

Biomass Structure and Allometry of *Abies nephrolepis* (Maxim) in Northeast China

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Above- and below-ground tree biomass structure and allometric relationships of *Abies nephrolepis* (Maxim) were assessed in an old secondary forest dominated by *A. nephrolepis*, *Pinus koraiensis*, *Quercus mongolica*, *Tilia amurensis*, *Fraxinus mandshurica* and *Acer mono* in northeast China. Based on the breast-height diameter (D), a total of 21 sample trees were divided into three tree size classes: the small trees ($1\text{ cm} \leq D < 10\text{ cm}$), the medium trees ($10\text{ cm} \leq D < 20\text{ cm}$) and the big trees ($D \geq 20\text{ cm}$). The greatest amount of live branch biomass was located in the middle and bottom layers of the crown, while the largest foliage biomass was found in the middle layer in each tree size category. The relative contribution of canopy biomass components (live branches and foliage) decreased with increasing tree size, while that of coarse root biomass remained almost constant. The relationship between above- and belowground biomass was linear. D and tree height (H) decreased with increasing competition intensity. The small trees had lower average crown ratio and higher average height-to-diameter ratio than those of the medium and big trees. The big trees had higher average stem to foliage mass ratio than those of the small and medium trees. Crown ratio, height-to-diameter ratio and stem to foliage mass ratio were not correlated with competition intensity in the same tree size class. Root to shoot mass ratio was almost constant among tree sizes. Allometric equations based on D gave higher correlations compared to those with other stem diameters: at tree base, at 30-cm height and at crown base.

Keywords biomass structure, aboveground competition, allometry, *Abies nephrolepis* (Maxim), tree size

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1 Introduction

Biomass estimation of forest trees has been subject to research for over a century (e.g., Kunze 1873, Burger 1929). More recently, the interest has been mainly due to the capacity of trees to sequester and store carbon (Cienciala et al. 2005). In addition, tree biomass is also an important indicator for assessing forest structure (Westman and Rogers 1977) and evaluating ecological and economic processes such as nutrient cycle, forest productivity and fuel inventories (Chambers et al. 2001, Bond-Lamberty et al. 2002). Tree biomass is usually divided into different components according to physiological functions, most commonly stems, live branches, foliage and roots. Although measuring actual tree biomass directly in the field is undoubtedly the most accurate method, it is labor-intensive, time-consuming, and destructive, and this practice is generally restricted to a small area and limited to small trees (Ketterings et al. 2001). The application of allometry produces a non-destructive and indirect measurement alternative for estimating tree compartments, and is often seen as a reliable approach (St. Clair 1993). As an essential tool for tree biomass estimation, allometry has also been used in the studies of forest production, forest fuel, and mapping and classifying regional forest carbon budgets (Schroeder et al. 1997, Ter-Mikaelian and Korzukhin 1997).

Diameter at breast height (D) has been found to be a simple and reliable predictor of biomass for both above- and below-ground compartments in most previous studies (Karizumi 1974, Santantonio et al. 1977, Ter-Mikaelian and Korzukhin 1997). However, other measured variables in the field have also been found useful for a particular compartment. e. g. the stem diameter at tree base for small trees and shrubs (Smith and Brand 1983, Bond-Lamberty et al. 2002), sapwood area for needle and branch biomass (Shinozaki et al. 1964, Pearson et al. 1984, Comeau and Kimmins 1989, Bormann 1990, Osawa 1990), and the stem diameter at low stem heights for coarse roots (Haynes and Gower 1995, Bond-Lamberty et al. 2002, Guan and Cheng 2003). Thus, it is necessary to apply and assess such alternative predictors for developing a reliable allometric equation for a target species.

