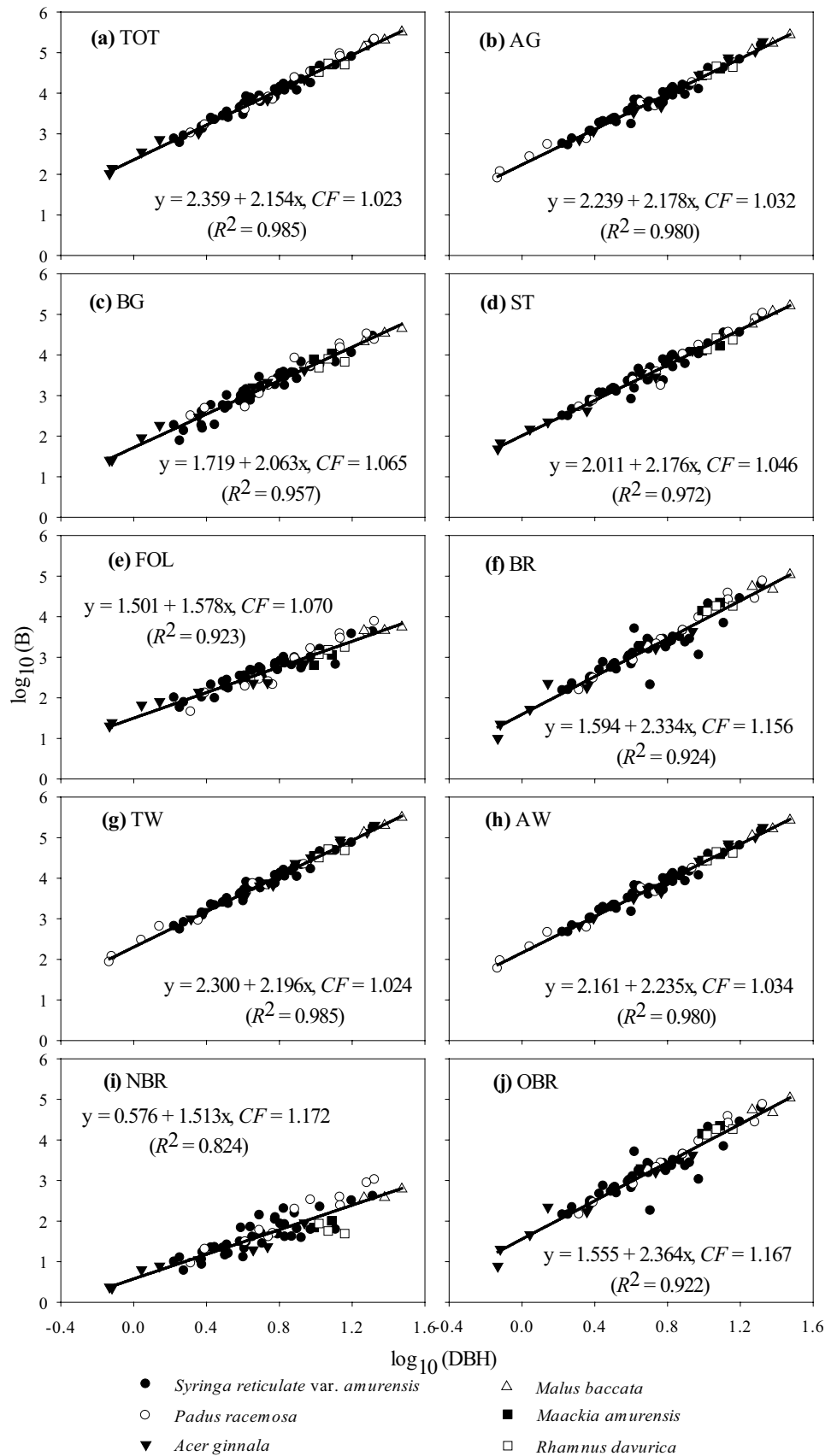
### Mixed-species and species-specific $DBH$ - $H$ component biomass equations

$DBH$ - $H$  combined equations were slightly better overall than  $DBH$ -only equations for most components (Table S2). Compared with  $DBH$ -only models,  $DBH$ - $H$  combined equations increased  $R^2$  from  $-1\%$  to  $+3\%$  (Fig. 3). However, adding  $\text{WD}$  as the second independent variable into the  $DBH$ -only models did not improve the regression for mixed tree species models (Table S3).

