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Biomass Equations for 24 Understory Species in Coniferous and Broadleaved Mixed Forests in Northeastern China

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Abstract: Understory plants are important components of forest ecosystem productivity and diversity. Compared to biomass models of overstory canopy trees, few are available for understory saplings and shrubs and therefore their roles in estimation of forest carbon pools are often ignored. In this study, we harvested 24 understory species including 4 saplings, 9 tree-like shrubs and 11 typical shrubs in coniferous and broadleaved mixed forest in northeastern China and developed the best fit allometric equations of above- and below-ground and total biomass by species-specific or multispecies using morphological measurements of basal diameter, height and crown area as independent variables. The result showed that single basal diameter, height or crown area had good explanatory power for both species-specific and multispecies ($p < 0.001$). The best-fit models included only basal diameter in sapling and tree-like shrubs, and combinations of crown area, height, and basal diameter in typical shrubs. The logarithmic model was most desired among the 4 model forms of linear, quadratic, multiple linear and logarithmic, for species-specific and multispecies. The models we developed should help the estimation of forest ecosystem carbon stocks, especially for belowground component, and provide tools for quantification of individual species biomass of understory plants.

Keywords: understory species; allometric biomass equation; species-specific and multispecies; temperate coniferous and broadleaved mixed forest; northeastern China

1. Introduction

Forests comprise the largest areas of terrestrial ecosystems and play an important role in maintaining an atmospheric CO₂ balance [1]. Accurate estimation of biomass in forest ecosystems is useful for achieving sustainable forest management, assessing forest growth conditions, adjusting forest structures, estimating forest productivity, nutrient and energy flows as well as monitoring its carbon cycle [2-6]. Forests have gained wide attention in the past decades because of their enormous capacity for carbon storage in the global carbon pool [7-9]. Understory species in the forest, composed of saplings and shrubs, serve as important components of forest ecosystems [10], play important roles in forest structures and functions [11], maintain species diversity, promote forest regeneration and improve forest production [10,12-15]. Compared with the biomass of overstory trees species, the biomass of saplings and shrubs is often neglected because of a lack of measurement technique and the difficulty in

their assessment [16].

Plant biomass can be determined through direct harvesting or estimated with allometric equations. Direct harvesting is more accurate, but is time-consuming and costly [16,17] and may not be practical or appropriate for understory plants. Comparatively, the use of allometric biomass is more practical and only requires the development of allometric biomass relationships of individual plants with their morphological variables, such as basal diameter, height or crown area [16,18-20]. A number of investigators have used allometric equations to develop species-specific or multispecies equations to measure biomass for forests [18,20-22], shrublands [17], alpine or subalpine ecosystems^{12,23} around the world. Currently, biomass equations for some shrub species have been developed for different ecosystems of the world [19,23,24]. However, biomass equations are scarce for understory species in closed forests [25], especially for temperate coniferous and broadleaved mixed forest ecosystem in northeastern China. We found that only a few species have been studied for biomass estimation [14,26,27]. Specially, there are several common shrub species in this ecosystem for which species-specific models have not yet been developed. As well, applicable multispecies models for this entire temperate forest area are lacking. Although Yang et al [26] and Li et al [14] have developed several species-specific and multispecies biomass equations, these are not enough for a comprehensive estimation of forest biomass in this region of China .

Model formulations and the choice of predictor variables that vary by species or study areas are two of the most important factors that must be considered when developed the allometric biomass equations [28]. Different models and variable types have been used to predict shrub or tree species biomass [20,29]. Generally, power models, linear models (single and multiple) and logarithmic models have often been used to develop biomass equations [14,17,24,29,30]. Particularly power models, transformed into logarithmic models, may be one of the most commonly applied of all models as can be found in numerous studies in different ecosystem worldwide [17,25,31-34]. A single independent variable, such as basal diameter, height, crown area or a combination of two variables has turned out to be the best fit to develop biomass equations for shrubs or sapling species [16,17,24,26,35].

Belowground biomass plays a key role in supplying forest ecosystem services such as those related to primary production, carbon storage, soil conservation and nutrient cycling[36], but has received less attention compared to aboveground biomass[37]. This is due to the difficulty in sampling and estimating destructive and not-standardized methods, the high labor and time consumption and costs as well as considerable variation and uncertainty in root sampling, especially for small and fine roots. Belowground biomass accounts for about 20-30% in tree species [38] and may be more for shrub or sapling species. It is therefore important that belowground biomass should be estimated for these species. Currently, almost all studies about establishing biomass equations for shrub or sapling species concentrated only on aboveground biomass [17,24,33,34,39]. Belowground biomass equations are few and far between [16,27]. Hence, we explored belowground biomass for twenty four understory species in temperate forests and developed equations for these species.

In this study, our primary aim was (1) to develop species-specific equations of above-and below-ground biomass as well as total biomass for twenty four understory species in the coniferous and broadleaved mixed forest in northeastern China; (2) to develop multispecies equations according to the classification of saplings, tree-like shrubs and typical

shrubs for these species and (3) to verify the prediction effectiveness of fitting the best fit model for multispecies. We wanted to provide a basic tool for accurately predicting understory species biomass and fill the information in the biomass study of understory species including tree saplings and shrubs. Also, we expect that more studies will be carried out for other species in other regions to supplement our pool of biomass models.

2. Material and methods

2.1. Study area

The study was carried out at the Jiaohe Experimental Forest (between 43°58'-44°05'N and 127°44.1'-127°44.7'E) in Jilin Province, in northeastern China, at an average elevation of 450 m. The area has a continental monsoon climate with a mean annual temperature of 3.8 °C and mean annual precipitation of 695.9 mm concentrated in the summer (June-August)[31,40]. The soil is mainly a dark brown forest soil. The study area is covered by a natural stands of secondary coniferous and broadleaved mixed forest consists of *Pinus koraiensis*, *Quercus mongolica*, *Tilia amurensis*, *Fraxinus mandshurica*, *Juglans mandshurica*, *Acer mandshuricum*, *Acer mono*, *Ulmus davidiana* var. *japonica*, *Betula platyphylla* and other trees. The understory vegetation is a rich mixture of species, with a shrub layer dominated by *Syringa reticulata* var. *amurensis*, *Acer barbinerve*, *Corylus mandshurica*, *Eleutherococcus senticosus*, *Philadelphus schrenkii*, *Sorbaria sorbifolia*, *Ribes* spp. and other species, while the herb layer is dominated by *Aegopodium alpestre*, *Adiantum* spp., *Cardamine leucantha*, *Meehanian fargesii*, *Pteridophyta*, *Carex* spp., *Brachybotrys paridiformis* and *Hylomecon japonica*.

