

Biomass allocation patterns and allometric relationships between components of the androdioecious *Acer tegmentosum*

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Received: 4 August 2015 / Accepted: 17 May 2016 / Published online: 17 June 2016
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Abstract

• **Key message** We present comparisons about biomass allocation between males and hermaphrodites of androdioecious *Acer tegmentosum* Maxim.. Different biomass allocation patterns were found, and males were shown to have a larger investment into coarse roots and foliage.

• **Context** Sexual dimorphism in differences of reproductive costs between genders has been widely reported for trees, but we still know little about allometric relationships between tree components in both genders.

• **Aims** We present biomass allocation patterns and relationships between components of the androdioecious *A. tegmentosum* in a broad-leaved mixed forest in northeastern China. The objectives of this study were to examine how gender affects the biomass structure of androdioecious species and how the gender-related reproductive efforts affect the allometric relationships.

• **Methods** We harvested 31 hermaphrodite and 29 male *A. tegmentosum* trees and opted for diameter at breast height, tree height, and crown length as the independent variables and various biomass components as the dependent variables. Five types of function were used to model allometry equations.

• **Results** Biomass allocation between genders was different, and the best biomass model for each biomass component varies between genders. Males have a higher investment in foliage and coarse root biomass than hermaphrodites, and hermaphrodites invested more in reproduction than males.

• **Conclusion** Biomass equations are strongly gender-related. Males tended to invest a larger fraction of the vegetative biomass into leaves and coarse roots.

Keywords *Acer tegmentosum* Maxim. · Biomass allocation · Allometric relationship · Androdioecious species

1 Introduction

In a sexual dimorphic reproductive system, androdioecy is very rare. This system consists of only two types of individual plants in breeding populations, i.e., male and cosexual plants (Yampolsky and Yampolsky 1922). Male plants produce male flowers, while cosexual plants produce perfect flowers. We chose a “hermaphrodite” to represent the second kind of plant. Lloyd (1979) pointed out that androdioecious plants have two forms in nature: (1) true functional androdioecy, where perfect flowers carry both female and male functions, and (2) morphological androdioecy, where the anthers of perfect flowers are indehiscent or barren, i.e., they are functionally dioecious or monoecious (Lloyd 1979; Anderson and Symon 1989; Swensen et al. 1998). Only seven species are known to exhibit true functional androdioecy (Vassiliadis et al. 2000). No matter which kind of androdioecy, hermaphrodites have to allocate their limited resources to both flowering and setting fruits, while males produce flowers only.

The theory of plant life history is largely concerned with optimal resource allocation between male and female functions (Allen and Antos 1993; Rocheleau and Houle 2001). It is assumed that there is a resource tradeoff between reproductive and vegetative distribution (Popp and Reinartz 1988; Allen and Antos 1993; Antos and Allen 1999; Obeso 2002; Torimaru and Tomaru 2012). A number of comparative studies have examined sexual dimorphism, although some

Handling Editor: Barry Alan Gardiner

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disagreement persists with this issue. Most reports indicate that a higher cost of reproduction should have some consequences, such as lower vegetative growth; hence, males will have a higher growth rate than females (Obeso et al. 1998; Antos and Allen 1999; Obeso 2002; Cornelissen and Stiling 2005). But the cost of fruit production seems to be not too high to limit vegetative growth in other species (Sakai 1990). Female plants have a powerful feedback mechanism to compensate for the higher reproductive effort by saving resources for stem and height growth (Petzold et al. 2013). For example, Nicotra (1999) reported that females grow faster than males. Sexual dimorphism may contribute to some intersexual secondary differences, which can be explained by the higher reproductive costs incurred by hermaphrodites than by males.

Most investigations have focused on reproductive costs, but little attention has been paid to sexual differences in biomass allocation patterns and relationships regarding the main tree architecture of cosexual species. Individuals may vary in their relative allocation to male and female functions (Lloyd 1979). Perhaps one of the most frequently observed differences between genders is that females allocate a greater proportion of biomass to reproduction components than do males (Meagher and Antonovics 1982; Popp and Reinartz 1988). Zhang et al. (2012) studied the biomass allocation of two dioecious shrub species of the genus *Rhamnus*. They found that females of these two species had more foliage, branch, and trunk biomass than males. Michiko et al. (2015) analyzed the

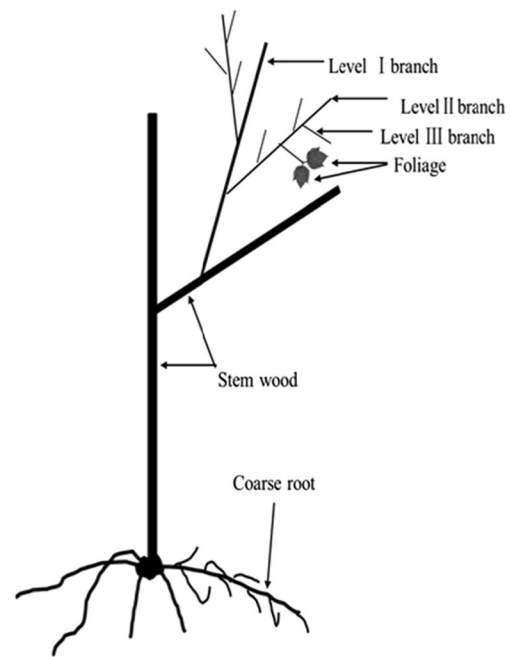


Fig. 1 Simplified scheme of the entire tree. We dissected each sample tree into different components including foliage, branches, stem wood, and coarse roots, and the branches were further classified as level 1, 2, and 3 branches, level 3 being the smallest and level 1 the biggest

allometric relationship between tree size and vegetative components of both genders. Their results demonstrate that females have greater leaf biomass than males. There are still

Table 1 Statistical summary of sample tree variables and biomass data for different genders