### Biomass allocation

Allocation differed significantly among the four components ( $P < 0.05$ ). Stems had the largest proportion of total biomass (45.5%), followed by branches (30.1%), roots (19.5%), and foliage (4.9%), with the mean root: shoot ratio of 0.24. Within specific component among the six tree species, belowground biomass overall converged, i.e., there were no significant difference among species, while the three above-ground components diverged. Stem biomass allocation of *M. amurensis* was the lowest while its branch biomass allocation was the largest. Foliage biomass allocation of *A. ginnala* was significantly higher than that of other species (Fig. 4).

**Fig. 2** Relationship between component biomass (B, g) and diameter at breast height (DBH, cm) after logarithmic transformation; TOT, AG, BG, ST, FOL, TW, AW, BR, NBR and OBR represent total, above-ground, belowground, stem, foliage, total woody tissues, aboveground woody tissues, total branch, new branch, and older branch biomass, respectively



**Table 3** Allometric equations relating biomass components (B, g) to diameter at breast height (DBH, cm) by species

Species	Component	N	a	b	R <sup>2</sup>	MSE	CF
<i>Syringa reticulata</i> var <i>amurensis</i> 1.7–20.7 cm	TOT	40	2.368	2.126	0.971	0.009	1.023
	AG	40	2.268	2.125	0.958	0.013	1.035
	BG	40	1.638	2.149	0.926	0.024	1.066
	ST	40	2.023	2.166	0.941	0.019	1.052
	FOL	40	1.522	1.572	0.903	0.017	1.047
	BR	40	1.730	2.085	0.806	0.068	1.197
	TW	40	2.317	2.160	0.971	0.009	1.025
	AW	40	2.203	2.167	0.955	0.014	1.039
	NBR	40	0.596	1.489	0.722	0.056	1.159
	OBR	40	1.704	2.100	0.801	0.071	1.208
<i>Padus asiatica</i> 2.1–21.1 cm	TOT	12	2.231	2.327	0.988	0.007	1.019
	AG	12	2.070	2.386	0.986	0.008	1.023
	BG	12	1.729	2.119	0.940	0.031	1.085
	ST	12	1.900	2.315	0.964	0.022	1.059
	FOL	12	1.010	2.125	0.945	0.017	1.046
	BR	12	1.428	2.575	0.978	0.016	1.044
	TW	12	2.203	2.338	0.989	0.008	1.023
	AW	12	2.030	2.404	0.988	0.008	1.021
	NBR	12	0.359	1.971	0.941	0.026	1.072
	OBR	12	1.398	2.594	0.977	0.017	1.046
<i>Acer ginnala</i> 0.7–8.7 cm	TOT	8	2.404	2.074	0.985	0.013	1.034
	AG	8	2.284	2.069	0.982	0.016	1.042
	BG	8	1.781	2.082	0.983	0.015	1.040
	ST	8	2.022	2.142	0.986	0.013	1.034
	FOL	8	1.616	1.239	0.946	0.017	1.046
	BR	8	1.608	2.297	0.945	0.060	1.174
	TW	8	2.325	2.155	0.984	0.014	1.039
	AW	8	2.176	2.177	0.981	0.018	1.050
	NBR	8	0.598	1.265	0.940	0.020	1.055
	OBR	8	1.550	2.366	0.939	0.072	1.209