2.2. Species selection

We surveyed understory species based on fixed plots (total area of plots: 130 ha) that were established in 2009-2010 by Zhao and his team [41-43] from which we selected twenty shrub species and four tree species representing eleven families as our research objects (Table 2). The twenty shrub species were divided, by morphology characteristics, to tree-like shrubs that have a single-stem and apparent trunk [10], and typical shrubs that are multi-stemmed, low-branching and not obvious in trunk [14]. Four tree species were small individual trees and defined as saplings. The names and types of sampled species are shown in Table 2. These are all broadleaved-deciduous and widely distributed in natural secondary coniferous and broadleaved mixed forests in northeastern China.

2.3. Species sampling

The number of plants selected for each species varied between 11 and 51 to cover ranges of their sizes in order to cover the widest possible range of plant sizes according to the data from our field plots. The species sampled were selected from the same forest style and we tried to keep the climatic and soil conditions as constant as possible[17]. The selected sample plants were measured and harvested in mid-August 2013 during the peak season of increasing biomass, when foliage biomass and canopy cover were relatively stable[11].

Measurements of several morphological variables, usually used to develop equations for estimating shrub biomass, were obtained from every individual plant sampled before harvesting: basal diameter (D: stem diameter at 5 cm above ground, cm); total height (H:

distance from the ground to the highest crown point, cm); maximum crown diameter (CD_1 , cm) and its perpendicular diameter (CD_2 , cm) as well as the number of ramifications (NR) from the root collar for clustered shrub species. Assuming an elliptical crown shape, crown area (CA, m^2) was calculated by crown diameters (CD_1 and CD_2) as follows:

$$CA = \pi \times (CD_1/2) \times (CD_2/2) / 10000 \quad (1)$$

where, CD_1 is the maximum crown diameter (cm) and CD_2 its perpendicular diameter (cm); 10000 is the constant for transforming the units from cm^2 to m^2 .

The individually sampled plants were cut down at ground level and the entire root system excavated, although at times, the fine roots could not be obtained in full. All plants were divided into stem, new-branches, older-branches, foliage and roots and their fresh weight (W, g) obtained in the field using a hanging scale (YP 30000, accuracy= 1 g when samples more than 100g or JT3101N, accuracy= 0.1 g when samples less than 100g). Subsamples of not less than 100 g of fresh weight from all components were selected from each sampling unit. When the dry mass amounted to less than 100 g, the entire component was used as the subsample. Then, all fresh component subsamples were weighed (using JT3101N, accuracy= 0.1 g), stored in envelop bags and brought to the laboratory, where the dry weight of each component subsample was obtained using an air-forced oven at $80^\circ C$ for 48 hours or more until reaching constant weight[11]. For each species, the water content was calculated using the dry mass/ fresh mass for each component. Then the water content of each component per species multiplied by the fresh mass of the component weighed in the field obtained the dry weight [30] of foliage (W_F), new-branches (W_{NB}), old-branches (W_{OB}), stems (W_S) and roots (W_R) of each species. We then obtained the biomass of the following components: branch dry weight (W_B) = $W_{NB} + W_{OB}$; aboveground dry weight (AGB) = $W_F + W_B + W_S$; total dry biomass (TB) = AGB + the belowground dry biomass (BGB=root biomass). We considered the entire root biomass as the belowground dry biomass.

2.4. Data analysis

First, species-specific allometric equations were constructed between morphological variables and dry biomass components (aboveground biomass, belowground biomass and total biomass). Second, allometric equations were developed by species groups of saplings, tree-like shrubs and typical shrubs. Seventeen equations in four model styles were chosen to fit the models using D, H and CA as the variables for aboveground biomass, underground biomass and total biomass for all twenty-four species (Table 1). Equations 7-9 and 14-17 in Table 1 are transformations from the following power function:

$$y = ax_1^b x_2^c x_3^d \quad (2)$$

where, y is the component biomass, x_1 , x_2 and x_3 are the morphological variables of D, H and CA; and a, b, c and d are constants to be calculated.

Table 1 Models for development of biomass allometric equations.

Code	Model style	Equation	Code	Model style	Equation
Eq.1	Linear	$y = a + b_1 x_1$	Eq.10	Multiple linear	$y = a + b_1 x_1 + c x_2$

Eq.2	Linear	$y = a + bx_2$	Eq.11	Multiple linear	$y = a + bx_2 + cx_3$
Eq.3	Linear	$y = a + bx_3$	Eq.12	Multiple linear	$y = a + bx_1 + cx_3$
Eq.4	Quadratic	$y = a + bx_1 + cx_1$	Eq.13	Multiple linear	$y = a + bx_1 + cx_2 + dx_3$
Eq.5	Quadratic	$y = a + bx_2 + cx_2$	Eq.14	Logarithmic	$\ln y = \ln a + b \ln x_1 + c \ln x_2$
Eq.6	Quadratic	$y = a + bx_3 + cx_3$	Eq.15	Logarithmic	$\ln y = \ln a + b \ln x_2 + c \ln x_3$
Eq.7	Logarithmic	$\ln y = \ln a + b \ln x_1$	Eq.16	Logarithmic	$\ln y = \ln a + b \ln x_1 + c \ln x_3$
Eq.8	Logarithmic	$\ln y = \ln a + b \ln x_2$	Eq.17	Logarithmic	$\ln y = \ln a + b \ln x_1 + c \ln x_2 + d \ln x_3$
Eq.9	Logarithmic	$\ln y = \ln a + b \ln x_3$			

y is the components biomass including aboveground biomass (AGB, g), belowground biomass (BGB, g) and total biomass (TB, g); x_1 , x_2 and x_3 are independent variables, i.e., basal diameter (D, cm), total height (H, cm) and crown area (CA, m²), respectively; a , b , c and d are constants to be calculated.

Given that logarithmic transformations introduce a systematic bias[44] and tends to underestimate[17]. Thus, a correction factor (CF) should be introduced in order to account for the inherent bias caused by the log transformation. The final back-transformed model was of the form:

$$y = CF \times ax_1^b x_2^c x_3^d \quad (3)$$

where,

$$CF = e^{(SEE^2/2)} \quad (4)$$

CF is the correction factor and SEE the standard error of the estimate; other variables have the same meaning as in equation (2).

The best models developed for species-specific or multispecies were selected on the basis of their Akaike Information Criterion (AIC)[45,46] which describes the trade-off between bias and variance in model construction. Simultaneously, the coefficient of determination (R^2), the fit index (FI), the standard error of the estimate (SEE) and the F value were used to evaluate the goodness of fit models.