Items	Male		Hermaphrodite	
	Mean \pm SD	Range	Mean \pm SD	Range
Number of trees	29	–	31	–
Sample tree variables				
DBH (cm)	7.83 \pm 3.02a	3.10–16.5	9.66 \pm 3.23b	4.10–18.0
DB (cm)	10.5 \pm 3.93a	4.10–19.8	12.5 \pm 3.68a	7.20–20.7
H (m)	8.62 \pm 2.17a	4.30–12.8	9.20 \pm 2.74a	3.50–13.4
CL (m)	5.56 \pm 1.92a	2.20–9.70	4.71 \pm 2.08b	1.90–9.60
CW1 (m)	4.98 \pm 1.60a	2.40–8.00	4.38 \pm 2.02a	2.00–9.40
CW2 (m)	4.92 \pm 1.56a	1.30–8.10	4.35 \pm 1.86a	1.70–8.90
CW (m)	4.95 \pm 1.51a	1.90–7.80	4.37 \pm 1.69a	1.90–8.50
Sample tree biomass data				
Foliage (kg)	0.967 \pm 0.828a	0.0300–3.10	0.803 \pm 1.964a	0.0528–4.11
Branch (kg)	5.00 \pm 5.12a	0.390–24.0	7.79 \pm 7.61a	0.789–29.0
Stem wood (kg)	9.91 \pm 8.43a	0.582–34.8	18.0 \pm 13.5b	1.59–45.3
Aboveground (kg)	15.9 \pm 14.0a	1.00–54.6	26.3 \pm 21.5b	3.36–79.7
Belowground (kg)	3.39 \pm 2.96a	0.380–12.0	3.32 \pm 2.44a	0.491–11.3
Total biomass (kg)	19.2 \pm 16.7a	1.38–65.6	29.6 \pm 23.6b	4.40–91.0

Different letters indicate significant differences between means at the 0.05 level

N number of sample trees, *DBH* diameter at breast height, *DB* diameter at tree base, *H* height, *CL* crown length, *CW1* crown width from south to north, *CW2* crown width from east to west, *CW* mean value of *CW1* and *CW2*

only a few studies revealing biomass allocation patterns and allometric relationship of androdioecious species.

In this study, we examined a basic biomass allocation pattern of the androdioecious *Acer tegmentosum* Maxim., relating biomass components for both genders. The specific objectives of this study were to investigate (1) whether the biomass structure of androdioecious species is gender-related and (2) whether the differences in reproductive efforts affect the allometric relationships of both genders.

2 Methods

2.1 Study site

The study was conducted at the Jiaohu experimental forest in Jilin province (43° 57.5' N, 127° 44.1'–127° 44.7' E) at an average elevation of 459 m, with a mean annual temperature of 3.8 °C. The region has a monsoon climate; precipitation is low in winter but at higher elevations in summer it is very high, with a mean annual precipitation as high as 695.9 mm. The soil is a dark brown forest soil. The study site is a multi-species near-mature forest dominated by *Pinus koraiensis* Sieb., *Fraxinus mandshurica* Rupr., *Tilia amurensis* Rupr., and *Acer mono* Maxim..

The androdioecious species *A. tegmentosum* in this study is common as a small tree at the study site. It is widely distributed in the conifer and broad-leaved mixed forests in north-eastern China. Both genders of *A. tegmentosum* blossom in early spring, with racemes of green flowers. For hermaphrodites, the fruits come with dipterous appearance and change from green to yellowish-brown when ripe in late August.

2.2 Sampling and measurements of biomass components

In May 2014, after identifying the sex of 60 flowering *A. tegmentosum* trees (29 males, 31 hermaphrodites) and marking their location, we counted the number of flowers of each tree. We took about 50 flowers to the laboratory, oven-dried them at 80 °C for 48 h, weighed their dry mass, and then estimated the total flower biomass.

All the sample trees (29 males and 31 hermaphrodites) were cut at ground level after measuring the diameter at breast height and diameter at tree base. After cutting, we dissected the entire plant into different components, i.e., vegetative parts such as foliage, branches, stem wood, and coarse roots, and the branches were further classified as level 1, 2, and 3 branches, level 3 being the smallest and level 1 the largest (Fig. 1), as well as fruits for hermaphrodites. We measured the fresh weights for each component separately in the field to the nearest 0.1 kg. We measured only coarse roots (diameter ≥ 5 mm), because harvesting fine roots is practically impossible and they have little impact on total root biomass.

The roots were cleaned and their fresh mass weighed. Simultaneously, 0.5–1 kg representative samples of each component were taken to the laboratory, oven-dried to a constant mass, and weighed for determination of their moisture content. Total dry matter of each component was calculated by the ratio of the samples (dry matter to fresh weight). Statistical summaries of sampled trees are presented in Table 1.

2.3 Data analysis

Analysis of covariance (ANCOVA) with DBH and gender as covariates was used to examine sexual differences in biomass proportion. The observations meet the assumptions of independence with equal error variances. A general non-linear biomass equation ($Y = pX_1^{p_1} X_2^{p_2} X_3^{p_3} \dots X_n^{p_n} \theta$) was used to develop equations for each gender relating tree component and belowground biomass (Xiao and Ceulemans 2004; Mesele et al. 2013; Nazanin and Taraneh 2013; Rosta et al. 2014; Fabiola et al. 2015), where Y is dry matter of a component and X_i the independent variables, p_0 – p_n are model coefficients, and θ represents the multiplicative error term. For each biomass component, equations were developed with different combination of independent variable: (i) DBH, (ii) tree volume index (DBH²H dm³), and (iii) the combination of DBH, H , and CL , where DBH is the diameter at breast height, H the tree height, and CL the crown length. After modelling, we checked whether the residuals were normally distributed.

Model selection was guided by an information criteria approach (Burnham and Anderson 2002). Employing an assumption of multivariate normality, Akaike's information criterion (AIC) is a way of selecting an equation from a set of alternative equations and was used to decide on the best model (Akaike 1974). Root mean square error (RMSE) was also

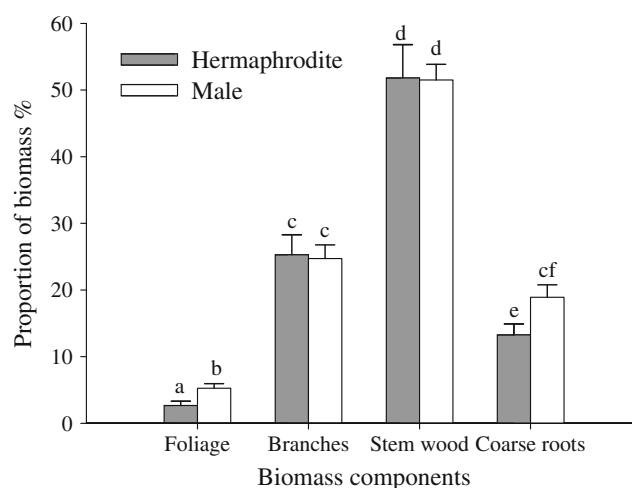


Fig. 2 Comparison of the biomass of selected components between hermaphrodite and male trees. Note 1: Proportion of biomass is defined as the ratio of biomass from corresponding components to total biomass. Note 2: The bars are standard deviations and different letters over the columns indicate significant differences ($p < 0.001$)