Abies nephrolepis (Maxim) with the common name of Eastern Siberian fir or Khingan fir, which is sometimes also referred to as *Abies sibirica* var. *nephrolepis*, is an important coniferous species native to the East Asia. It is mainly distributed in Russia, Korea and China (Li et al. 2005). In China, the species mainly occurs in the temperate mixed coniferous broad-leaved forests in the northeastern region and in the temperate broad-leaved deciduous forests of mountainous areas. It prefers a humid climate and acid soils. The essential oil of *A. nephrolepis* is widely applied in the perfume industry and medicine. Although there are some studies conducted on the oil and medicinal composition of the needles (Yang et al. 1990, Li et al. 2005), allometric relationships for above- and below-ground biomass components of *A. nephrolepis* are still lacking. Up to date, a complete and detailed biomass structure study has also not been reported as yet.

In this paper, a basic allometry at single tree level, relating biomass components to different independent variables that are usually available from field surveys is examined and the biomass structure of *A. nephrolepis* is analyzed based on a set of completely measured trees. First, the vertical distribution of live branch and foliage biomass is quantified, and biomass structure in relation to tree size and the effect of aboveground competition on the biomass structure are analyzed. Secondly, the assumption that allometric equations using D as an independent size variable is reliable for biomass estimation compared to other three easily measured variables is tested. And finally, tree size-independent and tree size-specific relations that can be used to predict different above- and below-ground biomass components are developed and compared.

2 Materials and Methods

2.1 Study Site

The study site is an old secondary forest dominated by *A. nephrolepis*, *Pinus koraiensis*, *Quercus mongolica*, *Tilia amurensis*, *Fraxinus mandshurica* and *Acer mono* in association with other subcanopy tree species located at Guangming

Forestry Center in Changbaishan Nature Reserve Zone in northeast China (42°21'N, 128°08'E, 748 m a.s.l.). It represents the typical forest type and landscape of deciduous broad-leaved and coniferous mixed forest. The climate in this region is classified as continental mountainous and monsoon-affected. Mean annual temperature is 3.6 °C. The highest monthly average temperature of 19.6 °C is observed in August while the lowest monthly average temperature of -15.4 °C in January. Extreme temperatures are 32.3 °C and -37.6 °C. Mean annual precipitation is 707 mm with a mean relative humidity of 66%. The distribution of precipitation over a year is relatively uneven. Wet season occurs from June to August. The soil is a brown forest soil and topography is flat to slightly undulating.

2.2 Sampling and Measurements

A permanent research plot covering an area of 200 m × 260 m was established at the site in July 2005 to represent *A. nephrolepis*, *P. koraiensis* and deciduous broad-leaved species dominated forest. The plot was further subdivided into 130 contiguous square subplots with 20 m × 20 m each. In each subplot, the species of all live and dead trees with woody stems exceeding 1 cm of their breast-height diameters were identified. The breast-height diameter, tree height and crown

dimensions of each tree were measured and recorded. Dominant tree species in the plot and their characteristics are shown in Table 1.

Twenty-one trees with *D*s between 3.4 and 35.6 cm were selected in close vicinity of the research plot for a destructive analysis of above- and below-ground biomass structure. The trees were chosen to represent the widest range of heights and competition situations existing in the plot. To achieve this, all recorded *A. nephrolepis* trees were divided into 5 classes with their heights and then 3 to 4 trees belonging to each class were destructively sampled. Trees with severe defects were not included. Each *A. nephrolepis* subject tree was located at the centre of an independent circular plot with a 10-m radius. The *D*s of all trees within this competition zone and their distances to the subject tree were both assessed. The study lasted about one month between July and August 2008.

Before the trees were cut at ground level, the stem diameters at tree base (D_B), at 30-cm height (D_{30}), and at breast height (D) were measured. After fallen, the diameter at the base of the live crown (D_C), live crown length (CL), crown widths from south to north (CW_1) and from east to west (CW_2) of the subject trees were immediately measured and recorded. Subsequently, their branches of the trees were stripped off.

Dead branches were separated from live ones and the live crown was divided into three sections

Table 1. Species composition, density, basal area, mean breast-height diameter (D) and maximum diameter of live trees which D is greater than 1 cm within the permanent research plot in the Changbaishan Nature Reserve Zone in northeast China.