These functions are defined as:

$$AIC = 2k + n \ln \left(\frac{1}{n} \sum_{i=1}^n (y_i - \hat{y}_i)^2 \right) \quad (5)$$

$$FI(R^2) = 1 - \frac{\sum_{i=1}^n (y_i - \hat{y}_i)^2}{\sum_{i=1}^n (y_i - \bar{y})^2} \quad (6)$$

$$F = \frac{\left(\sum_{i=1}^n (y_i - \bar{y})^2 - \sum_{i=1}^n (y_i - \hat{y}_i)^2 \right) / k}{\sum_{i=1}^n (y_i - \bar{y})^2 / (n - k - 1)} \quad (7)$$

where, k is the number of parameters, n the number of sampled individuals, y_i the observed value, \hat{y}_i the estimated value of the component biomass of sampling individual i

and \bar{y} the observed mean value of biomass.

FI is similar to the coefficient of determination (R^2) in linear regression models[47]. However, it is necessary to calculate FI because the R^2 may not be directly comparable among log-transformed and untransformed independent variables.

We only developed models about TB, AGB and BGB as functions of D, H and CA for all species, while the other component biomass models such as W_F , W_{NB} , W_{OB} , W_S and W_R are expected to be presented in subsequent studies.

All analyses were executed with R software (version 3.2.3; R Development Core Team 2014) using the *nls* package for model construction. The graphs were drawn using Sigmaplot 10.0 (Systat Software, Inc 2006).

3. Results

Among the twenty four species of the understory, four belong to sapling style species (total 117 individual plants), nine are tree-like shrubs (total 305 individual plants) and eleven are typical shrubs (a total of 206 individual plants or a total of 446 plants including ramifications). For the sapling species, the largest D, H and CA appeared in *Acer mono*, with their corresponding AGB and TB showing the highest values, although the largest BGB value was found in *Acer mandshuricum*. Similarly, *Syringa reticulata* var. *amurensis* exhibited the largest D, H and CA among tree-like shrubs as well as the BGB, AGB and TB. Among the typical shrubs investigated, *Acer barbinerve* showed the largest values of BGB, AGB and TB per plant in correspondence with their D, H and CA, which were much greater than for other species. However, the number of ramifications of *Ribes mandshuricum* and *Viburnum burejaeticum* per plant were maximum (both 11) of all shrub-like species. Names, family, number of sampled species, the number of ramifications (only for typical shrubs), the range of values of biometric variables (D, H and CA) as well as the component biomass (BGB, AGB and TB) per species are shown in Table 2.

Table.2 Range of sizes and biomass components by individual species.

Species	Family	Style	N	NR	D (cm)	H (cm)	CA(m ²)	BGB(g)	AGB(g)	TB(g)
<i>Acer mandshuricum</i>	Aceraceae	sapling	30	-	0.497-7.100	11-650	0.039-7.304	1.3-1737.5	4.6-5101.4	6.0-6838.9
<i>Acer mono</i>	Aceraceae	sapling	32	-	0.528-7.481	65-650	0.079-18.064	4.6-1598.3	3.9-5655.1	9.0-7253.3
<i>Carpinus cordata</i>	Betulaceae	sapling	28	-	0.490-5.531	35-630	0.071-7.791	3.5-997.8	4.5-3970.4	8.1-4968.2
<i>Ulmus laciniata</i>	Ulmaceae	sapling	27	-	0.256-5.769	45-585	0.118-12.566	1.3-816.5	1.3-4262.2	2.6-5078.7
<i>Corylus mandshurica</i>	Corylaceae	tree-like	36	-	0.275-4.859	35-530	0.031-5.498	1.1-1003.0	1.0-2566.2	2.0-3569.2
<i>Eleutherococcus senticosus</i>	Araliaceae	tree-like	26	-	0.293-1.457	32-220	0.070-0.440	0.9-50.1	1.7-76.5	2.6-126.5
<i>Euonymus alatus</i>	Celastraceae	tree-like	21	-	0.445-3.395	55-280	0.035-3.613	2.0-270.0	3.4-1009.6	5.8-1279.6
<i>Euonymus verrucosus</i>	Celastraceae	tree-like	51	-	0.199-5.689	36-505	0.008-11.486	0.5-1040.1	1.4-2933.4	2.0-3973.5
<i>Prunus padus</i>	Rosaceae	tree-like	39	-	0.543-5.883	85-605	0.059-6.350	5.0-2052.8	21.1-4720.1	26.1-6772.9
<i>Rhamnus schneideri</i>	Rhamnaceae	tree-like	26	-	0.710-4.935	85-360	0.061-4.909	6.3-736.7	19.0-3149.4	27.9-3886.1
<i>Sorbaria sorbifolia</i>	Rosaceae	tree-like	41	-	0.460-1.817	52-195	0.047-1.649	2.1-89.8	0.9-142.7	6.4-312.8
<i>Syringa reticulata</i> var. <i>amurensis</i>	Oleaceae	tree-like	37	-	0.533-7.933	42-630	0.001-12.456	3.4-2646.7	4.1-8041.0	10.2-10687.7

<i>Viburnum sargentii</i>	Caprifoliaceae	tree-like	28	-	0.357-3.720	46-390	0.021-6.432	2.8-705.0	12.6-1683.0	18.4-2189.9
<i>Deutzia parviflora</i> <i>var. amurensis</i>	Saxifragaceae	typical	15	1-5	0.284-1.835	37-200	0.059-2.238	2.4-143.9	4.9-284.9	7.2-415.9
<i>Lonicera chrysantha</i>	Caprifoliaceae	typical	18	1-8	0.318-3.487	30-240	0.094-1.649	1.1-125.3	3.8-254.6	4.9-372.1
<i>Lonicera maackii</i>	Caprifoliaceae	typical	16	1-6	0.767-9.514	80-280	0.330-5.718	8.0-822.2	35.9-2509.0	44.0-3167.8
<i>Lonicera praeflorens</i>	Caprifoliaceae	typical	24	1-4	0.322-5.672	70-255	0.090-2.270	3.7-341.5	4.2-1220.9	8.0-1470.1
<i>Philadelphus schrenkii</i>	Saxifragaceae	typical	25	1-4	0.492-4.679	13-250	0.189-4.155	2.8-166.8	9.2-445.0	12.1-562.8
<i>Ribes komarovii</i>	Saxifragaceae	typical	11	1-8	0.698-6.637	135-220	0.196-1.492	23.4-415.3	63.1-517.1	95.0-932.4
<i>Ribes mandshuricum</i>	Saxifragaceae	typical	13	1-11	0.921-9.932	70-190	0.050-1.035	13.2-365.1	15.4-563.1	28.6-928.2
<i>Ribes maximoviczianum</i>	Saxifragaceae	typical	22	1-5	0.383-2.767	67-160	0.008-1.225	1.1-58.8	4.0-143.3	5.2-202.1
<i>Spiraea fritschiana</i>	Rosaceae	typical	27	1-10	0.505-5.893	60-160	0.045-1.035	1.9-110.0	3.1-222.3	5.0-332.4
<i>Viburnum burejaeticum</i>	Caprifoliaceae	typical	12	1-11	0.585-9.328	80-280	0.063-2.827	3.8-265.1	10.7-505.4	14.7-663.0
<i>Acer barbinerve</i>	Aceraceae	typical	23	1-6	0.387-18.782	65-810	0.024-19.635	2.6-4507.0	3.1-17042.7	5.7-21549.7

