



# Effects of stand age on tree biomass partitioning and allometric equations in Chinese fir (*Cunninghamia lanceolata*) plantations

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## Abstract

Although stand age affects biomass partitioning and allometric equations, the size of these effects and whether it is worth incorporating stand age into allometric equations, requires further attention. We sampled a total of 90 trees for 10 Chinese fir (*Cunninghamia lanceolata*) plantations at seven stand age classes to obtain the data of tree component biomass using destructive harvesting. A multilevel modeling approach was applied to examine how stand age effects differ among tree components and predictor variables (diameter at breast height, *DBH* and tree height, *H*). Age class-specific allometric equations and the best fitting generalized equation that included stand age as a complementary variable were developed for each tree component. Large differences in both the intercept and slope for different stand age classes indicated that stand age affected allometric models. Branch and leaves were more sensitive to the environment and were the tree components most affected by stand age. Age class-specific allometric equations fitted well ( $R^2 > 0.65$ ,  $p < 0.001$ ) using *DBH* and the combined form  $DBH^2H$  as predictor variables. Including stand age as a complementary variable improved the fit of generalized allometric equations. Stem, aboveground and total tree biomass predicted by the multilevel model and generalized equation were comparable to the observed data. However, the multilevel model and generalized equations had a relatively low predictive capacity for branch, leaf and root biomass. These results could improve our capacity to evaluate carbon sequestration and other ecosystem functions in plantations.

**Keywords** Multilevel modeling · Shoot:root ratio · Stand age · Tree component biomass · Total tree height · Young planted seedlings

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## Introduction

Afforestation and reforestation are valuable approaches to enhance carbon (C) sequestration for mitigating the effects of climate change and to improve other ecosystem services. As a result, the area of planted forests worldwide has increased by over 105 million ha since 1990 and accounted

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for 291 million ha in 2015 (FAO 2016). These planted forests are not only the main source of timber, firewood, fiber and other raw materials, but also help to alleviate the huge timber demand pressure on natural forests (Borges et al. 2014). In addition, planted forests offer functions relating to clean water provision, hydrological process regulation, soil conservation and erosion control, and landscape connection (Bauhus et al. 2010). Accurate estimates of tree and stand biomass are critical to evaluate ecosystem functions (i.e. production and nutrient cycling) (Fatemi et al. 2011; Ishihara et al. 2015), the roles of forests in the global C cycle (MacFarlane 2015), and ecosystem services (i.e. bioenergy and biomass products) (de-Miguel et al. 2014), as well as environmental improvement for local residents (MacFarlane 2015).

Allometric equations are the common method used to convert forest plot inventory data into tree and stand biomass (Peichl and Arain 2007; Xiang et al. 2016) and provide predictions for validating biomass estimates from models and remote sensing (Forrester et al. 2017b; Dutcă et al. 2018). However, previous studies have indicated that allometric relationships differ by tree species (Xiang et al. 2016), site conditions such as climate and soil nutrients (Dutcă et al. 2018), and stand structure in terms of stand density or species composition that influences the interactions (competition vs. facilitation) among individual trees or tree species within complex forests (Forrester et al. 2017a). Developing allometric equations with high accuracy and precision for biomass estimates is still a challenge (Dutcă et al. 2018).

Allometric equations usually relate a tree biomass component (foliage, branch, stem and root) to easily measured dimensional variables, such as diameter at breast height (DBH), tree height ( $H$ ) and crown width (Zianis et al. 2011; Hounzandji et al. 2015). Most equations are fitted using a power function such that the tree biomass component is estimated by using  $DBH$  as a predictor variable (Pilli et al. 2006). A review of biomass equations for Sub-Saharan African forests reported that only 24% of equations contained more than one explanatory variable, the majority using only  $DBH$  (Henry et al. 2011). Since the height–diameter ratio reflects tree shape and is partially affected by environmental conditions (Mensah et al. 2018), it is believed that including  $H$  as an additional predictor variable may explain site effects and may improve prediction accuracy (Dutcă et al. 2018), and precision by 55–65% compared with equations based on  $DBH$  alone (Picard et al. 2015). Meanwhile, wood density has also been suggested as a variable for allometric equations because it is highly heritable and not only explains some of the inter-specific variability in allometry but also biomass partitioning (Rozenberg et al. 2001; Poorter et al. 2012, 2015). Moreover, wood density is the parameter linking volume with tree biomass (Pilli et al. 2006). Given that allometric relationships are non-static, even within tree

species (MacFarlane 2015), simple dimensional measurements may not be sufficient for accurate estimation of tree biomass (Chave et al. 2005). The choice of allometric equations and predictor variables that should be included in the equation are key sources of uncertainty when estimating tree component biomass (Mavouroulou et al. 2014).

Stand age affects tree size, shape, biomass allocation, and consequently allometric relationships (Peichl and Arain 2007). As stands develop, there are considerable changes in micro-site conditions (e.g. such as light and soil nutrients) and the interactions among individual trees to acquire available resources. For example, young trees allocate more biomass to stem for height growth and to branches and leaves for canopy expansion in order to increase competitive advantages for light resources over their neighbors (Beaudet and Messier 1998; Messier and Nikinmaa 2000; Porté et al. 2002). Biomass accumulation in stems and branch generally increases because of the increasing amount of heartwood at the expense of foliage as stand ages. To balance the allocation of resources among tree components, roots grow and their biomass increases. Accordingly, tree shape (taper), crown structure and root systems vary with stand age so that allometric relationships between tree biomass components and dimensional variables differ greatly (Peichl et al. 2007; Fatemi et al. 2011). In addition, stem wood density may also increase with stand maturation (Saint-André et al. 2005). Therefore, when developing allometric equations for tree biomass components, the effects of stand age should be taken into account to minimize the bias. Several studies have examined the effects of stand age on allometric equations and developed age- or age class-specific allometric equations for *Eucalyptus* (Saint-André et al. 2005), *Pinus strobus* L. (Peichl et al. 2007), *Pinus rigida* (Seo et al. 2013), *Cryptomeria japonica* (Lim et al. 2013) and *Pinus bungeana* (Li et al. 2014). The degree of stand age effects on tree biomass partitioning and allometric equations can also vary with ecological niche and shade tolerance (Fatemi et al. 2011). It is still unclear under which conditions stand age-specific equations are important and which tree component and predictors in allometric equations are sensitive to the change in stand age.

Chinese fir (*Cunninghamia lanceolata*) is the principal native tree species extensively planted for the economic purpose of timber production as well as for environmental considerations such as C sequestration and soil erosion control in subtropical areas of southern China (Chen 1998; Chen et al. 2013). Owing to its high wood quality and termite resistance, Chinese fir has been cultivated for more than a thousand years to provide local materials for building construction, furniture and decoration, handcraft and infrastructure (Wu 1984; Wu et al. 2020). The data of the eighth national forest inventory (2009–2013) of China showed that the total area of Chinese fir plantations had reached 8.95

million hectares and covered the largest (about 12.9%) plantation area in China. Many local allometric equations have been developed for Chinese fir plantations in different areas, including Hunan (Chen 1998), Fujian (Chen et al. 2013), Guangxi (Xue 1996), Jiangxi and Anhui (Xie et al. 2016). However, stand age effects on allometric equations are often not examined, so it remains unclear which tree components are significantly affected by stand age. Furthermore, no allometric equations are available to estimate biomass for young small trees (i.e. planted seedlings) and this constrains the estimates of their production and C sequestration potentials in reforestation projects. Therefore, the objectives of this study were to: (1) investigate the effects of stand age on biomass partitioning among tree components, including young planted seedlings; (2) determine how stand age effects on allometric equations vary with tree components and predictor variables; and (3) examine if the predictive capacity of the generalized allometric equations for the whole age sequence is improved when stand age is included as a predictor variable compared to the equations for stand age classes of Chinese fir plantations.