Table 2 Regression coefficients ($p_0 - p_3$) for different equations used to estimate component biomass (g) with DBH (cm), DBH^2H (dm^3), H (m), and CL (m) for male *Acer tegmentosum* trees

Dependent variable, Y	Equation	Coefficients				RMSE	AIC
		p_0	p_1	p_2	p_3		
Flower	${}^L Y = p_0 \text{DBH}^{p_1}$	71.3*	1.53***	–	–	658	465
	$Y = p_0 (\text{DBH}^2 H)^{p_1}$	40.7 NS ^a	0.591***	–	–	720	470
	$Y = p_0 \text{DBH}^{p_1} H^{p_2}$	197 NS	1.81***	–0.731 NS	–	629	464
	$Y = p_0 \text{DBH}^{p_1} \text{CL}^{p_2}$	98.4*	1.72***	–0.409 NS	–	631	464
	$Y = p_0 \text{DBH}^{p_1} H^{p_2} \text{CL}^{p_3}$	157 NS	1.79***	–0.470 NS	–0.174 NS		466
Foliage	$Y = p_0 \text{DBH}^{p_1}$	18.6*	1.87***	–	–	318	422
	${}^L Y = p_0 (\text{DBH}^2 H)^{p_1}$	4.34*	0.829***	–	–	271	413
	$Y = p_0 \text{DBH}^{p_1} H^{p_2}$	2.68 NS	1.56***	1.15**	–	267	414
	$Y = p_0 \text{DBH}^{p_1} \text{CL}^{p_2}$	14.7*	1.90***	0.128 NS	–	288	405
	$Y = p_0 \text{DBH}^{p_1} H^{p_2} \text{CL}^{p_3}$	1.46 NS	1.56***	1.33***	0.147 NS	210	389
Branch	${}^L Y = p_0 \text{DBH}^{p_1}$	28.8**	2.40***	–	–	1204	500
	$Y = p_0 (\text{DBH}^2 H)^{p_1}$	4.21 NS	1.07***	–	–	1405	509
	$Y = p_0 \text{DBH}^{p_1} H^{p_2}$	20.2 NS	2.37***	0.180 NS	–	1194	501
	$Y = p_0 \text{DBH}^{p_1} \text{CL}^{p_2}$	23.0*	2.38***	0.144 NS	–	1189	501
	$Y = p_0 \text{DBH}^{p_1} H^{p_2} \text{CL}^{p_3}$	20.6 NS	2.39***	0.192 NS	–0.0710 NS	1191	503
Stem wood	$Y = p_0 \text{DBH}^{p_1}$	221**	1.82***	–	–	2974	552
	$Y = p_0 (\text{DBH}^2 H)^{p_1}$	47.8**	0.830***	–	–	1922	527
	$Y = p_0 \text{DBH}^{p_1} H^{p_2}$	10.2**	1.32***	1.82***	–	1244	504
	$Y = p_0 \text{DBH}^{p_1} \text{CL}^{p_2}$	80.0*	1.66***	0.726***	–	2259	538
	${}^L Y = p_0 \text{DBH}^{p_1} H^{p_2} \text{CL}^{p_3}$	10.3**	1.22**	1.79***	0.238***	1006	493
Aboveground	$Y = p_0 \text{DBH}^{p_1}$	239**	1.99***	–	–	3550	562
	${}^L Y = p_0 (\text{DBH}^2 H)^{p_1}$	47.51***	0.890***	–	–	1917	529
	$Y = p_0 \text{DBH}^{p_1} H^{p_2}$	28.9**	1.69***	1.20***	–	2065	531
	$Y = p_0 \text{DBH}^{p_1} \text{CL}^{p_2}$	112**	1.88***	0.531***	–	2715	549
	$Y = p_0 \text{DBH}^{p_1} H^{p_2} \text{CL}^{p_3}$	28.5**	1.64***	1.19***	0.140 NS	1798	527
Belowground	$Y = p_0 \text{DBH}^{p_1}$	56.5*	1.94***	–	–	1123	496
	${}^L Y = p_0 (\text{DBH}^2 H)^{p_1}$	10.7*	0.881***	–	–	909	483
	$Y = p_0 \text{DBH}^{p_1} H^{p_2}$	4.37 NS	1.61***	1.43***	–	868	483
	$Y = p_0 \text{DBH}^{p_1} \text{CL}^{p_2}$	20.6 NS	1.82***	0.666**	–	963	489
	$Y = p_0 \text{DBH}^{p_1} H^{p_2} \text{CL}^{p_3}$	4.39 NS	1.58***	1.42***	0.0610 NS	865	485
Total biomass	$Y = p_0 \text{DBH}^{p_1}$	294**	1.98***	–	–	4326	574
	$Y = p_0 (\text{DBH}^2 H)^{p_1}$	57.7***	0.890***	–	–	2458	541
	${}^L Y = p_0 \text{DBH}^{p_1} H^{p_2}$	32.8**	1.68***	1.24***	–	2226	537

Table 2 (continued)

Dependent variable, <i>Y</i>	Equation	Coefficients				RMSE	AIC
		<i>p</i> ₀	<i>p</i> ₁	<i>p</i> ₂	<i>p</i> ₃		
	$Y = p_0 \text{ DBH}^{p_1} \text{ CL}^{p_2}$	132**	1.87***	0.563***	–	3241	559
	$Y = p_0 \text{ DBH}^{p_1} \text{ H}^{p_2} \text{ CL}^{p_3}$	32.5**	1.63***	1.23***	0.131 NS	2099	536

The best model for each biomass component is marked by prefixing the symbol \mathcal{L}

RMSE root mean square error, AIC Akaike’s information criterion

p* < 0.05; *p* < 0.01; ****p* < 0.001

^aNon-significant, *p* > 0.05

used for the selection of the best equation (Fayolle et al. 2013; Vahedi 2016). The formulas are defined as:

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

$$\text{RMSE} = \sqrt{\frac{1}{n} \sum_{i=1}^n (y_i - \hat{y}_i)^2} \tag{2}$$

where *k* is the number of parameters, *n* the number of trees, *y_i* the observed value, and \hat{y}_i the estimated value for a tree *i*, respectively.