N-number of individual samples, NR-number of ramifications, D- basal diameter, H-total height, CA-crown area, BGB-belowground biomass (also root biomass), AGB-aboveground biomass, and TB- total biomass.

3.1. Biomass models by species-specific

The optimal equations of AGB, BGB and TB by species, their corresponding parameters, goodness of fit statistics and correction factors are shown in Table 3. Most species-specific regression models relating components biomass with measured variables were statistically highly significant ($p < 0.001$). However, the optimal models styles were not the same for all species (Table 3).

Table 3. The best fit equations for AGB, BGB and TB of twenty four species.

Species	Components	Equations	lna	a or a ¹	b	c	d	R ²	FI	SEE	CF	p	F
<i>A. mandshuricum</i>	BGB	Eq.7	3.348	28.4	2.416			0.934	0.954	0.470	1.117	<0.001	364.9
	AGB	Eq.7	4.495	89.6	2.498			0.945	0.916	0.439	1.101	<0.001	447.3
	TB	Eq.7	4.773	118.2	2.479			0.944	0.928	0.443	1.103	<0.001	434.2
<i>A. mono</i>	BGB	Eq.4		80.4	-102.8	40.7		0.982	0.982	61.170		<0.001	795.2
	AGB	Eq.14	-2.990	0.051	1.498	1.306		0.991	0.934	0.208	1.022	<0.001	1653
	TB	Eq.7	3.819	45.6	2.406			0.976	0.953	0.317	1.051	<0.001	1243
<i>C. cordata</i>	BGB	Eq.7	2.788	16.3	2.319			0.977	0.969	0.270	1.037	<0.001	1108
	AGB	Eq.7	3.492	33.7	2.712			0.988	0.981	0.230	1.027	<0.001	2082
	TB	Eq.7	3.908	49.8	2.595			0.989	0.981	0.206	1.022	<0.001	2369
<i>U. laciniata</i>	BGB	Eq.16	3.050	21.499	1.554	0.437		0.992	0.963	0.190	1.018	<0.001	1416
	AGB	Eq.16	3.752	42.6	2.103	0.382		0.997	0.976	0.132	1.009	<0.001	4219
	TB	Eq.16	4.202	66.8	1.889	0.430		0.997	0.974	0.131	1.009	<0.001	3865
<i>C. mandshurica</i>	BGB	Eq.16	4.115	61.2	1.202	0.538		0.923	0.963	0.495	1.130	<0.001	196.9
	AGB	Eq.7	3.617	37.2	2.669			0.985	0.983	0.246	1.031	<0.001	2290

	TB	Eq.15	-2.163	0.110	1.467	0.640	0.981	0.984	0.267	1.036	<0.001	832.9
	BGB	Eq.7	2.687	14.7	1.919		0.848	0.626	0.398	1.082	<0.001	133.9
<i>E. enticosus</i>	AGB	Eq.8	-5.771	0.003	1.874		0.889	0.773	0.372	1.072	<0.001	192.9
	TB	Eq.7	3.720	41.3	2.067		0.880	0.731	0.373	1.072	<0.001	176.7
	BGB	Eq.7	2.522	12.5	2.337		0.909	0.878	0.565	1.173	<0.001	189.4
<i>E. alatus</i>	AGB	Eq.4		113.5	-260.9	152.7	0.993	0.993	20.5		<0.001	1223
	TB	Eq.16	4.089	59.7	2.124	0.260	0.980	0.981	0.229	1.027	<0.001	437.2
	BGB	Eq.7	2.789	16.3	2.401		0.971	0.992	0.345	1.061	<0.001	2930
<i>E. verrucosus</i>	AGB	Eq.7	3.614	37.1	2.508		0.985	0.995	0.257	1.033	<0.001	3198
	TB	Eq.7	4.008	55.1	2.451		0.988	0.997	0.222	1.025	<0.001	4071
	BGB	Eq.7	2.859	17.4	2.815		0.961	0.958	0.380	1.075	<0.001	899.9
<i>P. padus</i>	AGB	Eq.7	3.904	49.6	2.471		0.981	0.975	0.228	1.026	<0.001	1916
	TB	Eq.7	4.234	69.0	2.559		0.982	0.992	0.229	1.027	<0.001	2047
	BGB	Eq.7	2.694	14.8	2.293		0.951	0.846	0.320	1.052	<0.001	469.5
<i>R. schneideri</i>	AGB	Eq.16	4.231	68.8	1.876	0.381	0.974	0.901	0.260	1.034	<0.001	426.4
	TB	Eq.16	4.509	90.9	1.865	0.360	0.981	0.923	0.219	1.024	<0.001	580.8
	BGB	Eq.7	2.884	17.9	2.435		0.971	0.967	0.347	1.062	<0.001	1155
<i>S. reticulata</i> var. <i>amurensis</i>	AGB	Eq.16	3.720	41.3	2.383	0.162	0.976	0.920	0.356	1.065	<0.001	689.1
	TB	Eq.7	3.941	51.5	2.611		0.981	0.935	0.301	1.046	<0.001	1770
	BGB	Eq.4		32.115	-80.4	62.4	0.936	0.936	5.846		<0.001	279.5
<i>S. sorbifolia</i>	AGB	Eq.7	3.755	42.7	3.002		0.987	0.961	0.128	1.008	<0.001	2906
	TB	Eq.7	4.104	60.6	2.816		0.985	0.986	0.128	1.008	<0.001	2544
	BGB	Eq.7	4.114	61.2	1.949		0.701	0.744	0.860	1.447	<0.001	61.0
<i>Viburnum</i> <i>sargentii</i>	AGB	Eq.8	-6.037	2.4E-03	2.229		0.910	0.851	0.391	1.079	<0.001	264.3
	TB	Eq.8	-5.858	2.9E-03	2.258		0.908	0.887	0.403	1.085	<0.001	255.1
	BGB	Eq.5		116.2	-2.189	0.009	0.993	0.993	83.280		<0.001	1406
<i>A. barbinerve</i>	AGB	Eq.5		948.0	-12.475	0.040	0.994	0.994	288.600		<0.001	1633
	TB	Eq.5		1064.0	-14.660	0.049	0.995	0.995	331.700		<0.001	1986
	BGB	Eq.8	-6.798	1.1E-03	2.188		0.692	0.786	0.614	1.207	<0.001	56.3
<i>D. parviflora</i> var. <i>amurensis</i>	AGB	Eq.16	4.158	64.0	1.712	0.296	0.958	0.940	0.253	1.033	<0.001	271.5
	TB	Eq.11		-63.9	149.8	78.6	0.917	0.917	32.930		<0.001	132.3
	BGB	Eq.7	2.888	18.0	1.624		0.903	0.821	0.413	1.089	<0.001	148.1
<i>L. chrysantha</i>	AGB	Eq.7	3.655	38.6	1.846		0.930	0.625	0.391	1.080	<0.001	213.1
	TB	Eq.7	4.055	57.7	1.767		0.937	0.705	0.355	1.065	<0.001	237.6
	BGB	Eq.7	2.885	17.9	1.598		0.824	0.656	0.607	1.203	<0.001	65.7
<i>L. maackii</i>	AGB	Eq.16	4.739	114.3	0.806	0.932	0.968	0.914	0.247	1.031	<0.001	195.6
	TB	Eq.16	4.913	136.0	0.907	0.842	0.958	0.904	0.287	1.042	<0.001	148.2
<i>L. praeflorens</i>	BGB	Eq.16	3.740	42.1	0.695	0.909	0.852	0.591	0.608	1.203	<0.001	60.5