## Materials and methods

### Study site description

This study was carried out in the Huitong National Forest Ecosystem Research Station (lat 27° 50' N, long 109° 45' E) in southwestern Hunan Province, China. The study site is within one of the major production areas of Chinese fir. A large area of Chinese fir plantations was established at this site in the 1960s due to the huge timber demand for economic growth. Since the 1980s, plantations have matured, been harvested and subsequently reforested. As a result, the study area has a chronosequence of Chinese fir plantations

at different stand ages and allows us to obtain biomass data over the entire life cycle of the forests.

The study area has a humid mid-subtropical monsoon climate with an annual mean temperature 15–17 °C, ranging from an average of 4.3 °C during the coolest month (January) to 29.4 °C during the warmest month (July). Mean annual precipitation is from 1270 mm to 1650 mm, occurring mostly between April and August (meteorological data obtained from the Huitong National Forest Ecosystem Research Station). The soil type is a well-drained clay loam red soil developed on slate and shale parent rock classified as Alliti-Udic Ferrosols corresponding to Acrisol in the World Reference Base for Soil Resources (Institute of Soil Science, CAS 2001). The elevation ranges from 290 m to 410 m above sea level.

### Biomass measurement

Tree biomass measurement was conducted in October (autumn) 2017, after the growing season had ended. We established seventeen 20 m × 20 m quadrat sample plots, including one plot in plantations aged 7, 10, 31, 38, and 50 years, three plots each in plantations aged 4 and 18 years, and two plots each in plantations aged 15, 21, and 27 years. Diameter at breast height (1.3 m) (*DBH*), total height (*H*), height to the lowest living branch, and crown width were recorded for all trees in the plots. Within each plot, 3–7 trees covering the *DBH* range were selected and destructively harvested for biomass measurements (including coarse roots). A total of 90 trees were sampled in this study. The stands were grouped into age classes at 5-year intervals before 30 years and the stands older than 30 years were combined to one age class. Information about stand characteristics and the number of sample trees in the stands is presented in Table 1.

The sample trees were felled at ground level using a hand saw. First the *H*, crown width, *DBH*, and diameter at the

**Table 1** Stand age, age class, stand density, average diameter at breast height (1.3 cm, *DBH*), average tree height (*H*), total basal area (BA), stem wood density (WD, mean ± SD) and sample sizes harvested for biomass measurement in Chinese fir plantations

Stand age (year)	Age class	Stand density (stem ha <sup>-1</sup> )	<i>DBH</i> (cm)	<i>H</i> (m)	BA (m <sup>2</sup> .ha <sup>-1</sup> )	WD (g.cm <sup>-3</sup> )	Sample number
4	Class 1 (0–5 years)	3119	3.2	1.7	2.51	0.333 ± 0.058	15
7	Class 2 (6–10 years)	2490	9.6	8.7	18.01	0.280 ± 0.042	6
10	Class 2 (6–10 years)	2175	11.6	9.8	22.97	0.280 ± 0.042	6
15	Class 3 (11–15 years)	2370	13.5	12.8	33.91	0.318 ± 0.036	12
18	Class 4 (16–20 years)	1958	15.3	13.8	35.98	0.339 ± 0.054	15
21	Class 5 (21–25 years)	1635	16.5	13.8	34.94	0.309 ± 0.058	12
27	Class 6 (26–30 years)	1905	18.1	16.3	48.99	0.314 ± 0.057	12
31	Class 7 (> 30 years)	1560	18.5	16.6	41.91	0.329 ± 0.068	6
38	Class 7 (> 30 years)	1590	20.1	22.2	50.42	0.329 ± 0.068	3
50	Class 7 (> 30 years)	1305	23.3	22.2	55.62	0.329 ± 0.068	3

tree base, at half  $H$  and at the lowest living branch of the felled trees were recorded. Tree stems were then cut at 1.3 m and at 1-m intervals thereafter up to the apex. The branches were stripped from each stem section. The stem sections and the branches with leaves were weighed in situ. The sum of the weights of all stem sections from a given tree was the total fresh stem mass. Based on the branch size, three to five random samples of branches with leaves were collected for each stem section to estimate the fraction of branch and leaf biomass. Leaves were removed from the sampled branches. The fresh mass of the leaves and branches was measured separately to calculate the ratio of leaf to branch mass and to determine the total fresh biomass of foliage and branches. One disk per stem section and subsamples of leaves and branches were collected, put into cloth bags and transported to the laboratory.

Root biomass was determined using a manual excavation method. The stump was excavated before excavating the rest of the roots by tracing them back to their root tips, as far as possible. Soil clinging to the stump and roots was removed and the roots were weighed in situ. Subsamples of stump and roots were collected and brought to the laboratory.

The samples of stem, branch, leaf, stump and roots were oven-dried at 80 °C until a constant weight to determine moisture content. The fresh mass of all tree components was converted into a dry mass (i.e. biomass) using their respective moisture content. Aboveground biomass was calculated as the sum of the stem, branch and leaf biomass, while root biomass was calculated as the sum of the stump biomass and that of other roots. All tree component biomass was summed up to calculate total tree biomass.

## Data analysis and allometric equation fitting

The average values of tree component biomass, percentage of tree component biomass to total tree biomass, and the ratios of root: shoot (aboveground), leaf: stem, and branch: stem were computed for each stand age. These values were then plotted against stand age to examine how they change with stand age. In addition, tree component biomass was plotted against aboveground biomass to see how they were correlated.

Wood density did not differ significantly among age classes (Table 1) and was not used to develop allometric equations. Thus, we included  $DBH$  alone,  $H$  alone, the combined form  $DBH^2H$ , and  $DBH$  together with  $H$  as predictor variables to develop allometric equations. All data were natural logarithmically transformed ( $\ln$ ) to ensure a linear relationship between variables and to meet the requirements

of heteroskedasticity (Picard et al., 2012; Dutcă et al., 2018). In this study, the following four types of models were used to develop basic allometric equations:

$$\ln(B_i) = \beta_{i0} + \beta_{i1} \times \ln(DBH) + \varepsilon_i \quad (1)$$

$$\ln(B_i) = \beta_{i0} + \beta_{i1} \times \ln(H) + \varepsilon_i \quad (2)$$

$$\ln(B_i) = \beta_{i0} + \beta_{i1} \times \ln(DBH^2H) + \varepsilon_i \quad (3)$$

$$\ln(B_i) = \beta_{i0} + \beta_{i1} \times \ln(DBH) + \beta_{i2} \times \ln(H) + \varepsilon_i \quad (4)$$

where  $B$  = biomass,  $i$  = tree components (stem, branch, leaf, root, aboveground and total tree);  $\beta_{i0}$  is the intercept of the regression;  $\beta_{i1}$  and  $\beta_{i2}$  are the slopes of the regression; and  $\varepsilon_i$  is the residual error. Because  $DBH$  and  $H$  are highly correlated, the variance inflation factor (VIF) was calculated by using the R package 'CAR' (version 2.1-2) to identify the collinearity in Eq. (4) (Ouyang et al. 2019).