The equation is  $\log_{10}B = a + b(\log_{10}DBH)$ , where  $B$  is biomass component, DBH the diameter at breast height,  $a$  and  $b$  are parameters. TOT, AG, BG, ST, FOL, TW, AW, BR, NBR and OBR represent total, aboveground, belowground, stem, foliage, total woody tissues, aboveground woody tissues, total branch, new branch, and older branch biomass, respectively. Sample diameter range, sample size ( $N$ ), adjusted determination coefficient ( $R^2$ ), mean square error (MSE), and the logarithmic correction factor (CF) are given

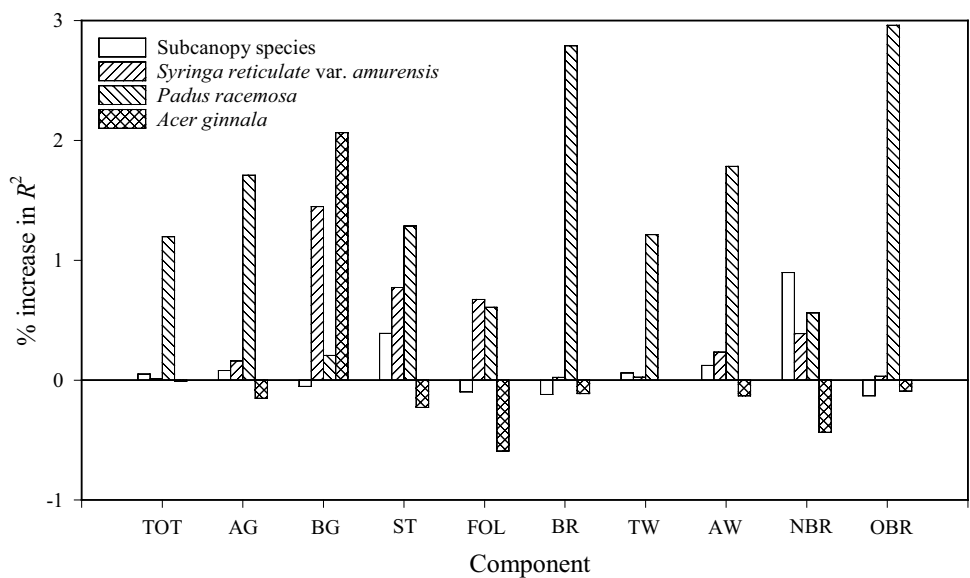
### Errors in individual and stand biomass estimations due to replacing subcanopy equations with canopy equations

How much error would be caused using biomass equations for canopy species to estimate individual subcanopy species and stand biomasses when subcanopy species equations were not available? To answer this question, biomass estimations were compared for *B. platyphylla*, *U. davidiana* var. *japonica*, *A. mono* and subcanopy mixed species. At the individual scale, total biomass equations for the four equations were used to estimate biomass in a DBH range of 1–30 cm (roughly the upper limit of subcanopy DBH). When DBH < 10 cm, there were few differences among the four