Tree species	Density (no. ha ⁻¹)	Percentage of total density (%)	Basal area (m ² ha ⁻¹)	Percentage of total basal area (%)	Mean D (cm)	Maximum D (cm)
<i>Abies nephrolepis</i>	560	14.75	2.90	8.40	6.93	45.7
<i>Pinus koraiensis</i>	152	4.00	2.32	6.72	9.32	78.0
<i>Picea jezoensis</i>	41	1.08	0.90	2.61	12.28	65.8
<i>Acer mono</i>	443	11.67	2.16	6.26	5.19	66.1
<i>Fraxinus mandshurica</i>	55	1.45	2.20	6.37	19.23	88.5
<i>Ulmus</i> var. <i>japonica</i>	43	1.13	0.40	1.16	8.31	53.4
<i>Tilia amurensis</i>	237	6.24	6.42	18.60	14.58	71.5
<i>Populus daviana</i>	85	2.24	0.80	2.32	40.22	80.7
<i>Betula platyphylla</i>	138	3.63	5.56	16.11	23.27	51.9
<i>Quercus mongolica</i>	50	1.32	2.46	7.13	19.67	82.5
Others	1993	52.49	8.40	24.33	4.20	105.0
Totals	3797	100.00	34.52	100.00	-	-

with equal length (the top, middle and bottom section). The fresh branch mass of each section was determined in the field using a hanging balance. From each section, two branches were randomly selected to be sub-samples in order to determine fresh to oven-dried mass ratios, as well as the contribution of biomass from large branches (diameter >2 cm), small branches (<2 cm) and shoots (twigs with foliage) to the biomass of each crown section. The fresh mass of the branch sub-samples was measured with an electronic balance. The sub-samples were oven-dried to a constant weight (the weight differences between consecutive weight measurement are not significant and the same criteria are applied to other samples below) at 65 °C. For about a half of them (randomly chosen one branch from the two sub-samples of each crown section), shoots from those chosen sub-samples were further sub-sampled by removing all foliage from twigs in order to determine foliage to twig mass ratio. Fresh to oven-dried mass ratios of large branches, small branches, twigs and foliage were applied to correct the total crown fresh mass and to determine the contribution of each crown component to the total biomass.

After all of the branches were removed, a total tree length measured from the ground to the base of the terminal bud (*H*) was recorded. And the crown ratio (*CR*) was defined as *CL/H* for further analysis. According to the *D* differentiations, all sample trees were divided into three tree sizes: small trees (1 cm ≤ *D* < 10 cm), medium trees (10 cm ≤ *D* < 20 cm) and big trees (*D* ≥ 20 cm). The primary parameters of each category are shown in Table 2.

Each stem of the sample trees was then divided into ten sections with equal length. The fresh mass of each stem section was determined in the field using a hanging balance. From each section, a stem disc of 2 cm width was selected as a sub-sample to determine the fresh to oven-dried mass ratio for each stem section. The bark of each stem disc was separated from the wood. The fresh mass of the bark and the wood parts was assessed and then they were put into an oven to dry to a constant weight at 65 °C to calculate the fresh to oven-dried mass ratio. The dry mass of each stem was calculated with the ratio. A bark to wood biomass ratio was calculated.

Table 2. Ranges of primary parameters for the sample trees in different tree sizes.

Tree size	N ^{a)}	A ^{b)} (yrs)	D ^{c)} (cm)	D _c ^{d)} (cm)	D ₃₀ ^{e)} (cm)	D _B ^{f)} (cm)	H ^{g)} (m)	CL ^{h)} (m)	H/D (m m ⁻¹)	CR ⁱ⁾ (m m ⁻¹)	CI ^{j)}	CW ₁ ^{k)} (m)	CW ₂ ^{l)} (m)
Small trees	9	18–31	3.4–9.9	3.2–9.1	4.0–11.0	4.6–12.3	2.7–10.3	1.6–7.5	0.74–1.05	0.46–0.74	5.42–22.7	2.3–3.7	2.3–3.0
Medium trees	6	43–65	11.1–19.9	9.6–17.5	11.8–21.4	13.3–24.8	7.9–17.2	6.3–11.6	0.66–0.86	0.67–0.90	1.32–4.8	3.6–5.5	2.6–4.1
Big trees	6	82–125	21.0–35.6	17.3–27.8	22.7–40.5	27.0–46.5	18.9–22.1	12.7–14.0	0.54–0.90	0.63–0.76	0.53–3.1	5.6–7.5	4.3–6.5