Three approaches were taken to fit allometric equations. At first, a multilevel modeling approach was employed to develop allometric equations. According to rotation length and tree growth process, the protocol for the forest resource inventory of China divides the development stages of Chinese fir plantations into different stand age classes at a 5-year interval (i.e. 0–5, 6–10, 11–15, 16–20, 21–25, 26–30, 31–35, etc.). In this study, Chinese fir plantations at different stand ages were grouped into seven stand age classes so that the number of sampled trees was balanced to meet the requirement of mixed effects models. Stand age class rather than stand age was used as a random factor to examine whether stand age classes affect the parameters of allometric equations. For multilevel modeling, individual trees were nested within stand age classes (groups) (Finch et al. 2014). Random coefficient models allow both slopes and intercepts to vary randomly from one stand age class to another (Finch et al. 2014). The nlme package (Pinheiro et al. 2020) in the statistical software R 3.9.1 (R Development Core Team 2019) was used to fit multilevel models to estimate a random intercept, random slope, and the relationship between tree biomass component and the fixed effect of predictor variables (Finch et al. 2014; Harrison et al. 2018). The codes for the models containing different predictor variables are as follows:

$$M1 : \text{lme}(\text{fixed} = \ln(B_i) \sim \ln(DBH), \text{random} = \sim \ln(DBH)|\text{group}) \quad (5)$$

$$M2 : \text{lme}(\text{fixed} = \ln(B_i) \sim \ln(H), \text{random} = \sim \ln(H)|\text{group}) \quad (6)$$

$$M3 : \text{lme}(\text{fixed} = \ln(B_i) \sim \ln(DBH^2H), \text{random} = \sim \ln(DBH^2H)|\text{group}) \quad (7)$$

$$M4 : \text{lme}(\text{fixed} = \ln(B_i) \sim \ln(DBH) + \ln(H), \text{random} = \sim \ln(DBH) + \ln(H)|\text{group}) \quad (8)$$

where  $B$  = biomass,  $i$  = tree components (stem, branch, leaf, root etc.); group represents stand age class. In the case where a model did not reach a solution (converge), the default method and control option were changed into “method = “ML”, control = list(maxIter = 100, msMaxIter = 100, opt = “optim”)” (Finch et al. 2014). The intercept variance ( $\tau_{i0}$ ) and slope ( $\beta_{i1}$  and  $\beta_{i2}$ ) variances ( $\tau_{i1}$  and  $\tau_{i2}$ ) occurring between stand age classes, and residuals ( $\sigma$ ) of the variance within stand ages were used to evaluate the effects of stand age classes on allometric models (Finch et al. 2014).

Secondly, specific allometric equations were developed for seven stand age classes. Models (1)–(4) were fitted using the data of tree component biomass ( $B_{st}$ ,  $B_{br}$ ,  $B_{lf}$ ,  $B_{rt}$ ,  $B_{ab}$ , and  $B_{tl}$ ) for each stand age class. In addition, Models (1)–(4) were fitted for the young age class (0–5 years) but in contrast to the models for older trees, the predictor variable  $DBH$  was replaced by basal diameter at the ground surface ( $DG$ ).

Finally, all tree data were pooled together to develop generalized allometric equations across stand age. Equations (1)–(4) were fitted for each tree component (i.e.  $B_{st}$ ,  $B_{br}$ ,  $B_{lf}$ ,  $B_{rt}$ ,  $B_{ab}$  and  $B_{tl}$ ) using the pooled data without considering stand age. Then stand age was introduced as a complementary variable into Eqs. (1)–(4) for all tree compartments to examine whether biomass estimates were improved. The individual effects of stand age and interactive effects with other predictor variables (i.e.  $DBH$ ,  $H$  and  $DBH^2H$ ) were taken into account when fitting the generalized allometric equations.

$$\ln(B_i) = \beta_{i0} + \beta_{i1} \times \ln(DBH) + \beta_{i2} \times \text{age} + \beta_{i3} \times \text{age} \times \ln(DBH) + \varepsilon_i \quad (9)$$

$$\ln(B_i) = \beta_{i0} + \beta_{i1} \times \ln(H) + \beta_{i2} \times \text{age} + \beta_{i3} \times \text{age} \times \ln(H) + \varepsilon_i \quad (10)$$

$$\ln(B_i) = \beta_{i0} + \beta_{i1} \times \ln(DBH^2H) + \beta_{i2} \times \text{age} + \beta_{i3} \times \text{age} \times \ln(DBH^2H) + \varepsilon_i \quad (11)$$

$$\ln(B_i) = \beta_{i0} + \beta_{i1} \times \ln(DBH) + \beta_{i2} \times \ln(H) + \beta_{i3} \times \text{age} + \beta_{i4} \times \text{age} \times \ln(DBH) + \beta_{i5} \times \text{age} \times \ln(H) + \varepsilon_i \quad (12)$$

where  $B_i$  represents tree component biomass as explained in Eqs. (1)–(4),  $\beta_{i0}$ – $\beta_{i5}$  are the fitted parameters, and  $\varepsilon_i$  is the residual error. Only two common equations (i.e. (1) and (3)) fitted the pooled data of all stand ages and the best fitted generalized equations that included stand age for each tree component are presented in this study to examine whether the fitness and predictive capacity are improved.

The Akaike’s information criterion (AIC) was calculated, and the standard error of residuals ( $RSE$ ) was recorded to

determine the model fitness. At the same time, to compare the performance of equations developed using the three approaches, each tree component biomass predicted by multilevel models, age class-specific equations and the best fitted generalized equations were plotted against the observed values. Since Eq. (1) using  $DBH$  as a predictor variable and Eq. (3) using  $DBH^2H$  as a predictor variable are commonly used allometric equations, we chose these two models fitted by multilevel modeling and stand age class-specific equations for the comparison. We randomly separated 90% of the data to fit the models and then used the remaining 10% to test predictive ability of the fitted models.

Logarithmic transformation for regression introduces inherently biased estimates of biomass (Montagu et al. 2005); thus a back transformation of linear models for prediction requires bias correction. The systematic bias was adjusted using a correction factor (CF) that was computed by the equation (Baskerville 1972):

$$CF = \exp(RSE^2/2) \quad (13)$$

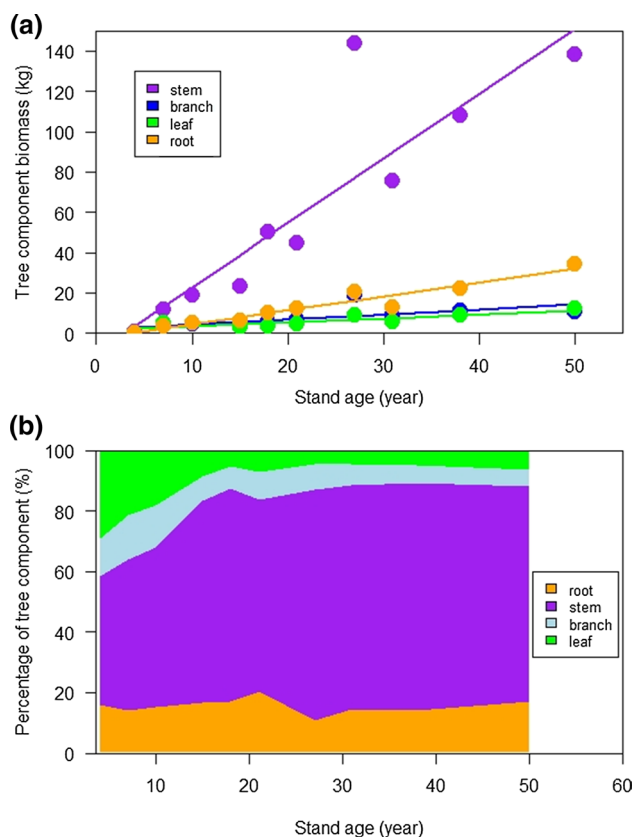
where  $RSE$  is the standard error of residuals obtained from the regression procedure. All statistical analyses were performed using the statistical software R 3.9.1 (R Development Core Team 2019).