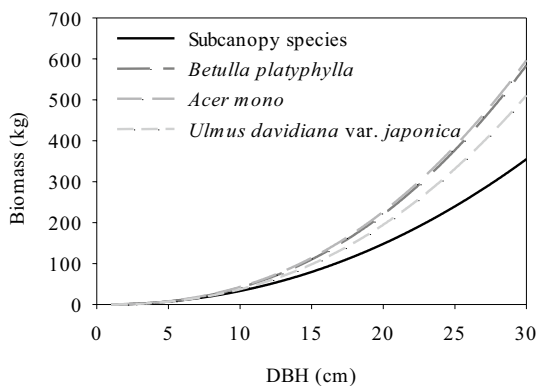
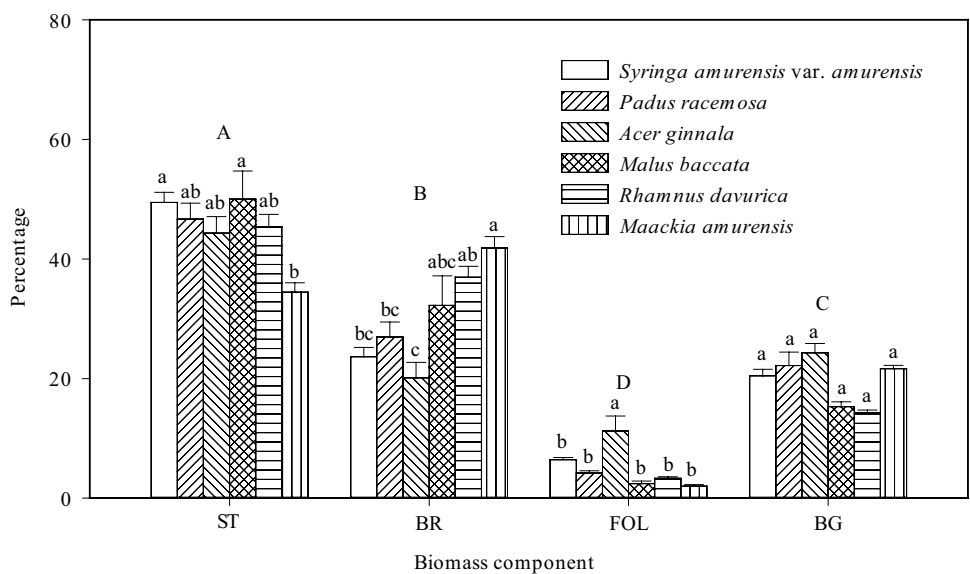
equations. However, the absolute difference in predicted values progressively increased with DBH (Fig. 5). For a DBH of 30 cm, the equation for *A. mono* led to the largest error (68.0%), while for *U. davidiana* var. *japonica* had the least error (43.9%).

At a stand scale, errors in biomass due to replacing subcanopy tree equations with canopy tree equations were quantified for 100 plots. The results showed that the errors were within 1% in 60% of the plots; however, the errors were higher than 10% in about 5% of the plots, with the maximum error up to 19.2%. Interestingly, errors in plot biomass were significantly positive with the percentage of basal area shared by subcanopy species compared to the whole stand (Table 4). Using the *DBH-only* model for mixed species,

**Fig. 3** Percent increase in the coefficient of determination ( $R^2$ ) after adding height into the DBH-only biomass equations; DBH is diameter at breast height; TOT, AG, BG, ST, FOL, TW, AW, BR, NBR and OBR represent total, aboveground, belowground, stem, foliage, total woody tissues, above-ground woody tissues, total branch, new branch, and older branch biomass, respectively



**Fig. 4** Comparison of biomass allocation among species and organs. ST, BR, FOL and BG represent stem, branch, foliage and belowground biomass, respectively. Error bars represent standard error. Different uppercase and lowercase letters represent significant differences between organs and between species, respectively



**Fig. 5** Variation in total biomass predicted by four equations (*Betula platyphylla*, *Ulmus davidiana* var. *japonica*, *Acer mono* and mixed species subcanopy equations) with DBH

the biomass density of subcanopy species of the 100 plots ranged from zero to 56.4 t ha<sup>-1</sup>, with a mean of 12.3 t ha<sup>-1</sup>.

### Adjustment factors

DBH-only biomass equations for *A. mono* were used as the base equations to calculate the adjustment factors. The results showed that the adjustment factors for most biomass components (except for the belowground component), were not a constant as indicated by the parameter  $n$  deviated from zero, but a continuous power function (Table 5). A negative sign of the power parameter,  $n$ , indicated a declining trend of AF; and a  $m$  higher than one, together with a negative  $n$ , indicated that the AF upward-adjusted biomass estimation

**Table 4** Relationship of errors when estimating biomass of subcanopy species using canopy species equations with the shared percentage of subcanopy species in stand basal area