a) number of sample trees
 b) tree age
 c) diameter at breast height
 d) diameter at crown base
 e) diameter at 30 cm height
 f) diameter at tree base
 g) tree height
 h) crown length
 i) crown ratio
 j) competition intensity
 k) crown width from south to north
 l) crown width from east to west

An entire root system of each sample tree was carefully excavated using a combination of pulley and manual digging (Bolte et al. 2004). Due to a high senescence rate, harvesting fine roots is unachievable. Only the coarse roots with a diameter ≥ 5 mm were excavated and their biomass was measured. The root systems were cleaned using a hose and fresh mass was weighed in the field using a hanging balance. About 500–1000 g of fresh coarse roots was randomly selected and delivered to the laboratory for measuring moisture content of the coarse roots and then oven-dried to a constant weight at 65 °C and the fresh to oven-dried mass ratio was calculated. The dry matter of the coarse roots in an entire root system was calculated with the ratio. To estimate the age of each sample tree, the rings on the basal disk were counted using a microscope.

2.3 Data Analyses

For each subject tree, competition intensity (CI) from neighbouring trees within a dynamic competition zone was computed using the Iterative Hegyi Index which has been found superior when compared with other sophisticated competition indices, because it uses a dynamic competition zone and differentiates between ‘active’ and ‘passive’ competitors (Lee and Gadaw 1997). Therefore, the index was chosen to analyze the competition status in this paper. The Iterative Hegyi Index was calculated in the following three steps (Lee et al. 2004):

- 1) Determine the dynamic radius of a competition zone for the subject tree, CZR :

$$CZR = k \cdot \sqrt{\frac{10000}{N}} \quad (1)$$

where N is the density (no ha^{-1}) of a circular competition zone with a 10-m radius, k is a constant set to 2.

- 2) Iterative selection of competitors within the dynamic radius:

Competitors should have a big enough relative size so that they can affect the subject tree growth. i.e., $d_j > 0.3d_i$ (where d_j is the D of competitor j , d_i is the D of subject tree i); then the active competitors which are not shaded by other trees are

determined so that they directly face the subject tree. Passive competitors are defined as those that are hidden behind one of the active competitors when viewed from the subject tree.

- 3) Calculate the Iterative Hegyi Index or competition intensity for the subject tree i , CI :

$$CI = \sum_{j=1}^n d_j / (d_i \times dist_{ij}) \quad (2)$$

where n is the number of active competitors within the density-dependent competition zone and $dist_{ij}$ is the distance from subject tree i to competitor j .

In order to test the assumption that D is a reliable predictor of biomass components, D and three alternative variables (D_{30} , D_B , D_C) were selected to be independent variables to establish the relationship between a predictor and biomass components. Allometry was approximated by power-form equation. A natural based log-transformation of the data was adopted to estimate the parameters of biomass allometric equation (i.e., $\ln B = a + b \ln X$; B is dry matter of a component and X is stem diameters at different tree height) using the ordinary least squares method. Although either the natural logarithm or the base 10 logarithm can be applied for the transformation functions, a pre-test was found that the natural logarithm could have better results. Therefore, the natural logarithm as a transformation function is used throughout. The significance of each regression was tested using the adjusted coefficient of determination (R^2_{adj}). Root mean square error (RMSE) and Akaike's Information Criterion (AIC) were also used to evaluate the goodness of fit.

A correction factor (CF) was computed for all equations to correct for the systematic bias due to log-transformation (Sprugel 1983). Statistical analyses were performed with the R version 2.12.0 (R Development Core Team 2010). Significance was evaluated at the $P=0.05$ and 0.01 probability levels.