## Results

### Biomass partitioning among tree components at different stand ages

Average biomass of all tree components tended to increase with stand age, ranging from 0.76 kg to 143.98 kg for stem,

0.19 kg to 19.14 kg for branch, 0.44 kg to 8.92 kg for leaf, and 0.24 kg to 20.77 kg for root (Fig. 1a). As usual, stem was the largest biomass pool across all stand ages and its percentage to total tree biomass tended to increase with age from 42.63% to 73.57% (Fig. 1b). In contrast, the percentage of leaf biomass to total tree biomass decreased with age from 29.08% to 4.96%. The percentage of branch biomass also tended to decrease from 12.26% to 6.34%. However, the contribution of root biomass to total tree biomass tended to



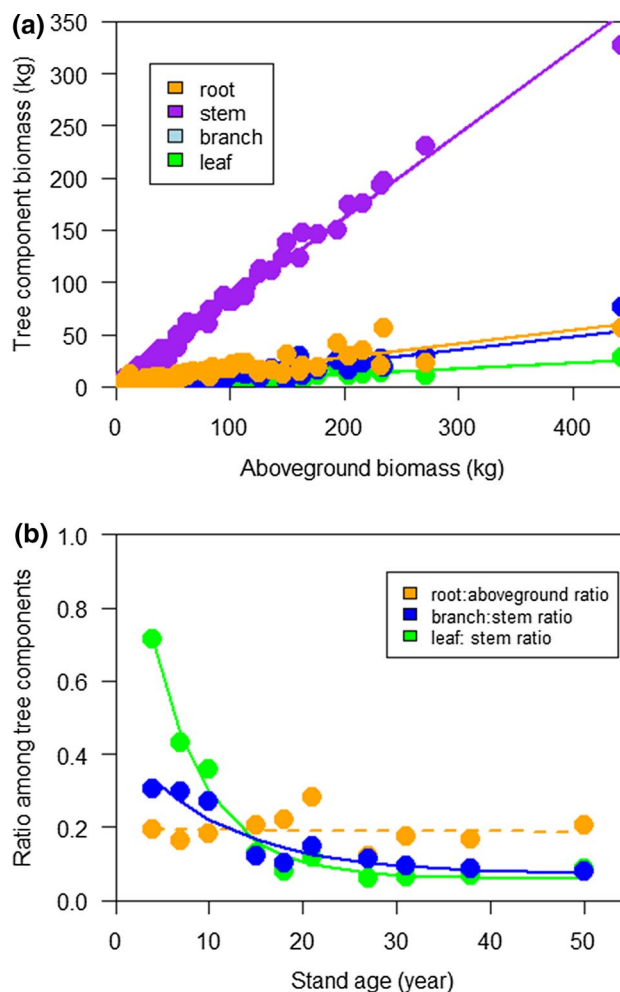
**Fig. 1** Changes in average tree component biomass (a) and the change in percentage of component biomass to total tree biomass in relation to age (b) in Chinese fir plantations

increase initially from 16.02% to 20.49%, and then decreased slightly to 15.13% (Fig. 1b).

The biomass of stems, branches, leaves, and roots showed significant linear relationships ( $p < 0.001$ ) when regressed with aboveground biomass (Fig. 2a). The regression slope was highest for stem biomass (0.81) and was lowest for leaf biomass (0.06). The slopes were intermediate for branch (0.12) and root (0.13) biomass (Fig. 2a). The average ratio of root to shoot (aboveground) biomass did not change significantly ( $p = 0.903$ ) and was about 0.19 averaged over all stand ages (Fig. 2b). A sharp decline in the ratio of leaf to stem biomass was observed between the 4-year-old stand and about 20-year-old stands and thereafter the ratio tended to be relatively stable (about 0.06). The ratio of branch to stem biomass decreased before age 30 years and then declined slightly before an equilibrium (about 0.08) in older stands (Fig. 2b).

### Multilevel models and stand age effects

When using *DBH* as a single predictor variable, allometric equations fitted by multilevel models had lower AICs than that using *H* as a predictor variable (Table 2), indicating that



**Fig. 2** Relationships between stem, branch, leaf, root and aboveground biomass (dry weight, kg) (a); and changes in the ratios of root: shoot (aboveground), leaf: stem, and branch: stem (b) in Chinese fir plantations with stand age

*DBH* is more reliable than *H* for predicting tree component biomass. Compared with *DBH*-based equations, including *H* as an additional variable for the combined form  $DBH^2H$  or separately largely improved predictions (i.e. decrease in AICs and RSE) for stem and aboveground biomass, but slightly decreased precision (i.e. increase in AICs and RSE) for branch and leaf biomass. The predictions for root and total biomass were marginally improved when including *H* as the combined form  $DBH^2H$ , and were slightly worsened when including *H* as a separate variable.

Allometric equations fitted by multilevel models showed that intercept variances were larger than slope variances (Table 2). The largest source of random variation in tree component biomass was the variation between stand age classes, with higher variances than within a stand age class. Among tree components, leaf biomass exhibited the highest variances for both intercepts and slopes between stand

**Table 2** Regression coefficients ( $\beta_{10}$ ,  $\beta_{11}$  and  $\beta_{12}$ ) with standard errors (in parentheses) and fit statistics of multilevel allometric equations for Chinese fir plantations at different age classes

Dependent variable	Predictors	$\beta_{10}$	$\beta_{11}$	$\beta_{12}$	Intercept variance ( $\tau_{10}$ )	Slope $\beta_{11}$ variance ( $\tau_{11}$ )	Slope $\beta_{12}$ variance ( $\tau_{12}$ )	RSE ( $\sigma$ )	AIC	VIF	CF
ln ( $B_{st}$ )	ln (DBH)	- 2.865 (0.244) ***	2.420 (0.103) ***		0.502	0.223		0.177	- 7.224		1.016
	ln (H)	- 4.455 (0.300) ***	3.124 (0.110) ***		0.528	0.186		0.272	39.699		1.038
	ln (DBH <sup>2</sup> H)	- 3.552 (0.259) ***	0.905 (0.036) ***		0.559	0.080		0.159	- 28.204		1.013
ln ( $B_{bv}$ )	ln (DBH) + ln (H)	- 3.611 (0.214) ***	1.752 (0.175) ***	0.990 (0.178) ***	0.396	0.288	0.189	0.159	- 31.187	6.538	1.013
	ln (DBH)	- 5.981 (0.820) ***	2.802 (0.277) ***		1.922	0.636		0.433	132.647		1.098
	ln (H)	- 6.555 (0.882) ***	3.110 (0.305) ***		1.616	0.482		0.591	186.399		1.191
ln ( $B_{fp}$ )	ln (DBH <sup>2</sup> H)	- 6.575 (0.932) ***	1.016 (0.104) ***		2.148	0.232		0.453	142.225		1.108
	ln (DBH) + ln (H)	- 5.341 (0.607) ***	3.282 (0.645) ***	- 0.716 (0.621)	1.192	1.400	1.173	0.412	134.472	9.246	1.089
	ln (DBH)	- 4.615 (0.823) ***	2.238 (0.271) ***		1.950	0.621		0.373	114.996		1.072
ln ( $B_{tl}$ )	ln (H)	- 5.413 (0.870) ***	2.615 (0.284) ***		1.736	0.472		0.490	158.516		1.128
	ln (DBH <sup>2</sup> H)	- 5.165 (0.908) ***	0.821 (0.098) ***		2.127	0.219		0.388	121.753		1.078
	ln (DBH) + ln (H)	- 4.354 (0.707) ***	2.420 (0.501) ***	- 0.266 (0.456)	1.487	1.013	0.579	0.366	120.942	4.428	1.069
ln ( $B_{ub}$ )	ln (DBH)	- 3.660 (0.126) ***	2.179 (0.060) ***		0.001	0.068		0.308	65.330		1.049
	ln (H)	- 4.411 (0.170) ***	2.531 (0.075) ***		0.024	0.055		0.390	102.265		1.079
	ln (DBH <sup>2</sup> H)	- 3.968 (0.128) ***	0.774 (0.019) ***		0.015	0.0175		0.310	63.574		1.049
ln ( $B_{ut}$ )	ln (DBH) + ln (H)	- 3.911 (0.162) ***	1.897 (0.335) ***	0.400 (0.388)	0.139	0.561	0.656	0.301	69.256	38.734	1.046
	ln (DBH)	- 2.591 (0.221) ***	2.401 (0.112) ***		0.457	0.261		0.181	- 8.076		1.017
	ln (H)	- 3.912 (0.437) ***	3.001 (0.156) ***		0.911	0.315		0.285	52.56		1.041
ln ( $B_{tt}$ )	ln (DBH <sup>2</sup> H)	- 3.227 (0.288) ***	0.893 (0.039) ***		0.643	0.088		0.171	- 28.997		1.015
	ln (DBH) + ln (H)	- 3.210 (0.289) ***	1.810 (0.172) ***	0.865 (0.175) ***	0.608	0.247	0.002	0.169	- 22.234	2.294	1.014
	ln (DBH)	- 2.294 (0.142) ***	2.356 (0.082) ***		0.283	0.198		0.178	- 21.267		1.016
ln ( $B_{tt}$ )	ln (H)	- 3.536 (0.411) ***	2.922 (0.145) ***		0.815	0.272		0.290	59.616		1.043
	ln (DBH <sup>2</sup> H)	- 2.873 (0.239) ***	0.870 (0.033) ***		0.513	0.077		0.174	- 20.757		1.015
	ln (DBH) + ln (H)	- 2.744 (0.217) ***	1.886 (0.163) ***	0.670 (0.166) ***	0.433	0.212	0.001	0.173	- 14.830	3.107	1.015