	AGB	Eq.16	4.748	115.3	1.047	0.874		0.974	0.753	0.280	1.040	<0.001	390.2
	TB	Eq.16	5.095	163.2	0.946	0.886		0.965	0.768	0.312	1.050	<0.001	287
	BGB	Eq.9	4.009	55.1	0.727			0.399	0.354	0.703	1.280	<0.001	14.6
<i>P. schrenkii</i>	AGB	Eq.9	4.719	112.1	0.948			0.623	0.576	0.581	1.184	<0.001	36.3
	TB	Eq.9	5.107	165.1	0.954			0.651	0.560	0.550	1.163	<0.001	41.1
	BGB	Eq.7	3.602	36.7	1.252			0.974	0.980	0.157	1.012	<0.001	339.7
<i>R. komarovii</i>	AGB	Eq.7	4.163	65.3	2.646			0.970	0.980	0.173	1.015	<0.001	575.9
	TB	Eq.7	4.819	123.9	0.941			0.818	0.868	0.342	1.060	<0.001	40.5
	BGB	Eq.9	5.395	220.4	0.992			0.948	0.828	0.265	1.036	<0.001	202.2
<i>R. mandshuricum</i>	AGB	Eq.7	3.354	28.6	1.299			0.739	0.943	0.630	1.219	<0.001	31.1
	TB	Eq.7	3.955	52.2	1.291			0.844	0.956	0.452	1.108	<0.001	59.7
	BGB	Eq.7	3.154	23.4	2.165			0.675	0.464	0.457	1.110	<0.001	64.3
<i>R. maximoviczianum</i>	AGB	Eq.11		-20.3	57.6	28.1		0.910	0.910	4.5		<0.001	151.4
<i>m</i>	TB	Eq.11		-26.1	82.2	26.7		0.921	0.921	5.3		<0.001	174.6
	BGB	Eq.17	-9.757	5.8E-05	1.274	2.211	-1.038	0.750	0.888	0.439	1.101	<0.001	23.1
<i>S. fritschiana</i>	AGB	Eq.17	-8.237	2.4E-04	1.166	2.212	-0.587	0.923	0.987	0.252	1.032	<0.001	92.0
	TB	Eq.17	-8.188	2.8E-08	1.181	2.223	-0.718	0.907	0.971	0.267	1.036	<0.001	74.4
	BGB	Eq.10		-54.8	26.7	0.383		0.979	0.979	12.8		<0.001	183
<i>V. burejaeticum</i>	AGB	Eq.10		-124.2	48.4	1.006		0.970	0.970	110.1		<0.001	131.2
	TB	Eq.12		-174.2	1.566	189.3		0.967	0.967	41.5		<0.001	118.8

¹ a' is only associated with logarithmic models and calculated as $a' = \exp(\ln a)$. Otherwise, the a was used.

Among species-specific optimal equations for AGB, BGB and TB, the models of the style of Eq.7 were the most commonly used from all alternative equations, i.e., 32 equations among 72 equations, accounting for almost for 45% of all equations. Next in line was Eq.16, with 14 equations accounting for almost 20% of all equations. As well, equations.4-5 and 8-15 were used, with 26 accounting for slightly more than 35%. It is to be noted that of these optimal models more than 75% (56 of 72) belong to a logarithmic style model. D was the best predictor variable for component biomass among species-specific equations and occurred in 58 optimal equations. CA was the second best predictor variable, used in 21 optimal equations, while, H was the least often used. The R^2 of all optimal equations varied between 0.675 for BGB in *R. maximoviczianum* and 0.997 for AGB and TB in *U. laciniata*. FI values, calculated based on predicted and observed values, varied from 0.464 for BGB in *R. maximoviczianum* to 0.996 for TB in *E. verrucosus*.

For most species, the R^2 values of the best fitted models for AGB and TB exceeded 0.9; the exceptions were *E. enticosus*, *P. schrenkii*, *R. komarovii* and *R. mandshuricum*). The lowest R^2 value scored was for AGB in *R. mandshuricum* ($R^2=0.739$). R^2 values of BGB, which ranged between 0.675 (*R. maximoviczianum*) and 0.992 (*U. laciniata*), were relatively smaller than those of AGB and TB in most species with the exception of *R. komarovii*, *R. mandshuricum* and *V. burejaeticum* (Table 3).