The biomass equation of canopy species	Stand biomass error at the plot level (%)		Correlation coefficients between error and shared percentage of subcanopy species in basal area
	Mean error	Maximum error	
<i>Betula platyphylla</i>	2.161	18.111	0.798**
<i>Ulmus davidiana</i> var. <i>japonica</i>	1.018	11.206	0.649**
<i>Acer mono</i>	2.662	19.211	0.865**

\*\*values are statistically significant at the 0.01 level

**Table 5** Canopy to subcanopy species biomass adjustment factors

Component	<i>m</i>	<i>n</i>
TOT	1.288	-0.227
AG	2.035	-0.357
BG	0.418	0.082
ST	1.352	-0.232
FOL	1.886	-0.370
BR	5.056	-0.600
TW	2.581	-0.360
NBR	8.254	-0.819
OBR	4.837	-0.578

*Acer mono* is used as the base equation. The adjustment factor is  $AF = mDBH^n$ , where *AF* is the adjustment factor, *m* and *n* parameters (see Eq. 7 for adjustment factor and parameters definitions). TOT, AG, BG, ST, FOL, TW, BR, NBR and OBR represent total, aboveground, belowground, stem, foliage, total woody tissues, total branch, new branch and older branch biomass, respectively

when DBH was small but downward-adjusted when DBH was large.

## Discussion

We developed biomass equations for common subcanopy species for secondary forests in northeast China, and quantified errors in biomass estimations of individual species and at the stand scale when estimating the biomass of subcanopy species with the canopy species equations. He et al. (2018) reported biomass equations for one subcanopy species, *M. amurensis*, in a primary forest in temperate northeast China. Our results provide a guideline for developing biomass equations for subcanopy species in other forest types, and contribute to accurately estimating forest biomass and C stocks, thus helping to improve predictions of C sink.

## Mixed species versus species-specific biomass equations

Previous studies have had no consensus on the priority of species-specific biomass equations over mixed-species equations. Some studies found that mixed-species biomass equations had equal or better results (MacFarlane 2015), while other studies found that the accuracy of species-specific biomass equations were higher (Wang 2006; Duncanson et al. 2015; He et al. 2018). Our results were intermediate, with some species-specific biomass component equations that fitted better than that for mixed species. One possible explanation of the better fitting of mixed-species biomass equations in some components was that very few individual trees with abnormal forms dominated the equation, while mixed-species equations represented a wider range of tree forms (MacFarlane 2015) with a larger sample size, and thus weakened the effect of abnormal individual trees. For practical purposes, mixed-species equations are more convenient in temperate forests of northeast China.

## DBH-only versus DBH-H biomass equations

DBH was used as an independent variable in most biomass equations because of the simple and stable allometric relationship between DBH and biomass (Gower et al. 1999; Dong et al. 2015). In this study,  $R^2$  slightly increased after adding H into the *DBH-only* equations for most biomass components. The results were similar to those for shrub species in the same site (Li et al. 2010), but slightly different from canopy species on the same site, for which the  $R^2$  of the *DBH-H* equations were always higher than the *DBH-only* models (Wang 2006). In theory, the greater the difference in height curves, the higher the increase of adding H as the second predictive variable. Tree forms of subcanopy species tended to be convergent (Fig. 1), while that of canopy species were quite different (Wang 2006). Therefore, adding H improved the  $R^2$  more for mixed-canopy species models but not for subcanopy tree species. In addition,  $R^2$  did not increase significantly after adding WD into the mixed-species equations (Table S3). This was because WD of the subcanopy species in this study was in a very narrow range (0.46–0.55 g·cm<sup>-3</sup>) (Table S4).