Residual standard error (RSE), Akaike information criterion (AIC), variance inflation factor (VIF) for the model of DBH and H separately, and logarithmic correction factor (CF). Asterisk \*\*\* after the coefficients indicates the significance level at  $p < 0.001$  and no asterisk indicates no significance at level of  $p > 0.05$

age classes, followed by branch biomass, stem biomass, aboveground and total biomass, whereas root biomass had the lowest variances for both intercepts and slopes between stand age classes (Table 2). Including *DBH* as the single predictor variable in the allometric equations yielded lower variances between stand age classes for stem, root, aboveground and total tree biomass, but a higher variance between stand age classes for branch and leaf biomass compared with using *H* as the single predictor variable. Adding *H* in combined form  $DBH^2H$  to allometric equations increased the variance between stand age classes for tree component biomass, except for stem biomass compared with using *DBH* alone, but the reverse pattern occurred for stem, root, aboveground and total biomass when comparing with using *H* alone (Table 2). For stem, branch and leaf biomass, using both *DBH* and *H* as separate predictor variables resulted in the lowest variance of intercept between stand age classes.

### Age class-specific allometric equations and generalized allometric equations

Across the seven stand age classes, biomass of all tree components was significantly related to *DBH*. The determination coefficients ( $R^2$ ) of stem, aboveground and total tree biomass were larger than 0.95, except for age class 7, with  $R^2$  lower than 0.85. The determination coefficients of branch, leaf and root biomass varied greatly with age classes, with the lowest values for leaf biomass at age class 3 ( $R^2=0.67$ ) and root biomass at age class 4 ( $R^2=0.69$ ) (Table S1). When using *H* as a single predictor variable, the relationships for all tree biomass components were significant but were weaker than using *DBH* as a single predictor variable. The allometric equations using *H* as a predictor variable did not fit well in older stands after age class 4 (Table S2). Adding *H* in the

combined form  $DBH^2H$  improved the fit of allometric equations, except for branch and leaf biomass in older stands (age class 6 and age class 7) (Table S3). When both *DBH* and *H* were included as separate predictor variables, the fit was improved but the *H* effects on allometric equations were not significant (Table S4).

For the smallest age class, the allometric equations fitted well for all tree biomass components, whether diameter at the ground surface (*DG*) (Fig. S1) or the combined *DG* and *H* was used as the predictor variables. The determination coefficient ( $R^2$ ) was higher than 0.85 (Table 3).

When the data for all trees were pooled together to develop the generalized allometric equations, using *DBH* and  $DBH^2H$  as the predictor variables had a high determination coefficient ( $R^2 > 0.85$ ) for stem, branch, root, aboveground and total tree biomass, but a low determination coefficient ( $R^2 = 0.83$  and  $0.81$ ) for leaf biomass (Table 4). The equations using *DBH* as a predictor variable provided better fits for branch and leaf biomass than those using  $DBH^2H$  as a predictor variable. But for stem, root, aboveground and total biomass, the equations using  $DBH^2H$  as a predictor variable had the best fits. Including stand age as a complimentary predictor variable greatly improved the fit of the generalized equations for all tree components (Table 4 and Fig. 3). But predictor variables included in the generalized allometric equations varied with tree components (Table 4).

### Comparison of three modeling approaches

The biomass values predicted by multilevel models, age class-specific equations and generalized equations for stem, aboveground and total tree were comparable to the observed biomass values, except aboveground biomass predicted using the generalized equation (Fig. 4 and Table S5). For

**Table 3** The parameters ( $\beta_{i0}$  and  $\beta_{i1}$ ) with standard errors (in parenthesis) for allometric equations [ $\ln(B_i) = \beta_{i0} + \beta_{i1} \times \ln(DG)$ ] (model 1) relating component biomass  $i$  ( $B_i$ , g) to basal diameter at ground level (*DG*, cm) and [ $\ln(B_i) = a + b \times \ln(DG^2H)$ ] (model 2) relating  $B_i$  to combined predictors of *DG* and tree height (*H*, cm) for young Chinese fir trees at age of 4 years

Component	Model	$\beta_{i0}$	$\beta_{i1}$	AIC	RSE	$R^2$	CF
Stem	Model 1	2.182 (0.224)***	2.762 (0.158)***	5.859	0.259	0.959	1.034
	Model 2	2.579 (0.258)***	0.930 (0.068)***	12.684	0.325	0.930	1.054
Branch	Model 1	1.445 (0.368)***	2.378 (0.260)**	20.675	0.424	0.855	1.094
	Model 2	1.671 (0.270)***	0.833 (0.071)***	14.126	0.341	0.907	1.048
Leaf	Model 1	2.722 (0.204)***	2.118 (0.144)***	2.979	0.235	0.939	1.028
	Model 2	3.017 (0.212)***	0.716 (0.056)***	6.830	0.267	0.921	1.036
Root	Model 1	2.073 (0.222)***	2.171 (0.156)***	5.463	0.255	0.932	1.033
	Model 2	2.348 (0.198)***	0.742 (0.052)***	4.834	0.250	0.935	1.032
Aboveground	Model 1	3.314 (0.177)***	2.456 (0.125)***	-1.197	0.205	0.965	1.021
	Model 2	3.646 (0.186)***	0.833 (0.049)***	2.979	0.235	0.954	1.028
Total tree	Model 1	3.574 (0.165)***	2.401 (0.116)***	-3.403	0.190	0.968	1.018
	Model 2	3.895 (0.171)***	0.815 (0.045)***	0.374	0.216	0.959	1.023