3 Results

3.1 Biomass Structure

Mean dry matter of each tree component increases with tree size (Table 3). Total tree biomass (expressed as dry matter) increased from 13.4 kg tree⁻¹ for the class of the small trees to 90.9 and 333.3 kg tree⁻¹ for the classes of the medium and big trees, respectively.

As expected, stem wood biomass had the biggest contribution to total above-ground biomass, amounting to 5.4, 36.3 and 149.2 kg tree⁻¹ for the small, medium and big trees, respectively. The canopy biomass, including foliage and live branches, was heavier than the stem bark and the

coarse root biomass for all classes (Table 3).

The vertical biomass distributions of live branches and foliage are shown in Fig. 1. Live branch biomass was mostly allocated in the middle and bottom layers of the crown for each tree size. Based on the results of the Wilcoxon test, there was no significant difference between the live branch biomass in the middle and in the bottom section ($P > 0.05$). However, foliage biomass located in the top and in the bottom layers of the crown was significantly lower than in the middle section ($P < 0.05$). There was no significant difference between the foliage biomass in the top and bottom sections ($P > 0.05$). Generally, most of the live branch and foliage biomass is located in the middle and bottom sections of the crown.

Table 3. Biomass (kg dry matter/tree) structure of *A. nephrolepis* in different tree sizes (mean ± S.D.).

Components	Small trees	Medium trees	Big trees
Foliage	1.8 ± 1.4	12.1 ± 7.8	23.3 ± 10.5
Live branches	2.5 ± 1.9	17.8 ± 14.4	53.8 ± 33.4
Dead branches	0.3 ± 0.3	1.8 ± 1.0	9.8 ± 8.6
Stem wood	5.4 ± 5.0	36.3 ± 24.9	149.2 ± 72.1
Stem bark	1.2 ± 1.0	7.5 ± 4.1	34.9 ± 25.1
Total aboveground	11.1 ± 9.3	75.5 ± 51.8	270.9 ± 142.6
Coarse roots	2.4 ± 2.0	15.4 ± 6.2	62.4 ± 32.4
Total tree	13.4 ± 11.2	90.9 ± 57.7	333.3 ± 174.9

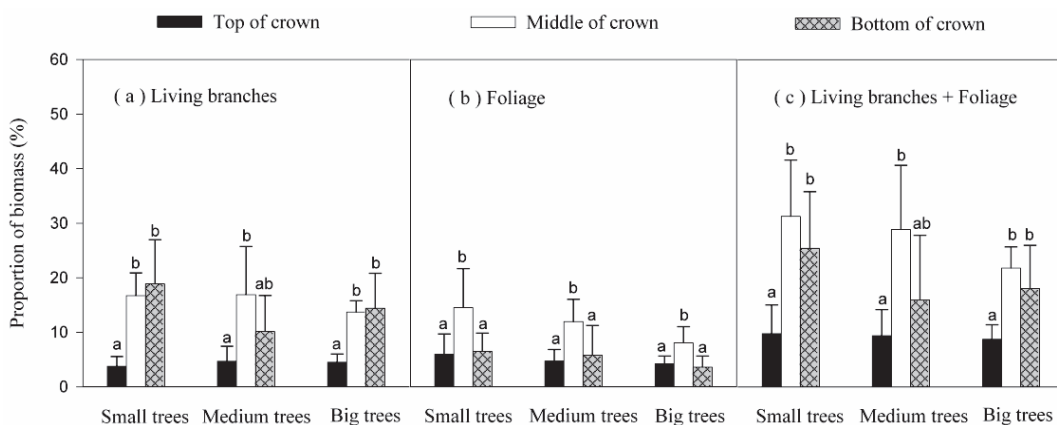


Fig. 1. Vertical biomass distributions of live branches (a), foliage (b) and their summation (c) in different layers of the live crown under different size classes. The distribution defined as a proportion of biomass components from corresponding crown section to the total live crown biomass. The bars are standard deviations and the different letters over the columns indicate significant differences ($P < 0.05$).

Fig. 2. Relative contribution of above- and below-ground biomass components to total biomass in different tree sizes.