3.2. Biomass equations by multispecies for three groups

As single independent variables D, H and CA were all highly significant for AGB, BGB and TB for three multispecies groups of saplings, tree-like shrubs and typical shrubs ($p < 0.001$). However, the explanatory capabilities of these three variables varied for different components and groups (Fig.1). Among the three groups models of multispecies considered, the sapling multispecies (Fig. 1a, b and c) and tree-like shrub multispecies (Fig.1d, e and f) had higher explanatory capabilities than the typical shrubs (Fig. 1g, h and i) for the three independent variables, with the sapling multispecies slightly higher than for the tree-like shrub multispecies. For the biomass components of each group multispecies, the explanatory capabilities for AGB and TB of three variables were similar and higher than for BGB. Of the three independent variables involved, D had usually the highest explanatory capabilities for all components and groups of multispecies, followed by the H and the lowest in CA (Fig. 1).

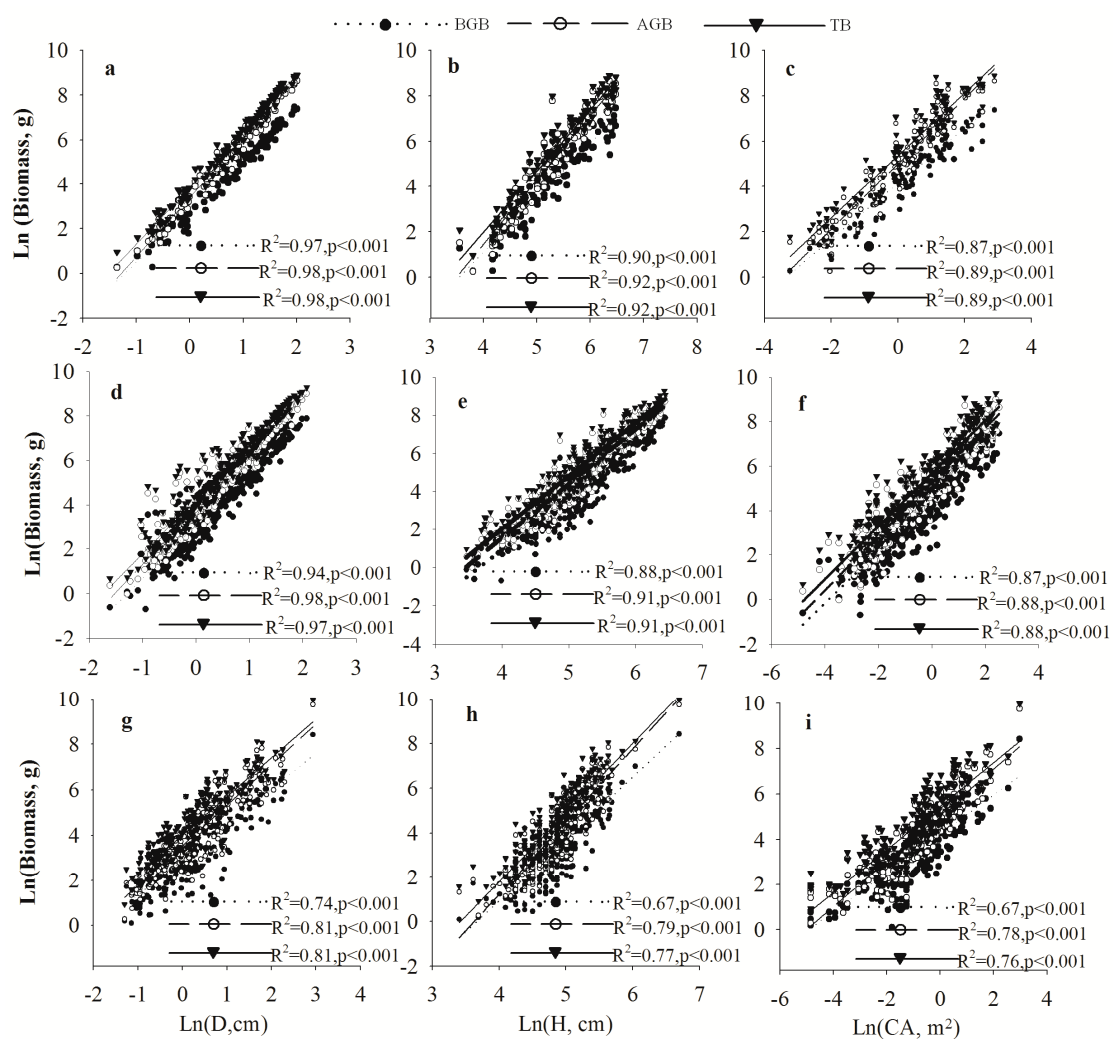


Figure 1. Belowground biomass (BGB, g), aboveground biomass (AGB, g) and total biomass (TB, g) as functions of basal diameter D (cm), total height H (cm) or crown area CA (m^2) of saplings (a, b and c), tree-like shrubs (d, e and f) and typical shrubs (g, h and i) in the understory. The total number of sampled plants was the same for three biomass components, 117 for saplings, 305 for tree-like shrubs, and 206 for typical shrubs. The various symbols and colors represent different biomass components, a black solid circle represents for BGB, a white hollow circle for AGB and a black inverted triangle for TB.

Goodness fit (R^2 and p-value) of the regression models are provided for BGB (dotted line), AGB (medium dash line) and TB (solid line) for the three single independent variables, i.e., D, H and CA.

We developed multispecies regression models of BGB, AGB and TB for three different groups of understory species, i.e., saplings, tree-like shrubs and typical shrub and selected the best fitting multispecies models based on AIC and RMSE for BGB, AGB and TB of the three groups of multispecies, with their goodness fit and statistical descriptors shown in Table 4. These models are all of a logarithmic form, using multiple-variables, except for the multispecies model of BGB for saplings. Similarly as in the best fitting species-specific models, D was the most commonly used variable for all optimum multispecies models (all models used this variable) (Table 4). These optimum models displayed high explanatory capability (all $R^2 > 0.8$) with p values < 0.001 . Although the best-fit typical shrub models had more plant size variables (all three variables) than sapling or tree-like shrub models, their explanatory capabilities were lower. Biomass variability among individual plants was greater in typical shrubs than in saplings and tree-like shrubs.

Table 4. The best fit equations for biomass components of AGB, BGB and TB by three species groups of understory plants.