If there was no difference in the model form between genders, we demonstrated the occurrence of different allometric patterns by randomly selecting 1000 numbers from the minimum to the maximum independent variables we sampled, and then we calculated the values of biomass for both genders with the selected best equations. A general *t* test was used to check the differences between the populations of the two biomass groups. After all the data were transformed by natural logarithms, we tested the statistical differences between regressions for component biomass with the Chow test (Dantas et al. 2013; Khanam et al. 2015; Jadin et al. 2016).

All analyses were performed with R, version 3.2.3 (R Development Core Team 2014). R package *nls* was used for modelling, and the R library “gap” was used for Chow test analyses.

3 Results

3.1 Vegetative biomass components in both genders as a proportion of total biomass

No significant difference was found in total biomass between male and hermaphrodites (*F* = 3.78, *p* = 0.571). We examined

the component biomasses of both hermaphrodites and males as a proportion of total biomass and found it gender-specific. Compared with males, hermaphrodites have a smaller ratio of foliage biomass to total biomass, while in terms of below-ground biomass, the percentage of coarse roots biomass is higher in males than in hermaphrodites (Fig. 2).

3.2 Gender-related biomass equations

All allometric equations of both genders, based on DBH, are significant (Tables 2 and 3). According to the evaluation of AIC and RMSE, the forms of the best model for stem wood and total biomass equations are different between genders, and the DBH²H independent variable model was found to be the best fit for foliage, branch, and aboveground and belowground biomass for both genders we sampled. In terms of flower and branch biomass, the DBH model proved to be best. Both the Chow test and *t* test showed significant difference between genders for the same equation form, except for branch biomass (Table 4). These results indicated that the biomass models were significantly different between male and hermaphrodite trees, suggesting that biomass equations are gender-related for flower, foliage, branch, and above-ground and belowground components.

3.3 Allometry in vegetative/reproductive components

We analyzed the relationships of vegetative components and independent variable for both sexes (see Fig. 3). The results showed that the biomass of the various parts differs in their allometric relationships. For vegetative components, the values of both parameters (multiplier and power parameter) are higher for males than for hermaphrodites in foliage and coarse root biomass (Fig. 3 and Table 4). In terms of above-ground biomass, males have a lower power parameter (0.890) but higher multiplier (47.5). There were no significant

Table 3 Regression coefficients (p_0 – p_3) for different equations used to estimate component biomass (g) with DBH (cm), DBH^2H (dm^3), H (m), and CL (m) for hermaphrodite *Acer tegmentosum* trees

Dependent variable, Y	Equation	Coefficients				RMSE	AIC
		p_0	p_1	p_2	p_3		
Flower	${}^L Y = p_0 \text{DBH}^{p_1}$	64.2*	2.02***	–	–	2569	580
	$Y = p_0 (\text{DBH}^2 H)^{p_1}$	22.9 NS	0.820***	–	–	2581	581
	$Y = p_0 \text{DBH}^{p_1} H^{p_2}$	41.1 NS	1.87***	0.352 NS	–	2522	582
	$Y = p_0 \text{DBH}^{p_1} \text{CL}^{p_2}$	63.4 NS	2.03***	–0.0101 NS	–	2569	583
Fruit	$Y = p_0 \text{DBH}^{p_1} H^{p_2} \text{CL}^{p_2}$	21.0 NS	1.97***	0.670 NS	–0.211 NS	2464	582
	${}^L Y = p_0 \text{DBH}^{p_1}$	99.1*	2.72***	–	–	35,012	743
	$Y = p_0 (\text{DBH}^2 H)^{p_1}$	17.3 NS	1.16***	–	–	32,226	738
	$Y = p_0 \text{DBH}^{p_1} H^{p_2}$	19.1 NS	2.34***	1.09 NS	–	32,219	740
Foliage	$Y = p_0 \text{DBH}^{p_1} \text{CL}^{p_2}$	95.3 NS	2.75***	–0.0200 NS	–	35,006	745
	$Y = p_0 \text{DBH}^{p_1} H^{p_2} \text{CL}^{p_3}$	1.56 NS	2.90***	2.06**	–0.730**	27,538	732
	$Y = p_0 \text{DBH}^{p_1}$	0.341*	3.24***	–	–	484	477
	${}^L Y = p_0 (\text{DBH}^2 H)^{p_1}$	0.0420*	1.39***	–	–	447	472
Branch	$Y = p_0 \text{DBH}^{p_1} H^{p_2}$	0.0501 NS	2.82***	1.25 NS	–	447	474
	$Y = p_0 \text{DBH}^{p_1} \text{CL}^{p_2}$	1.20 NS	2.04***	1.01*	–	392	466
	$Y = p_0 \text{DBH}^{p_1} H^{p_2} \text{CL}^{p_3}$	0.0511 NS	1.63**	1.54 NS	1.24 NS	376	466
	${}^L Y = p_0 \text{DBH}^{p_1}$	17.5*	2.58***	–	–	3620	602
Stem wood	$Y = p_0 (\text{DBH}^2 H)^{p_1}$	4.18 NS	1.07***	–	–	3596	602
	$Y = p_0 \text{DBH}^{p_1} H^{p_2}$	8.53 NS	2.38***	0.521 NS	–	3507	602
	$Y = p_0 \text{DBH}^{p_1} \text{CL}^{p_2}$	33.1 NS	2.01***	0.470*	–	3264	598
	$Y = p_0 \text{DBH}^{p_1} H^{p_2} \text{CL}^{p_3}$	39.4 NS	2.02***	–0.0901 NS	0.494 NS	3262	600
Aboveground	$Y = p_0 \text{DBH}^{p_1}$	184*	1.97***	–	–	5061	623
	$Y = p_0 (\text{DBH}^2 H)^{p_1}$	56.8*	0.831***	–	–	3232	595
	${}^L Y = p_0 \text{DBH}^{p_1} H^{p_2}$	30.4*	1.44***	1.31***	–	2960	592
	$Y = p_0 \text{DBH}^{p_1} \text{CL}^{p_2}$	261*	1.65***	0.270*	–	4467	617
Belowground	$Y = p_0 \text{DBH}^{p_1} H^{p_2} \text{CL}^{p_3}$	24.7 NS	1.49***	1.41***	–0.0931 NS	2917	593
	$Y = p_0 \text{DBH}^{p_1}$	153 NS	2.20***	–	–	8028	651
	${}^L Y = p_0 (\text{DBH}^2 H)^{p_1}$	42.2 NS	0.920***	–	–	6181	635
	$Y = p_0 \text{DBH}^{p_1} H^{p_2}$	35.8*	1.79***	1.04*	–	6181.19	637
Belowground	$Y = p_0 \text{DBH}^{p_1} \text{CL}^{p_2}$	233*	1.82***	0.310*	–	6965.57	645
	$Y = p_0 \text{DBH}^{p_1} H^{p_2} \text{CL}^{p_3}$	46.0 NS	1.73***	0.932**	0.101 NS	6100.71	638
	$Y = p_0 \text{DBH}^{p_1}$	26.8*	2.06***	–	–	1212.42	534
	${}^L Y = p_0 (\text{DBH}^2 H)^{p_1}$	11.1*	0.821***	–	–	1132.56	530
Belowground	$Y = p_0 \text{DBH}^{p_1} H^{p_2}$	13.3 NS	1.76***	0.611 NS	–	1124.51	532
	$Y = p_0 \text{DBH}^{p_1} \text{CL}^{p_2}$	35.1 NS	1.82***	0.191 NS	–	1171.21	534
Belowground	$Y = p_0 \text{DBH}^{p_1} H^{p_2} \text{CL}^{p_3}$	11.7 NS	1.78***	0.670 NS	–0.0422 NS	1123.54	533