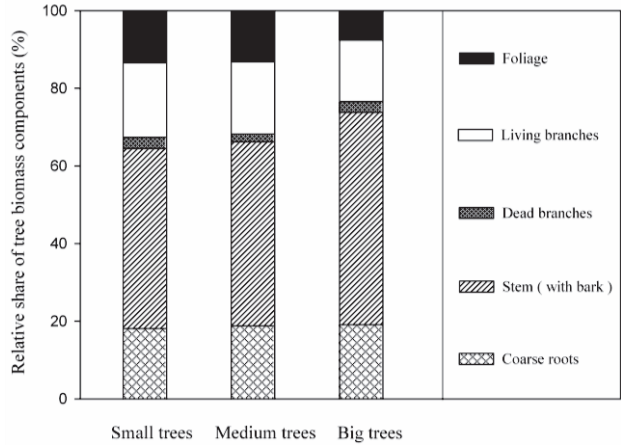
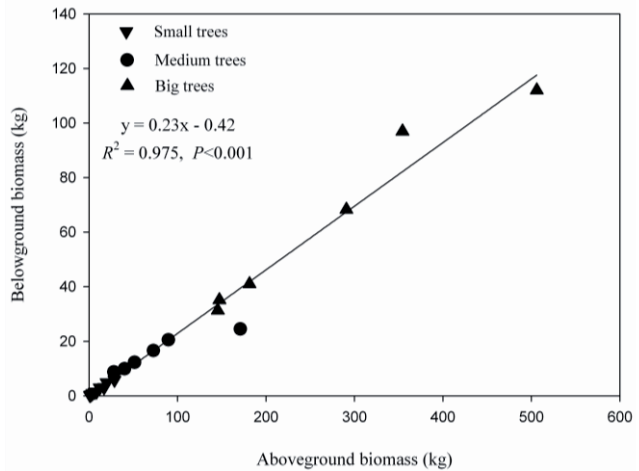


Fig. 3. Relationship between above-ground biomass and belowground biomass.



Coarse root biomass increased with tree size from 2.4 kg tree⁻¹ for the small size to 15.4 and 62.4 kg tree⁻¹ for the medium and big sizes, respectively. The biomass of coarse roots exceeded foliage biomass and approached live branch biomass for the small and medium sizes. It also exceeded the total biomass of foliage and stem bark as well as live branch biomass for the big size (Table 3).

Relative contribution of stem (with bark) biomass to total tree biomass increases from 46.4% for the small class to 47.5% and 55.6% for the medium and big classes. The relative proportion of live branch biomass decreases from 19.2% for the small class to 18.7% and 15.3% for the medium

and big classes. However, the proportion of foliage biomass decreases from 13.4% for the small to 13.1% and 7.4% for the medium and big classes. The proportion of dead branch biomass decreases for the small to medium trees and increases again for the big trees. The contribution of coarse root biomass increases marginally with tree size, but differences of the relative contribution were not significant among tree sizes (Fig. 2).

Individual root to shoot mass ratio of all sample trees ranged from 0.14 to 0.31, with an average value of 0.23. There was a significant ($P < 0.001$) linear relationship with a slope of 0.23 between above-ground and below-ground biomass for all sample trees (Fig. 3).