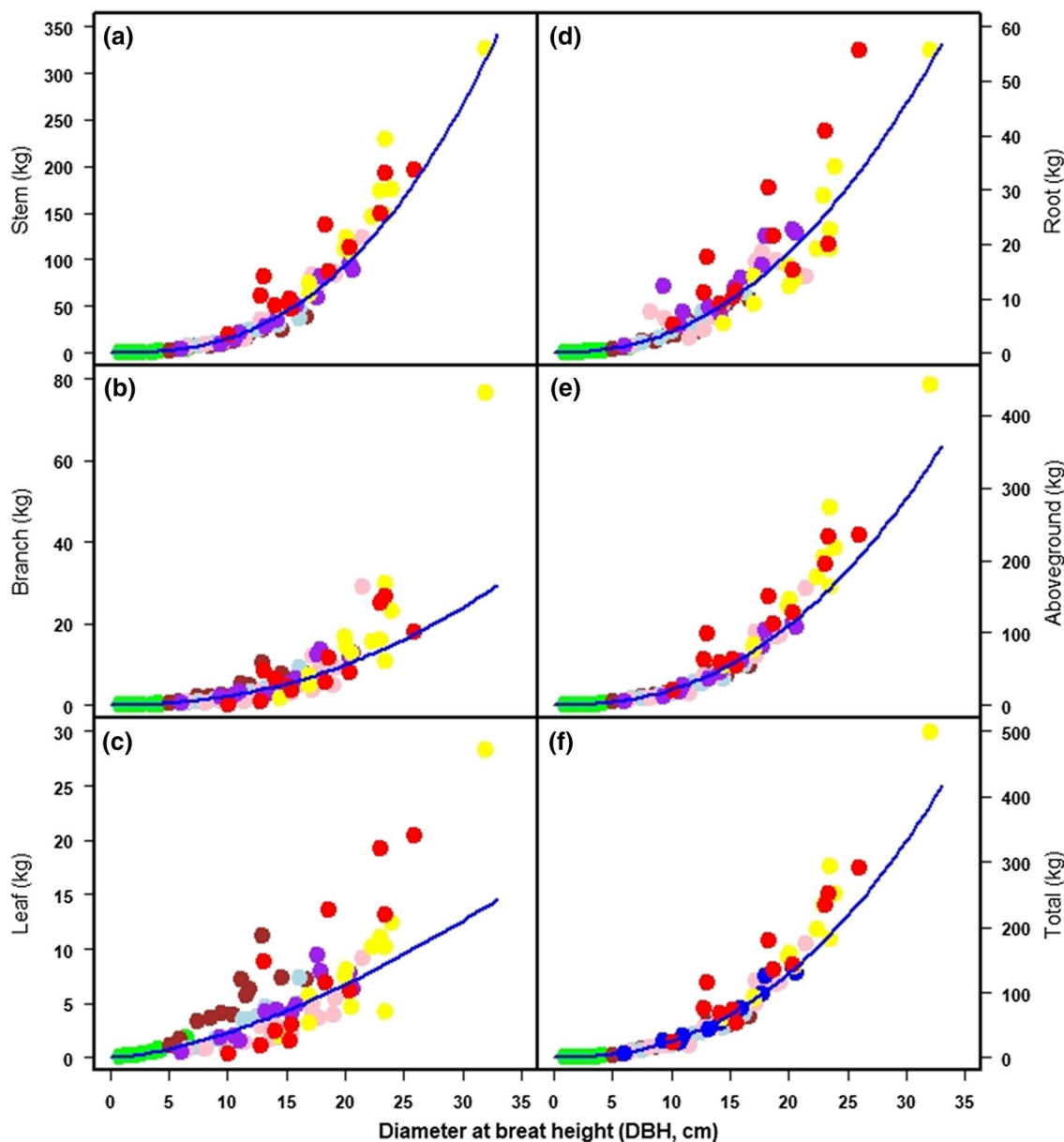
The number of sample trees was 15; RSE is residual standard error;  $R^2$  is the adjusted coefficient of determination; CF is logarithmic correction factor. Asterisks \*\* and \*\*\* after the coefficients indicate the significance level at  $p < 0.01$  and  $p < 0.001$ , respectively



**Table 4** Regression coefficients ( $\beta_{10}$ ,  $\beta_{11}$ ,  $\beta_{12}$  and  $\beta_{13}$ ) with standard errors (in parentheses) and fit statistics for generalized allometric equations

Dependent variable	Predictors	$\beta_{10}$	$\beta_{11}$	$\beta_{12}$	$\beta_{13}$	AIC	RSE	$R^2$	CF
$\ln(B_{sk})$	$\ln(DBH)$	- 2.993 (0.098)***	2.511 (0.039)***			28.674	0.278	0.978	1.039
	$\ln(DBH^2H)$	- 3.258 (0.086)***	0.877 (0.012)***			- 1.883	0.234	0.985	1.028
	$\ln(DBH^2H) + age$	- 3.146 (0.074)***	0.817 (0.014)***	0.017 (0.003)***		- 33.244	0.195	0.990	1.019
$\ln(B_{br})$	$\ln(DBH)$	- 4.208 (0.190)***	2.171 (0.076)***			146.901	0.540	0.902	1.157
	$\ln(DBH^2H)$	- 4.381 (0.210)***	0.750 (0.028)***			158.376	0.576	0.889	1.180
	$\ln(DBH) + age + age^2 \ln(DBH)$	- 3.439 (0.239)***	1.992 (0.110)***	- 0.140 (0.027)***	0.045 (0.009)***	126.040	0.475	0.926	1.119
$\ln(B_{fr})$	$\ln(DBH)$	- 2.712 (0.188)***	1.542 (0.076)***			144.973	0.534	0.826	1.153
	$\ln(DBH^2H)$	- 2.820 (0.205)***	0.531 (0.028)***			154.192	0.563	0.808	1.172
	$\ln(DBH) + age + age^2 \ln(DBH)$	- 1.995 (0.236)***	1.406 (0.108)***	- 0.137 (0.026)***	0.043 (0.009)***	123.644	0.468	0.870	1.116
$\ln(B_{cl})$	$\ln(DBH)$	- 3.770 (0.122)***	2.234 (0.049)***			67.436	0.346	0.960	1.062
	$\ln(DBH^2H)$	- 3.995 (0.123)***	0.779 (0.017)***			63.014	0.337	0.962	1.058
	$\ln(DBH) + age$	- 3.673 (0.111)***	2.041 (0.060)***	0.019 (0.004)***		48.964	0.310	0.968	1.049
$\ln(B_{sh})$	$\ln(DBH)$	- 2.309 (0.090)***	2.342 (0.036)***			14.681	0.257	0.979	1.034
	$\ln(DBH^2H)$	- 2.548 (0.087)***	0.817 (0.012)***			0.588	0.237	0.982	1.028
	$\ln(DBH^2H) + age + age^2 \ln(DBH^2H)$	- 2.078 (0.100)***	0.735 (0.015)***	- 0.054 (0.012)***	0.008 (0.001)***	- 36.576	0.190	0.989	1.018
$\ln(B_{cl})$	$\ln(DBH)$	- 2.099 (0.084)***	2.325 (0.034)***			2.111	0.239	0.982	1.029
	$\ln(DBH^2H)$	- 2.335 (0.080)***	0.811 (0.011)***			- 12.597	0.220	0.985	1.024
	$\ln(DBH^2H) + age + age^2 \ln(DBH^2H)$	- 1.937 (0.095)***	0.736 (0.014)***	- 0.042 (0.011)***	0.006 (0.001)***	- 44.903	0.182	0.990	1.017

Each equation is presented with Akaike's information criterion (AIC), residual standard error (RSE), coefficient of determination ( $R^2$ ), and logarithmic correction factor (CF). Asterisk \*\*\* after the coefficients indicates the significance level at  $p < 0.001$