Tropical and temperate forests usually show contrasting results on the selection for biomass models because tree structures differ greatly between climate zones (Duncanson et al. 2015). Tree species are rich and numerous in tropical and subtropical forests, which makes it difficult to establish species-specific biomass equations. To increase the accuracy of biomass equations, additional variables besides DBH are often considered in mixed-species biomass equations in these forests. For example, in tropical forests, equations including H improved biomass prediction in both individual trees and plots (Feldpausch et al. 2012). Aboveground biomass equations, including DBH, H and WD, performed well in 58 sites across forest types and bioclimatic conditions in the pantropics (Chave et al. 2015). In subtropical forests of China, WD and H were also essential for aboveground biomass mixed-species equations across 41 species, in addition to DBH (Xu et al. 2015). In addition to the above variables, adding crown dimensions in tropical and subtropical biomass equations could also reduce errors (Goodman et al. 2014; Xu et al. 2015). The height curve and WD among regions and species have great variability in tropical and subtropical regions, in contrast to our site where the H curve and WD are similar among subcanopy species. Collectively, biomass equations of mixed tree species in tropical and subtropical forests may need to include more variables to improve the superiority of simulation and applicability in different regions, which may be not necessary in temperate forests.

#### Effect of interspecific variation in biomass allocation on fitting mixed-species equations

The six subcanopy species were similar in only root biomass allocation, while they diverged in the three aboveground components (Fig. 4). One possible reason for the higher biomass allocation in branches of *M. amurensis* was the greater canopy openness (Wang, personal observation), which changed the relative allocation between stem and canopy. For example, young *B. platyphylla* trees with lower stand density had more branch biomass compared with those in the natural forests (Wang et al. 2018). Open-grown, multiple-stemmed species in shelterbelts also had a higher allocation to branches than to trunks (Zhou et al. 2007). Interspecific variation in biomass allocation may affect the goodness of fitting mixed-species component biomass equations. In general, young components (e.g., foliage and new branches) were more variable and site specific than that of older components (Bond-Lamberty et al. 2002; Forrester et al. 2017), thus they fitted poorest among the components with mixed-species equations (Fig. 2). Large differences in biomass allocation in particular components may reduce the superiority of fitting mixed-species equations, but the effect on the total

biomass or the total woody tissue biomass may be little. This was supported by the results of applying forest-derived equations to estimate the biomass of open-grown trees; the whole tree biomass curves tended to converge, although trunk and branch biomass curves diverged down and up, respectively, from their forest-derived counterparts (Zhou et al. 2015).

#### Adjustment factor

According to Zhou et al. (2015), forest-derived biomass equations can be adjusted for open-grown tree species. The canopy species biomass equations can also be adjusted for subcanopy tree species. Because of higher openness, open-grown trees had lower trunk biomass and higher crown biomass. This meant a total biomass balance led to a result that adjustment factors close to 1.2 in two of the three studied species (Zhou et al. 2015). However, compared with canopy trees, subcanopy species had a lower increasing H rate against DBH (Fig. 1). This indicated that the biomass would be overestimated when replacing subcanopy tree equations with canopy tree equations (Fig. 5). This difference in the H curve against DBH between canopy and subcanopy species led to a continuous power function of the adjustment factor (Table 4). By this method, the biomass equations for canopy tree species were easily adjusted to that for subcanopy tree species, which can effectively reduce labor and time but retain high accuracy in application.

#### Conclusions

Using destructively sampled data, it was found that DBH was a good predictor of biomass for subcanopy tree species. Adding H as a second predictor only slightly improved the model compared with the *DBH-only* models for most biomass components because of the similar H curves for these species. Adding WD did not improve the models because of the narrow range of WD. The biomass allocation of the six species diverged in three aboveground components (stems, branches, and foliage) while it converged in belowground biomass. Estimating biomass with equations for canopy species instead of those for subcanopy species could result in errors for individual tree biomass up to 68.8% for a DBH of 30 cm, and as up to 19.2% for stand biomass. Errors in biomass estimation due to canopy species biomass equations could be corrected by applying adjustment factors. It was concluded that biomass equations for subcanopy species are indispensable, particularly when the subcanopy species share a large proportion of stand basal area, usually characterized by a relatively open canopy or lower stand density.

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