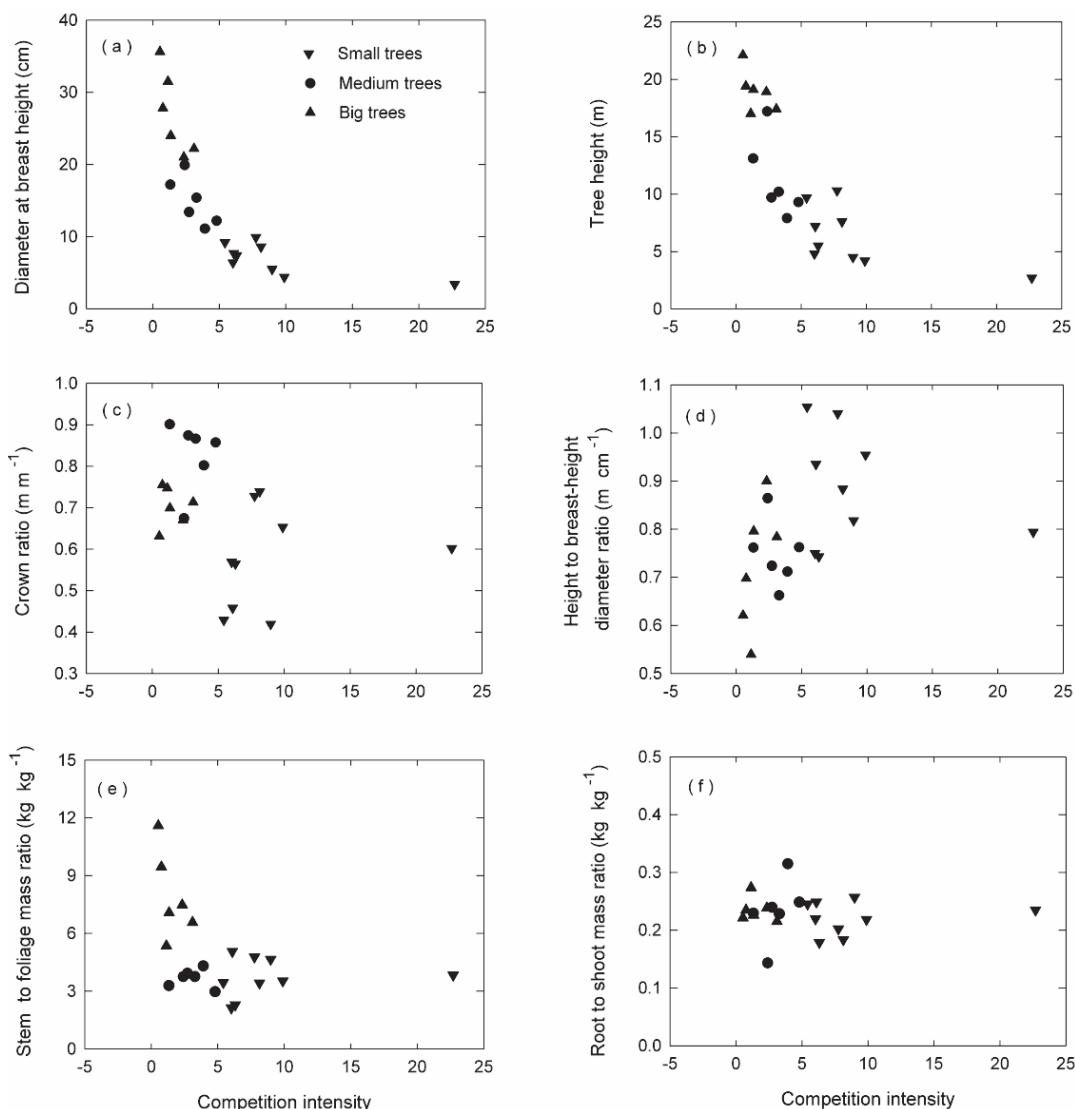


Fig. 4. Relationships of breast-height diameter (a), tree height (b), crown ratio (c), tree height to breast-height diameter ratio (d), stem to foliage mass ratio (e) and root to shoot mass ratio (f) against aboveground competition intensity.

The influence of aboveground competition on the biomass structure was analyzed (Fig. 4). The relations between the tree dimensions and competition intensity were represented by exponential functions and were highly significant ($P < 0.001$) for D and H when considering all sample trees. Obviously, both D and H decreased with CI (Fig. 4a and b). Average values of crown ratio (CR)

and height to breast-height diameter ratio (H/D) differed significantly among tree sizes according to the Wilcoxon test (not shown). The small trees had lower average CR (0.57) than those of the medium trees (0.83) and big trees (0.70), while average H/D (0.89) higher than those of the medium trees (0.75) and big trees (0.72). Both CR and H/D were not correlated with competition

intensity in the same size class ($P > 0.05$) (Fig. 4c and d).