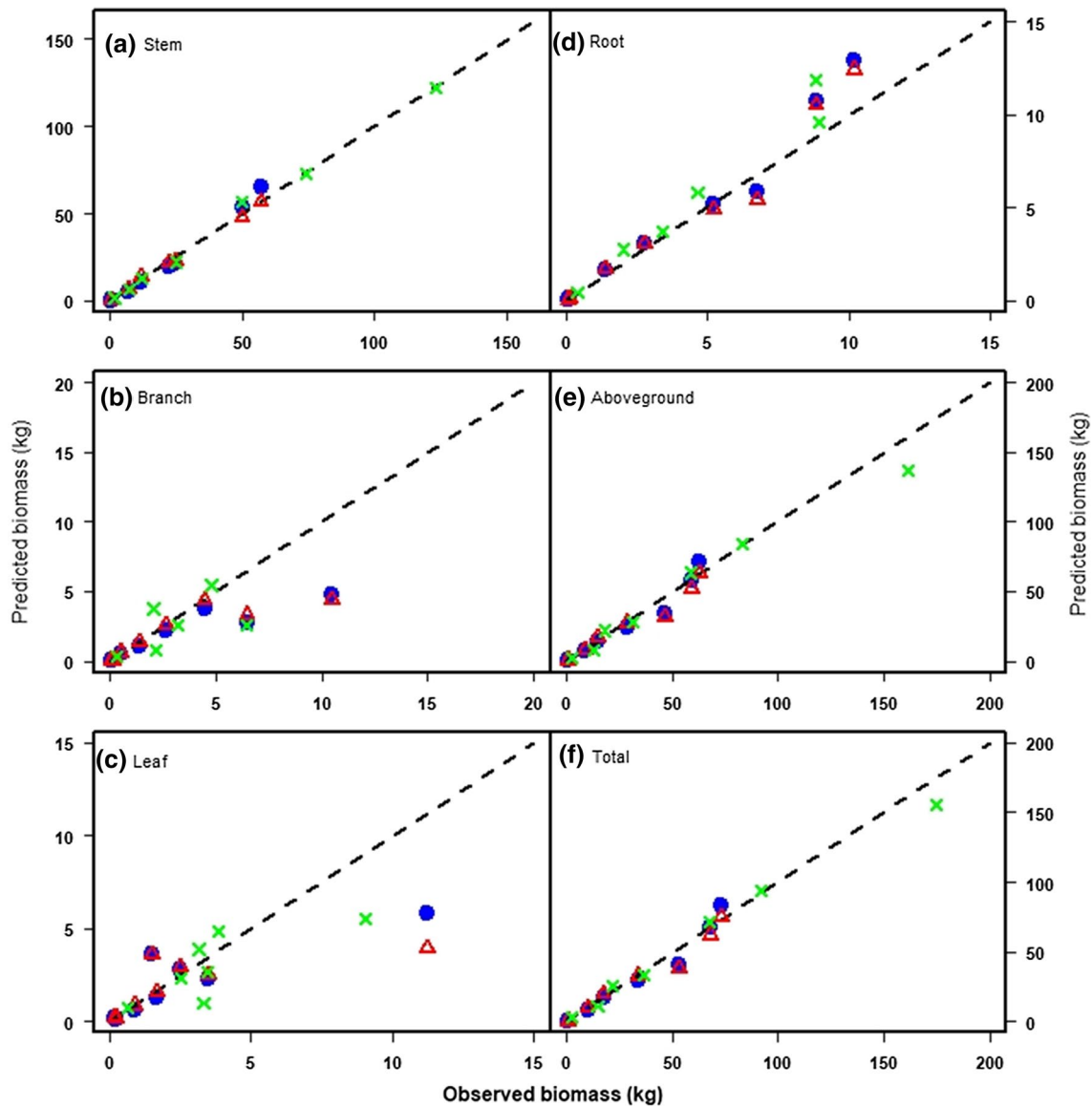


**Fig. 3** The observed biomass (kg) of stem (a), branch (b), leaf (c), root (d), aboveground (e) and total tree (f) plotted against diameter at breast height (1.3 m) (DBH, cm) together with the fitted curves using the DBH-based generalized equations in Chinese fir plantations at different age classes. Note: the color of dots is green for Class

1, brown for Class 2, light blue for Class 3, pink for Class 4, purple for Class 5, yellow for Class 6, and red for Class 7. The relationship between ground diameter and biomass for the <5 year class are presented in Fig S1

branches and roots, the biomass values predicted by age-specific equations were close to the observed values, while the multilevel models and generalized equations had similar estimations but poorly predicted biomass values (Fig. 4 and Table S5). For leaves, age-specific equations using *DBH* as

a predictor variable had close estimates for the observed biomass. The other four equations (two multilevel models, age-specific equation using  $DBH^2H$  as predictor variable, and generalized equation) poorly predicted leaf biomass (Fig. 4 and Table S5).



**Fig. 4** Comparison of the predicted stem (a), branch (b), leaf (c), root (d), aboveground (e), and total tree biomass (kg) (f) against the corresponding observed biomass (kg) in Chinese fir plantations. Note: the blue dots represent multilevel models, red triangles represent general-

ized additive models, and green crosses represent age class-specific models, using diameter at breast height (DBH, cm) as predictor variable

## Discussion

### Effects of stand age on tree biomass partitioning

The effects of stand age on biomass partitioning are the result of tree growth and the balance of resource allocation among tree components in a way that maintains the physiological activities and functions of each component (Landsberg and Sands 2011; Mensah et al. 2016). The aboveground partitioning pattern where the proportion of stem increases and proportions of leaf and branch biomass decrease with stand age (Fig. 1) is consistent with previous

studies (Saint-André et al. 2005; Peichl and Arain 2007; Seo et al. 2013; Lim et al. 2013; Li et al. 2014). This results firstly from the rapid foliage and branch expansion during early stages, which is crucial for light capture and tree survival (Fatemi et al. 2011; Peichl and Arain 2007). The higher leaf to stem ratio in younger trees or stands suggest that more resources (carbohydrate resources) might have been allocated to foliage for photosynthetic activities (Mensah et al. 2016). Then, as stands age, tree size increases due to ontogeny and more resources are allocated for stem growth (Mensah et al. 2016). Meanwhile, the canopy closes, crown sizes and hence leaf and

branch biomass increases proportionally less than stem mass (Mensah et al. 2016) which continues to increase due to physical adaption to ensure tree stability (Peichl and Arain 2007). Even through stem biomass was the largest biomass component, leaf and branch biomass is also important for C storage and should be included in C accounting in forests, in particular in young plantations.

The relative proportion and root:shoot ratio are usually applied to estimate root biomass due to the labor input and large time-consumption of direct root measurements (Lim et al. 2013). In this study, the relative proportion of root biomass increased initially and then decreased slightly before reaching a stable value, ranging from 15.13% to 20.49%. This is inconsistent with other studies where the relative proportion of root biomass decreased considerably after stand establishment and then stabilized to a certain value (Tobin and Nieuwenhuis 2005; Peichl and Arain 2007). The average ratio of root to shoot remained at about 0.19 for different stand ages. This is very similar to 0.205 reported for subtropical moist plantations in a meta-analysis (Mokany et al. 2006) and is in line with Li et al. (2014), who reported a relatively stable root:shoot ratio for *Pinus bungeana*. Therefore, variation in relative root biomass needs to be considered in order to avoid considerable error in root biomass and C stock estimates.

### Effects of stand age on allometric equations

Stand age effects on relationships between biomass and tree dimensions have been reported since the early 1970s (Saint-André et al. 2005). However, the fitted regression coefficients of allometric equations related to stand age are controversial, depending on tree components and species (Bond-Lamberty et al. 2002; Saint-André et al. 2005). Multilevel models were used in this study to examine which tree components were more influenced by stand age and how the effects varied with predictor variables.

The results showed that variances of both intercepts and slopes for all tree components were higher between stand age classes than within stand age classes, indicating the effects of stand age on allometric equations. Leaf and branch biomass exhibited higher variances of intercepts and slopes than stem, aboveground and total biomass, but root biomass had lower variances (Table 2). This not only reflects the change in tree growth but is also the result of the combined effect of tree age and tree social status (Saint-André et al. 2005). On the one hand, structural components (i.e. stem, branch and coarse root) change gradually over time while functional components (i.e. foliage, sapwood and fine roots) are more sensitive to the environment (Landsberg and Sands 2011) and competition from the neighboring trees (Dutca et al. 2018). On the other hand, trees of the same size but different age might have a distinct social status: dominant

in young stands and suppressed in old stands (Wirth et al. 2004; Saint-André et al. 2005). The suppressed and older trees of same size tend to decrease leaf and branch biomass (Fig. 3). Therefore, allometric equations for leaf and branch biomass exhibited larger variations in intercepts and slopes between stand age classes than stem, root, aboveground and total biomass (Table 2). Developing age-specific equations or generalized equations that include stand age effects is required to improve estimates of branch and leaf biomass.