Table 3 (continued)

Dependent variable, <i>Y</i>	Equation	Coefficients				RMSE	AIC
		<i>p</i> ₀	<i>p</i> ₁	<i>p</i> ₂	<i>p</i> ₃		
Total biomass	$Y = p_0 \text{ DBH}^{p_1}$	178*	2.19***	–	–	8615.40	656
	$^L Y = p_0 (\text{DBH}^2 H)^{p_1}$	50.8*	0.911***	–	–	6583.51	639
	$Y = p_0 \text{ DBH}^{p_1} H^{p_2}$	46.7 NS	1.79***	0.980***	–	6575.89	641
	$Y = p_0 \text{ DBH}^{p_1} \text{ CL}^{p_2}$	265*	1.83***	0.301*	–	7466.90	649
	$Y = p_0 \text{ DBH}^{p_1} H^{p_2} \text{ CL}^{p_3}$	57.9 NS	1.74***	0.883**	0.0801 NS	6526.81	643

The best model for each biomass component is marked by prefixing the symbol L

RMSE root mean square error, AIC Akaike’s information criterion

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

^aNon-significant, $p > 0.05$

differences in branch biomass. Due to their higher investment in foliage and coarse root biomass, male trees allocate more resources to vegetative biomass.

We defined reproductive biomass as the flower biomass for males and the sum of flower and fruit biomass for hermaphrodites. We found no significant differences in the number of flowers in both sexes. For total reproductive biomass, hermaphrodites invested more in reproduction than males in all the DBH classes observed (Fig. 4).

4 Discussion

4.1 Gender-dependent biomass allocation pattern

Many studies reported sexual dimorphism, which is a phenomenon frequently associated with the differences in gender allocation patterns, especially in dioecious species (Sakai 1990; Allen and Antos 1993; Nanami et al. 2005; Zhang

et al. 2014). Obeso (1998) reported that females allocate more resources to reproduction than males and exhibit a slower growth rate (Obeso et al. 1998). Shea et al. (1993) studied water tupelo trees (*Nyssa aquatic* Linnaeus.) and found that males were significantly larger in height and basal area than females, suggesting that males allocate more resources to vegetative growth than females. Similarly, Zhang et al. (2014) reported higher rates of stem grow in males for the diecious species *F. mandshurica* Rupr..

Reproductive costs of females are usually higher than those of males, which may contribute to differences in resource allocation. Females usually put more resources to defense and reproduction, while males allocate more resources towards vegetative growth (Verónica and Rodolfo 2010; Petzold et al. 2013). Life history theory of plants depends heavily upon how they allocate their limited resources to vegetative growth, reproduction, defense, and other capabilities (Roff 1993; Bazzaz et al. 2000). Therefore, there might be a tradeoff between reproductive and vegetative resource

Table 4 Summary of the allometric patterns of component biomass in males and hermaphrodites using the Chow test and *t* test

Component	Equation form	Chow test		<i>t</i> test	
		<i>F</i> value	<i>p</i> value	<i>t</i> value	<i>p</i> value
Flower	$Y = p_0 \text{ DBH}^{p_1}$	23.8	$p < 0.001$ ***	27.3	$p < 0.001$ ***
Foliage	$Y = p_0 (\text{DBH}^2 H)^{p_1}$	11.8	$p < 0.001$ ***	10.5	$p < 0.001$ ***
Branch	$Y = p_0 \text{ DBH}^{p_1}$	1.20	$p > 0.05$	0.761	$p > 0.05$
Aboveground	$Y = p_0 (\text{DBH}^2 H)^{p_1}$	112	$p < 0.001$ ***	–4.92	$p < 0.001$ ***
Belowground	$Y = p_0 (\text{DBH}^2 H)^{p_1}$	84.1	$p < 0.001$ ***	–52.0	$p < 0.001$ ***