Species group	Component	Best fit model	R^2	FI	SEE	CF	p	F
Sapling	BGB	$\ln\text{BGB}=2.752+2.259\ln\text{D}$	0.969	0.948	0.322	1.053	<0.001	3390
	AGB	$\ln\text{AGB}=3.626+2.258\ln\text{D}+0.242\ln\text{CA}$	0.986	0.914	0.253	1.033	<0.001	3787
	TB	$\ln\text{TB}=1.610+2.1221\ln\text{D}+0.470\ln\text{H}$	0.985	0.956	0.251	1.032	<0.001	3508
Tree-like shrub	BGB	$\ln\text{BGB}=-2.347+1.458\ln\text{D}+1.121\ln\text{H}$	0.914	0.933	0.574	1.179	<0.001	1599
	AGB	$\ln\text{AGB}=-1.952+1.532\ln\text{D}+1.194\ln\text{H}$	0.938	0.931	0.507	1.137	<0.001	2292
	TB	$\ln\text{TB}=-1.437+1.489\ln\text{D}+1.175\ln\text{H}$	0.942	0.951	0.479	1.121	<0.001	2451
Typical shrub	BGB	$\ln\text{BGB}=-1.549+0.8361\ln\text{D}+1.004\ln\text{H}+0.23\ln\text{CA}$	0.812	0.938	0.676	1.257	<0.001	472.5
	AGB	$\ln\text{AGB}=-2.240+0.787\ln\text{D}+1.312\ln\text{H}+0.33\ln\text{CA}$	0.925	0.970	0.463	1.113	<0.001	916.2
	TB	$\ln\text{TB}=-1.524+0.778\ln\text{D}+1.249\ln\text{H}+0.3\ln\text{CA}$	0.910	0.978	0.485	1.125	<0.001	752.5

The comparison between observed and predicted values (calculated from the optimum models and shown in Table 3) of AGB, BGB and TB for the three species groups of multispecies are displayed in Figure 2. As close as possible, the slopes of our linear regression models were approximately 1, implying that the predicted and observed values were very similar. The slopes of all regression models ranged between 0.9594 and 1.0080. Among the three species groups, the models for saplings and typical shrubs were better than those for tree-like shrubs in terms of slopes and error bias of regression model between observed and predicted values. For sapling multispecies models, the slopes of BGB, AGB and TB were 0.9999, 1.0003 and 1.0028, respectively, indeed very close to 1. Next were the typical shrub multispecies models, with slopes for BGB, AGB and TB of 1.0075, 1.0080 and 0.9990. Then, the slopes of tree-like shrubs multispecies models were 0.9695 for BGB, 0.9601 for AGB and 0.9594 for TB, respectively (Fig. 2).

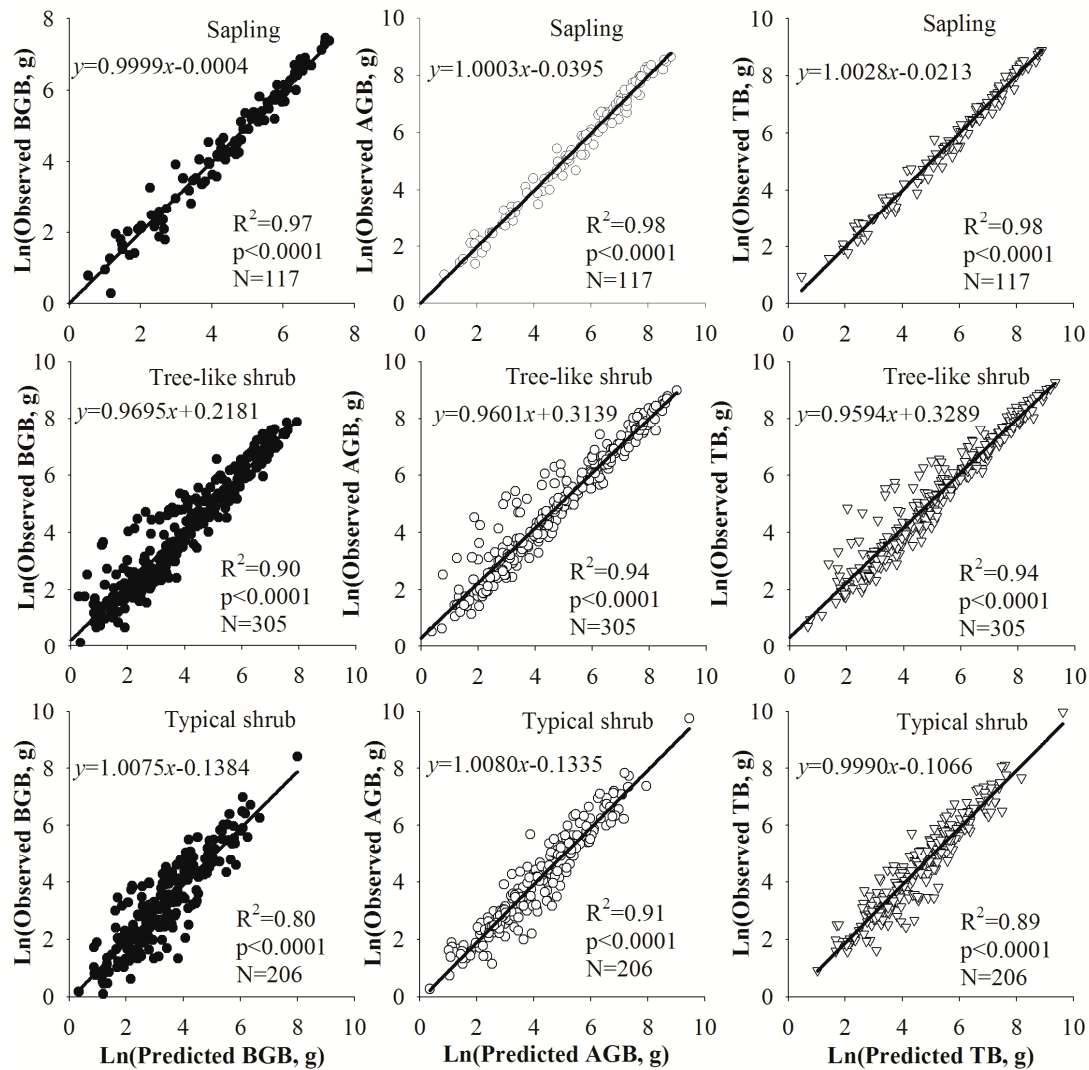


Figure 2. Ability of the best fit models to predict BGB, AGB and TB for species groups of saplings, tree-like shrubs and typical shrubs. Solid circles denote the BGB of the natural logarithmic transformation of three groups for multispecies; hollow circles represent for AGB and the hollow inverted triangles for TB. The black lines are simple regression models showing predicted values as functions of the observed values in a natural logarithm transformation. The coefficients of determination (R^2), p-values and the number of samples for each regression equation are shown in each sub-figure.