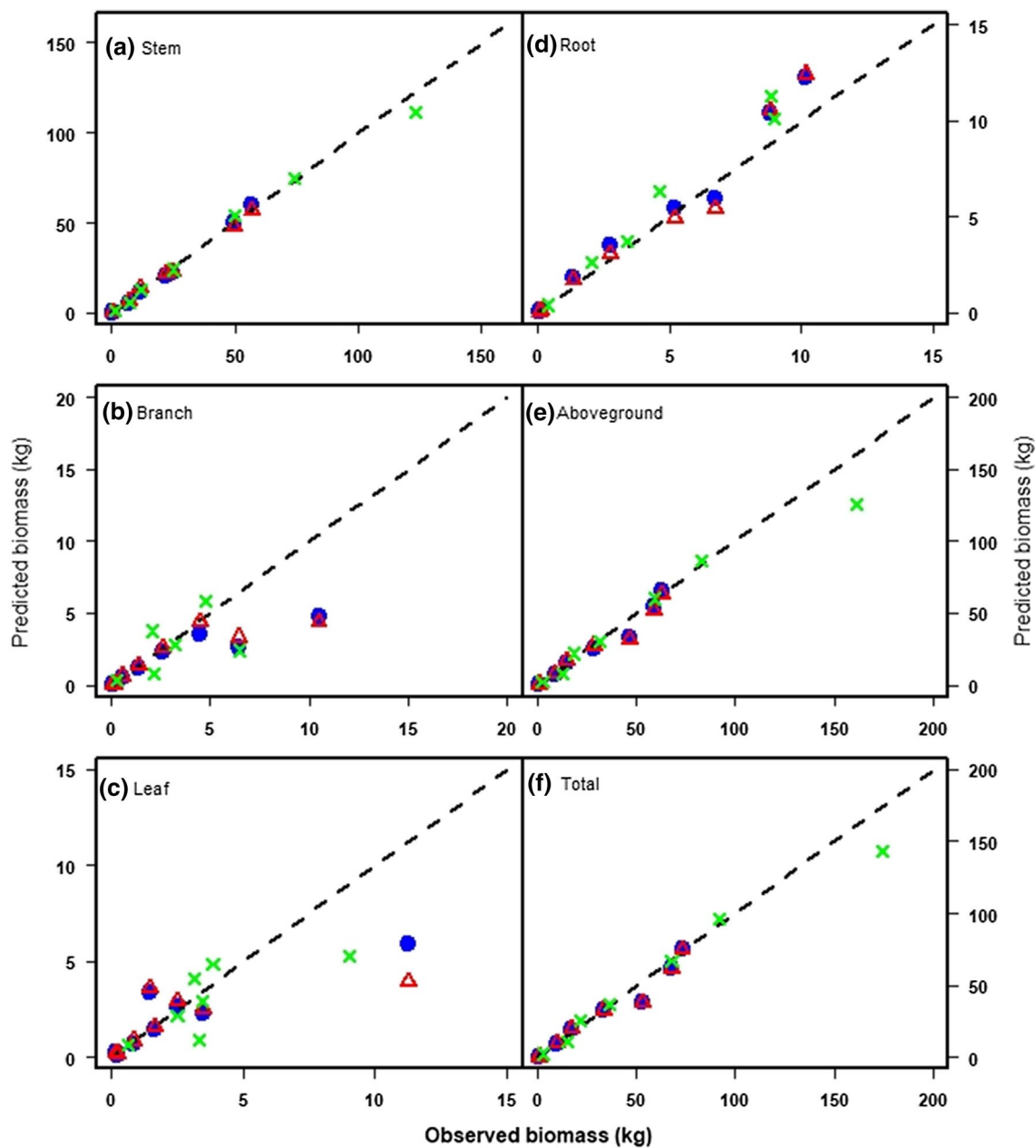
Multilevel models using *DBH* as a predictor variable had lower intercept and slope variances between stand age classes for stem, root, aboveground and total tree biomass than the models using *H* as a predictor variable (Table 2). However, the reverse pattern was found for branch and leaf biomass. This confirms that the biomass of large woody components is more strongly related to *DBH* and this relationship varies less between stand age classes than that of smaller and shorter-lived components (such as branch, leaf and root biomass) (Cole and Ewel 2006). Moreover, competition for canopy dominance may cause trees to allocate more photosynthates to increase tree height instead of radial growth (Fatemi et al. 2011). Thus, using *H* as a predictor variable explained less variance for branch and leaf biomass between stand age classes than using *DBH* as a predictor variable.

Including *H* as an additional predictor variable only reduced the variance between stand age classes for stem biomass. This may be because stem biomass is determined more by tree size (diameter and height) while the other components are determined by biomass allocation patterns that vary with stand age (Dutca et al. 2018).

### Age class-specific versus generalized allometric equations

Age class-specific allometric equations that had *DBH* as a single predictor variable were significant for all tree biomass components (Table S1). This result is consistent with other studies (Brown et al. 1989; Zianis and Mencuccini 2004; Basuki et al. 2009; Kuyah et al. 2012) where *DBH* was a strong predictor of tree component biomass. The proportion of variation in biomass that was explained by *DBH* was high ( $R^2 > 0.95$ ) for stem, aboveground and total tree biomass in stand age-specific allometric equations, but was relatively low and differed among stand age classes for branch, leaf and root biomass (Table S1). This indicates that branch, leaf and root biomass are more responsive to competition and environment (Cole and Ewel 2006; Xiang et al. 2016).

Age-specific allometric equations using *H* as a single predictor variable were also significant. Thus, tree height in combination with other dimensional variables (i.e. crown diameter) may be attractive for the development of allometric equations to predict biomass using the data retrieved



**Fig. 5** The predicted stem (a), branch (b), leaf (c), root (d), above-ground (e), and total tree biomass (kg) (f) plotted against the corresponding observed biomass (kg) in Chinese fir plantations. Note: the blue dots represent multilevel models, red triangles represent general-

ized additive models, and green crosses represent age class-specific models, using diameter at breast height (DBH, cm) and height (H, m) as composite variable ( $DBH^2H$ )

from remote sensing (Jucker et al. 2017). However, the determination coefficients were lower than using  $DBH$  as a predictor variable, in particular for older age classes. This is due to the fact that  $DBH$  explains a greater proportion of biomass variance than  $H$  (Dutca et al. 2018). Meanwhile, in older plantations tree height development slows so that tree  $DBH$  varies much more than height. Including  $H$  in the combined form  $DBH^2H$  generally improved the fit of age-specific allometric equations. This may be because the combined

$DBH^2H$  captures the variation in the  $DBH$ - $H$  ratio and tree architecture, and avoids multicollinearity problems between  $DBH$  and  $H$  as separate variables in allometric equations (Rojas-García et al. 2015; Dutca et al. 2018).

This study developed generalized allometric equations for tree component biomass across stand age. Adding stand age as a complementary variable in the generalized allometric equations improved the fit (Table 4) and the prediction of tree component biomass (Fig. 4 and Fig. 5).

This is consistent with the results reported by Saint-André et al. (2005), because of the increasing sample size and the consideration of stand age effects (Porté et al. 2002). When compared with the observed data, the three fitting approaches (multilevel, age-specific and generalized models) provided comparable predictions for stem, root, above-ground and total biomass. As for branch and leaf biomass, age class-specific allometric equations provided similar predictions but multilevel models and generalized allometric equations underestimated their values (Fig. 4 and Fig. 5). This confirms more variation in branch and leaf biomass in Chinese fir plantations (Cole and Ewel 2006; Xiang et al. 2016). Further improvement may be possible if stand structure and canopy architecture of individual trees are taken into account (Forrester et al. 2017b).

## Conclusions

As the age of Chinese fir plantations increased, the proportions of branch and leaf biomass decreased while the stem biomass proportion increased. The proportion of root biomass increased initially and then decreased to a stable state. Multilevel models indicated that stand age affected the intercept and slope of allometric equations. Branch and leaf biomass exhibited higher variances between stand age classes. Using *DBH* as a predictor variable had lower variances between stand age classes for stem, root, above-ground and total tree biomass, but using *H* as predictor variable explained less variance for branch and leaf biomass between stand age classes. Age-specific allometric equations fitted well using *DBH* and the combined form  $DBH^2H$ . Including stand age as a complementary predictor variable improved the fitness of generalized allometric equations. Stem, aboveground and total tree biomass predicted by the multilevel models and generalized equations were comparable to the observed data. Nevertheless, multilevel and generalized equations had relatively low predictive capacity for branch, leaf and root biomass. Therefore, multilevel models and the best generalized equations could be used to estimate stem, aboveground and total tree biomass, but age-specific equations are recommended to improve the estimates of branch, leaf and root biomass.

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