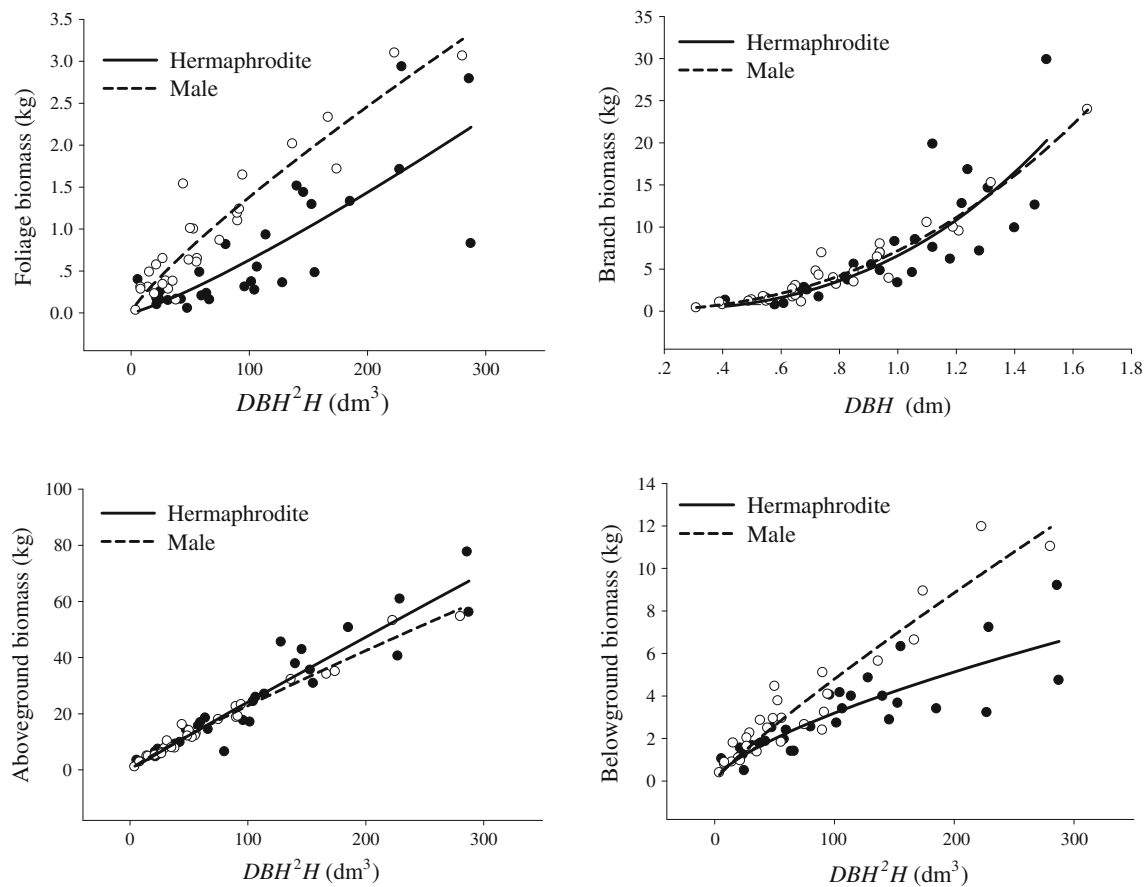


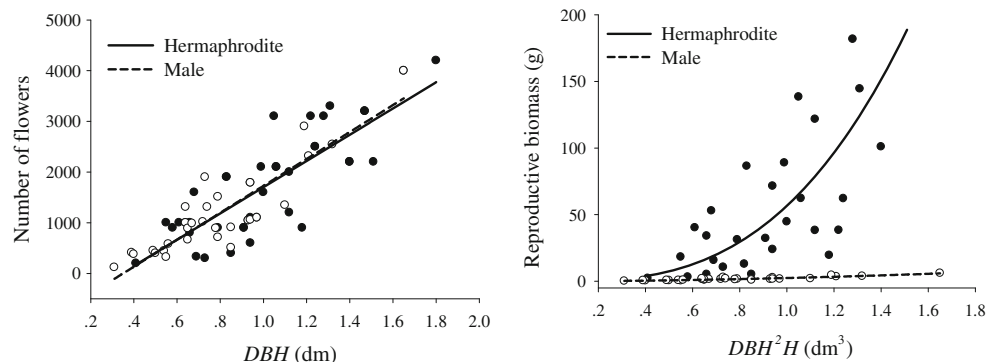
Fig. 3 Vegetative components as a function of DBH or DBH^2H for both male and hermaphrodite trees. For each regression of the components, the bivariate lines were fitted on the basis of the best model selected in Tables 2 and 3

allocation, where vegetative growth is affected by reproductive costs (Popp and Reinartz 1988; Rocheleau and Houle 2001). We assume that plants, which consume energy for both blooming and fruiting (female plants for dioecy, hermaphrodite for androdioecy), bear a higher cost of reproduction and hence ought to have a lower vegetative growth rate than males.

A number of comparisons have been made to examine the reproductive costs in sexual dimorphic species (Allen and Antos 1993; Cornelissen and Stiling 2005). However, less attention has been paid to the differences in biomass structure.

If indeed resource allocation differs between sexes, then this difference might have some consequences, of which total biomass allocation pattern might be one (Zhang et al. 2012). Our results are consistent with those of previous studies. We found that the proportion of vegetative component biomass varies between genders, with males having a larger proportion of foliage and belowground biomass, implying that hermaphrodites have a different biomass allocation strategy than males (Fig. 2). It turns out that males allocate more resources to vegetative foliage and coarse roots.

Fig. 4 Reproductive components as a function of DBH or DBH^2H for both male and hermaphrodite trees. The reproductive biomass was defined as the biomass of flowers for males while the sum of flower and fruit biomass for hermaphrodites. The bivariate lines were fitted for each regression



4.2 Different biomass equations between genders

Biomass equations are an effective way for predicting biomass. The biomass of individual trees can be estimated from regression equations as a function of height, DBH, or other independent variables (Catchpole and Wheeler 1992; Zianis and Mencuccini 2003; Zheng et al. 2015). Ter-Mikaelian and Korzukhin (1997) presented 803 biomass equations for 65 species in North America. Bond-Lamberty et al. (2002) reported that biomass allocation differs among components and established not only aboveground but also belowground biomass equations for six species in their temperate region. Biomass equations with DBH as an independent variable worked very well for the various components of *A. tegmentosum* and are consistent with previous studies for various other tree species (Ter-Mikaelian and Korzukhin 1997).

For androdioecious species, investigations into gender-independent biomass equations are rare. We opted for five types of equations to establish relations between biomass, vegetative and reproductive components, as well as tree attributes. Our results revealed different model forms for stem wood and total biomass (Tables 2 and 3) and different models for the same component biomass equation (except for branch biomass) between males and hermaphrodites (Table 4), suggesting that gender is a significant factor in biomass models. This result emphasized that, when establishing biomass equations for androdioecious species, sex roles are crucial in developing models.

4.3 Gender-related allometric relationships

As discussed earlier, males usually show a higher vegetative growth for vegetative components than hermaphrodites. Obeso (1998) found that males had a faster relative growth rate than females, which tended to have a lower relative growth rate in their fruit-bearing branches than males. Females have to allocate extra resources to successfully pollinated flowers. Similarly, Cornelissen and Stiling (2005) reported that male plants have better growth rates of vegetative organs. Our results show larger foliage and coarse root biomass in males than in hermaphrodites (Fig. 3 and Table 4), which agree with the findings of Popp and Reinartz (1988), Antos and Allen (1999), Rocheleau and Houle (2001), and Petzold et al. (2013).