4. Discussion

The model forms and prediction variables for developing biomass equations were derived from various investigations [6,17,34,39,47,48]. In our study, we choose three variables (basal diameter, total height and crown area) and four models (linear, quadratic, multiple and logarithmic regression) to develop species-specific and multispecies equations for BGB, AGB and TB. The independent variables D, H and CA have often been used to develop regression models for estimating biomass for shrub and sapling species [17,32,33,48]. In our study, the result showed that each of the three independent variables D, H and CA have a high explanatory ability for assessing AGB, BGB and TB in all species, entirely in agreement with similar variable-biomass relationships found for understorey species in other studies [14,27,32].

Stem basal diameter may be the best predictor variable to develop optimum biomass models for various understory species, specially for saplings or tree-like shrubs species, as shown in Tables 3 and 4. Occasionally crown area had to be considered for shrub-like species, specially for low-growth shrubs with multiple stem growth form, where it is difficult to measure each stem basal diameter individually [10,24,49]. Halpern et al. [49] found that basal diameter had the weakest prediction capability and the highest errors when used as the independent variable to estimate the biomass of small multiple-stem shrubs. In the semi-arid Chaco forest, Conti et al. [17] used crown area as well as crown-shaped variables to develop their species-specific and multispecies shrub models which proved to be the best, but suggested that the use of such models should be combined with total height and crown area (crown volume, $CV=H \times CA$) as a single variable to predict aboveground dry biomass of shrub species. In this study, we also found that crown area was usually found in combination with height or basal diameter for optimum typical shrub species-specific models, but hardly ever used alone. The addition of height or basal diameter in models developed for shrub-like species was suitable because crown area mainly explained variation associated with horizontal growth, but not associated with any variation [10,49].

Other studies have shown that crown volume (CV) and D^2H may be the suitable variables in addition to basal diameter, height and crown area [14,17,23,24,27,47,50]. For example, Paton et al. [23] developed log-log regression models for 22 shrub species in Monfragüe Natural Park in southwestern Spain, in which 12 species were fitted with CV as the independent variable in all optimum models. Fan et al. [27] studied fourteen saplings in the Changbai Mountain region of northeastern China, showing that an entire plant biomass can be modeled accurately with power models based on basal diameter or the product of the square of basal diameter and total height. Liu et al. [24] developed four allometric biomass equations for alpine shrub species in the Heihe River Basin of northwestern China and also showed that the optimum models of *Salix cupularis* and *Caragana jubata* were constructed, again using the product of the square of basal diameter and height. In our study, crown volume and the product of the square of basal diameter and height were not used for modeling, but may be applicable for some other species in any future studies. However, these variables may not be preferred when a single variable model can estimate biomass well enough given a combination of two variables that are difficult to measure in practice [17]. It may be an interesting investigation to develop biomass models with CV or D^2H as independent variables for those species where two or more than two variables are called for.

In most cases, multiple-variable models are shown to have better explanatory ability than single-variable models (see Tables S1, S2 and S3). However, the more variables included in models, the more difficult and laborious the effort would be to deal with in practice. This seems to imply that more attention should be paid to the range of each variable, that more field measurements should be made and that more deviation might be expected. Models with fewer variables are more convenient and preferred and therefore, we suggest that one should opt for models with few variables when adding a variable that does not improve goodness of fit significantly. So, the selection of best biomass models should be based on not only over-all model fitting, but also applicability of models. Appropriate models can be selected from Tables S1, S2 and S3 based on the purpose for which it is needed.

The results from our optimum models developed for AGB, BGB and TB for the twenty

four understory species show that power models, transformed by natural logarithms, were more often employed than other models for both species-specific plant communities and multispecies communities (Tables 3 and 4). The goodness of fit of the logarithmic models in these species should be no questioned, given that the validity of these models has been further confirmed in a number of other studies for various of woody plant species around the world [17,25,31,32,40,51,52].

In general, species-specific models show greater accuracy in estimating biomass components than multispecies models for a given individual species, especially for root biomass (BGB) as shown in our study and for foliage and branches (not shown), as confirmed in a few studies [10,14,53]. However, for a particular species for which no specific regression model has been developed, it may be possible to select a model from a species of similar morphological characteristics or a multispecies model from an appropriate species group [19,54].

Few belowground biomass equations are available for understory species [55,56] because of the difficulty of measuring root biomass [57]. In our study, we explored the belowground biomass of 24 understory species in northeastern China and developed their optimum equations. Between above- and below-ground biomass, the predicting power of the belowground biomass models was inferior to that of the aboveground models. This may have been caused by the fact that some serious uncertainties were introduced in the harvesting process [21], such as the roots of other plants may have been included in the sample or a few root samples could not be collected or were lost, especially small roots. It is important to ensure that root systems are harvested completely, accurately and competently as possible in field sampling for measuring an entire biomass.

In this study, we developed biomass models of understory plants by species-specific or multispecies for coniferous and broadleaved mixed forest, northeastern China. The optimum models of both species-specific and multispecies, provided in our study, can estimate below- and above-ground and total biomass quite accurately for our study region. Given the limits in the number and ranges of variables sampled and our restricted study region, it is not clear that whether these models can be used in other forest types or other regions. We will verify the applicability of these models and supplement more data for other forest types and other regions in any future investigations. Our work helps the estimation of forest ecosystem carbon stocks, especially for belowground component, and provides tools for quantification of individual species biomass of understory plants. Due to various research purposes or the limitations in measuring variables, our optimum models (shown in Tables 3 or 4) are not always and everywhere appropriate to use. We provide some alternative models in our supporting documents in Tables S1, S2 and S3. We furthermore urge that special attention should be paid to the range of each variable when these models are used. When a variable is beyond our range, we suggest that this should be taken into consideration and models revised before their use.

5. Conclusions

This work harvested 24 understory species including 4 saplings, 9 tree-like shrubs and 11 typical shrubs in coniferous and broadleaved forest in northeastern China and developed the best fit allometric equations of above- and below-ground biomass and total biomass by

species-specific and multispecies. The single basal diameter, height or crown area had good explanatory power for species-specific and multispecies. The logarithmic model was most desired for both components biomass. These best fit models has been developed in this study were all estimation above-and belowground and total biomass well. These models should contribute to estimating the forest ecosystem biomass and carbon stocks or sink as well as providing tools for quantification of individual biomass for understory species.

Supplementary Materials: The following are available online at www.mdpi.com/***, Table S1: The alternative biomass equations of specie-specific and multispecies biomass equations of understory saplings, Table S2: The alternative biomass equations of specie-specific and multispecies biomass equations of understory tree-like shrubs, Table S3: The alternative biomass equations of specie-specific and multispecies biomass equations of understory typical shrubs.

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