For reproductive components, there were no significant differences in the number of flowers between genders, as shown in Fig. 4. However, the total reproductive investment in biomass was higher for hermaphrodites than for males, as a result of fruit production. Hermaphrodite *A. tegmentosum* plants have higher reproductive costs and lower vegetative biomass. Not surprisingly, this result accords with the

predictions that there are clear tradeoffs between vegetative and reproductive matters.

Harris and Pannell (2010) reported that females of highly serotinous species were less branched than males in dioecious *Leucadendron*. Another study showed more branches and smaller leaves in males than in females (Midgley 2010). As the results in Figs. 3 and 4 demonstrate, hermaphrodites of *A. tegmentosum* have a lower value of foliage and coarse root biomass than males. In contrast, Zhang et al. (2012) reported that female plants have larger leaf, branch, and stem wood biomass than males, owing to their green flowers and fruits. In several studies, it has been demonstrated that green flowers and fruits are capable of photosynthesis and can supply a significant amount of their own carbon requirements (Bazzaz et al. 1979; Williams et al. 1985; Galen et al. 1993). For *A. tegmentosum* in this study, the reproductive components of hermaphrodite trees are also green, but they do not seem to contribute much to growth. García (1995) reported that the total amount of chlorophyll in fruits accounts for almost half the biomass of the aerial part of fruiting female plants, suggesting that photosynthetic activity of green fruits is far less than that of leaves. This phenomenon is likely to vary among species and depend on their reproductive features. Our results suggest that the sexual differences in allometric relationships might be related to differences in reproductive costs between hermaphrodites and males.

Compliance with ethical standards

Funding This research is supported by the Fundamental Research Funds for the Central Universities (Nos. BLYJ201608), the State Key Program of National Natural Science Foundation of China (41330530) and the National Basic Research Program of China (973 Program; 2011CB403203).

References

- Akaike H (1974) A new look at the statistical model identification. *IEEE T Automat Contr* 19:716–723. doi:10.1109/TAC.1974.1100705
- Allen GA, Antos JA (1993) Sex ratio variation in the dioecious shrub *Oemleria cerasiformis*. *Am Nat* 141:537–553. doi:10.1086/285490
- Anderson GJ, Symon DE (1989) Functional dioecy and andromonoecy in *Solanum*. *Evolution* 43:204–219. doi:10.2307/2409175
- Antos JA, Allen GA (1999) Patterns of reproductive effort in male and female shrubs of *Oemleria cerasiformis*: a 6-year study. *Ecology* 87: 77–84. doi:10.1046/j.1365-2745.1999.00331.x
- Bazzaz FA, Carlson RW, Harper JL (1979) Contribution to reproductive effort by photosynthesis of flowers and fruits. *Nature* 279:554–555. doi:10.1038/279554a0
- Bazzaz FA, Ackerly DD, Reekie EG (2000) Reproductive allocation in plants. In: Fenner M (ed) *Seeds: the ecology of regeneration in plant communities*. CABI Publishing, New York, pp 1–29
- Bond LB, Wang C, Gower ST (2002) Aboveground and belowground biomass and sapwood area allometric equations for six boreal tree

- species of northern Manitoba. *Can J Forest Res* 32:1141–1450. doi:10.1139/x02-063
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer, New York
- Catchpole WR, Wheeler CJ (1992) Estimating plant biomass: a review of techniques. *Aus J Ecol* 17:121–131. doi:10.1111/j.1442-9993.1992.tb00790.x
- R Development Core Team (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org/>.
- Cornelissen T, Stiling P (2005) Sex-biased herbivory: a meta-analysis of the effects of gender on plant-herbivore interactions. *Oikos* 111:488–500. doi:10.1111/j.1600-0706.2005.14075.x
- Dantas V de L, Batalha MA, Pausas JG (2013) Fire drives functional thresholds on the savanna-forest transition. *Ecology* 94:2454–2463. doi:10.1890/12-1629.1
- Fabiola RG, Bernardus HJ, De J, Pablo MZ, Fernando PP (2015) Database of 478 allometric equations to estimate biomass for Mexican trees and forests. *Ann Forest Sci* 72:835–864. doi:10.1007/s13595-015-0456-y
- Fayolle A, Doucet JL, Gillet JF, Bourland N, Lejeune P (2013) Tree allometry in Central Africa: testing the validity of pantropical multi-species allometric equations for estimating biomass and carbon stocks. *Forest Ecol Manag* 305:29–37. doi:10.1016/j.foreco.2013.05.036
- Galen C, Dawson TE, Stanton M (1993) Carpels as leaves: meeting the carbon cost of reproduction in an alpine buttercup. *Oecologia* 95:187–193. doi:10.1007/BF00323489
- García MB, Antor RJ (1995) Sex ratio and sexual dimorphism in the dioecious *Borderea pyrenaica* (Dioscoreaceae). *Oecologia* 101:59–67. doi:10.1007/BF00328901
- Harris MS, Pannell JR (2010) Canopy seed storage is associated with sexual dimorphism in the woody dioecious genus *Leucadendron*. *J Ecol* 98:509–515. doi:10.1111/j.1365-2745.2009.01623.x
- Jadin I, Meyfroidt P, Lambin EF (2016) International trade, and land use intensification and spatial reorganization explain Costa Rica's forest transition. *Environ Res Lett* 11:035005. doi:10.1007/s11027-015-9681-9
- Khanam T, Rahman A, Mola-Yudego B, Pykäläinen J (2015) Identification of structural breaks in the forest product markets: how sensitive are to changes in the Nordic region? *Mitig Adapt Strat Gl* 1–15. doi:10.1007/s11027-015-9681-9
- Lloyd DG (1979) Some reproductive factors affecting the selection of self-fertilization in plants. *Am Nat* 113:67–79. doi:10.1086/283365
- Meagher TR, Antonovics J (1982) The population biology of *Chamaelirium luteum*, a dioecious member of the lily family: life history studies. *Ecology* 63:1690–1700. doi:10.2307/1940111
- Mesele N, Mike S, Markku K (2013) Allometric equations for biomass estimation of Enset (*Ensete ventricosum*) grown in indigenous agroforestry systems in the Rift Valley escarpment of southern-eastern Ethiopia. *Agrofor Syst* 87:571–581. doi:10.1007/s10457-012-9577-6
- Michiko N, Tomohiro I, Michiko I, Kosei A, Tomoya O, Watanabe Y, Koji K, Chikage T, Keisuke I, Naomichi K, Kanae O, Megumi H, Saori T, Keigo H, Iku A, Kazuma K, Ayaka Y, Daisuke K, Michinari M (2015) Inter-specific and sexual differences in architectural traits of two dioecious *Lindera* species (Lauraceae). *Plant Ecol* 216:99–109. doi:10.1007/s11258-014-0419-7
- Midgley JJ (2010) Causes of secondary sexual differences in plants—evidence from extreme leaf dimorphism in *Leucadendron* (Proteaceae). *S Afr J Bot* 76:588–592. doi:10.1016/j.sajb.2010.05.001
- Nanami S, Kawaguchi H, Yamakura T (2005) Sex ratio and gender dependent neighboring effects in *Podocarpus nagi*, a dioecious tree. *Plant Ecol* 177:209–222. doi:10.1007/s11258-005-2210-2
- Nazanin S, Taraneh S (2013) A mixed integer non-linear programming model for tactical value chain optimization of a wood biomass power plant. *Appl Energy* 104:353–361. doi:10.1016/j.apenergy.2012.11.013
- Nicotra AB (1999) Sexually dimorphic growth in the dioecious tropical shrub *Siparuna grandiflora*. *Funct Ecol* 13:322–331. doi:10.1046/j.1365-2435.1999.00326.x
- Obeso JR (2002) The costs of reproduction in plants. *New Phytol* 155:321–348. doi:10.1046/j.1469-8137.2002.00477.x
- Obeso JR, Alvarez SM, Retuerto R (1998) Sex ratios, size distributions, and sexual dimorphism in the dioecious tree *Ilex aquifolium* (Aquifoliaceae). *Am J Bot* 85:1602–1608. doi:10.2307/2446488
- Petzold A, Pfeiffer T, Jansen F, Eusemann P, Schnittler M (2013) Sex ratios and clonal growth in dioecious *Populus euphratica* Oliv., Xinjiang Prov., Western China. *Trees* 27:729–744. doi:10.1007/s00468-012-0828-y
- Popp JW, Reinartz JA (1988) Sexual dimorphism in biomass allocation and clonal growth of *Xanthoxylum americanum*. *Am J Bot* 75:1732–1741. doi:10.2307/2444688
- Rocheleau AF, Houle G (2001) Different cost of reproduction for the males and females of the rare dioecious shrub *Corema conradii* (Empetraceae). *Am J Bot* 88:659–666. doi:10.2307/2657066
- Roff D (1993) Evolution of life histories: theory and analysis. Chapman and Hall, New York
- Rosta M, Tord J, Almeida S (2014) Biomass equations for tropical forest tree species in Mozambique. *Forests* 5:535–556. doi:10.3390/f5030535
- Sakai AK (1990) Sex ratios of red maple (*Acer rubrum*) populations in Northern Lower Michigan. *Ecology* 71:571–580. doi:10.2307/1940310
- Shea MM, Dixon EM, Sharitz RR (1993) Size differences, sex ratio, and spatial distribution of male and female water tupelo, *Nyssa aquatica* (Nyssaceae). *Am J Bot* 80:26–30. doi:10.2307/2445116
- Swensen SM, Luthi JN, Rieseberg LH (1998) Datisaceae revisited: monophyly and the sequence of breeding system evolution. *Syst Bot* 23:157–169. doi:10.2307/2419585
- Ter-Mikaelian MT, Korzukhin MD (1997) Biomass equations for sixty-five North American tree species. *Forest Ecol Manag* 97:1–24. doi:10.1016/S0378-1127(97)00019-4
- Torimaru T, Tomaru N (2012) Reproductive investment at stem and genet levels in male and female plants of the clonal dioecious shrub *Ilex leucoclada* (Aquifoliaceae). *Botany* 90:301–310. doi:10.1139/b2012-004
- Vahedi AA (2016) Artificial neural network application in comparison with modeling allometric equations for predicting above-ground biomass in the Hyrcanian mixed-beech forests of Iran. *Biomass Bioenergy* 88:66–76. doi:10.1016/j.biombioe.2016.03.020
- Vassiliadis C, Valero M, Saumitou LP (2000) A model for the evolution of high frequencies of males in an androdioecious plant based on a cross-compatibility advantage of males. *Heredity* 85:413–422. doi:10.1046/j.1365-2540.2000.00755.x
- Verónica CC, Rodolfo D (2010) Sex-related differences in reproductive allocation, growth, defense and herbivory in three dioecious *Neotropical Palms*. *Plos one* 5:1–9. doi:10.1371/journal.pone.0009824
- Williams K, Koch GW, Mooney HA (1985) The carbon balance of flowers of *Diplacus aurantiacus* (Scrophulariaceae). *Oecologia* 66:530–535. doi:10.1007/BF00379345
- Xiao CW, Ceulemans R (2004) Allometric relationships for below- and aboveground biomass of young Scots pines. *Forest Ecol Manag* 203:177–186. doi:10.1016/j.foreco.2004.07.062
- Yampolsky C, Yampolsky H (1922) Distribution of sex forms in the phanerogamic flora. *Bibliotheca genetica*, Leipzig

- Zhang CY, Wang J, Zhao X-H, Xia F-C, Gadow KV (2012) Sexual dimorphism in reproductive and vegetative allometry for two dioecious *Rhamnus* plants in north-eastern China. *Eur J For Res* 131: 1287–1296. doi:[10.1007/s10342-012-0598-5](https://doi.org/10.1007/s10342-012-0598-5)
- Zhang XN, Zhang C-Y, Zhao X-H (2014) Effect of sex ratio, habitat factors and neighborhood competition on stem growth in the dioecious tree *Fraxinus mandshurica*. *Ecol Res* 29:309–317. doi:[10.1007/s11284-013-1125-y](https://doi.org/10.1007/s11284-013-1125-y)
- Zheng CH, Mason EG, Jia LM, Wei SP, Sun CW, Duan J (2015) A single-tree additive biomass model of *Quercus variabilis* Blume forests in North China. *Trees* 29:705–716. doi:[10.1007/s00468-014-1148-1](https://doi.org/10.1007/s00468-014-1148-1)
- Zianis D, Mencuccini M (2003) Aboveground biomass relationships for beech (*Fagus moesiaca* Cz) trees in Vermios Mountain, Northern Greece, and generalised equations for *Fagus* sp. *Ann Forest Sci* 60: 439–448. doi:[10.1051/forest:2003036](https://doi.org/10.1051/forest:2003036)