Stem to foliage mass ratio ranged from 2.13 to 11.59. Average values of the ratio differed significantly among tree sizes. The big trees had higher average value (7.92) than those of the small trees (3.68) and medium trees (3.67). The ratio did not correlate with competition intensity in the same tree size ($P > 0.05$) (Fig. 4e). Root to shoot mass ratio remained almost constant with changing tree size. Average values of the ratio for the small trees, the medium trees and the big trees were 0.22, 0.23 and 0.23, respectively. The differences among trees sizes were not significant ($P > 0.05$) by the Wilcoxon test (not shown). Similarly, competition intensity did not affect root/shoot among tree sizes (Fig. 4f).

3.2 Allometric Relationships

All allometric equations, based on different stem diameters (D , D_{30} , D_B , D_C) are significant (Table 4). For coarse root mass, the correlations (R^2_{adj}) with D were somewhat improved when D_{30} was used as an independent variable, especially for the big trees. In addition, the correlations of allometric regressions using D_{30} or D_C were also higher than using D for the dry matter of live branches, foliage and coarse roots in the big trees. However, the majority of the equations based on the variables: D_{30} , D_B and D_C , did not always improve the correlations compared to those only D was used. These findings support the hold assumption that D -based allometry is a simple and reliable model for the estimation of above- and below-ground biomass.

The log-log biomass equations based on D for all sampled trees provide a highly significant fit for all biomass components (Fig. 5). The tree size-independent regressions could explain more than 95% of the variability for biomass components of total tree, total aboveground, coarse roots, stem wood, stem bark and live branches. The foliage biomass equation had the lowest coefficient of determination ($R^2_{adj} = 0.944$).

Regarding the biomass of aboveground components (stem wood, stem bark, live branches and foliage), the linearity of the size-independent equation is less confident as residuals (not shown) tended to be relatively high for the small and big

Table 4. Adjusted coefficient of determination (R^2_{adj}) in equations ($\ln B = a + b \ln X$) for each biomass component (B , kg) with four stem diameters (X , cm) in different tree sizes. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Components	Diameters (cm)	Adjusted coefficient of determination (R^2_{adj})		
		Small trees	Medium trees	Big trees
Stem wood	D	0.974***	0.981***	0.945***
	D_{30}	0.971***	0.962***	0.901**
	D_B	0.944***	0.958***	0.963***
	D_C	0.921***	0.974***	0.883**
Stem bark	D	0.930***	0.947***	0.975***
	D_{30}	0.944***	0.945***	0.926**
	D_B	0.889***	0.940***	0.968***
	D_C	0.858***	0.953***	0.910**
Live branches	D	0.949***	0.922**	0.880**
	D_{30}	0.926***	0.870**	0.905**
	D_B	0.929***	0.880**	0.823**
	D_C	0.948***	0.888**	0.912**
Foliage	D	0.966***	0.965***	0.750*
	D_{30}	0.949***	0.936***	0.782*
	D_B	0.900***	0.932***	0.742*
	D_C	0.943***	0.951***	0.826**
Coarse roots	D	0.968***	0.988***	0.952***
	D_{30}	0.976***	0.998***	0.965***
	D_B	0.949***	0.998***	0.962***
	D_C	0.881***	0.994***	0.973***
Total aboveground	D	0.989***	0.981***	0.981***
	D_{30}	0.985***	0.952***	0.958***
	D_B	0.958***	0.951***	0.976***
	D_C	0.945***	0.967***	0.949***
Total tree	D	0.988***	0.987***	0.980***
	D_{30}	0.985***	0.962***	0.964***
	D_B	0.959***	0.962***	0.977***
	D_C	0.936***	0.974***	0.958***

trees, especially for the foliage biomass. This implies that the size-specific equation maybe an option to these aboveground components.

The tree size-specific allometric regressions were further developed (Table 5). Above- and below-ground biomass components were highly correlated to D ($P < 0.001$). The correlations of biomass components to D for the big trees were slightly weaker than those for the small and medium trees. The relationships of aboveground components (stem wood, stem bark, live branches

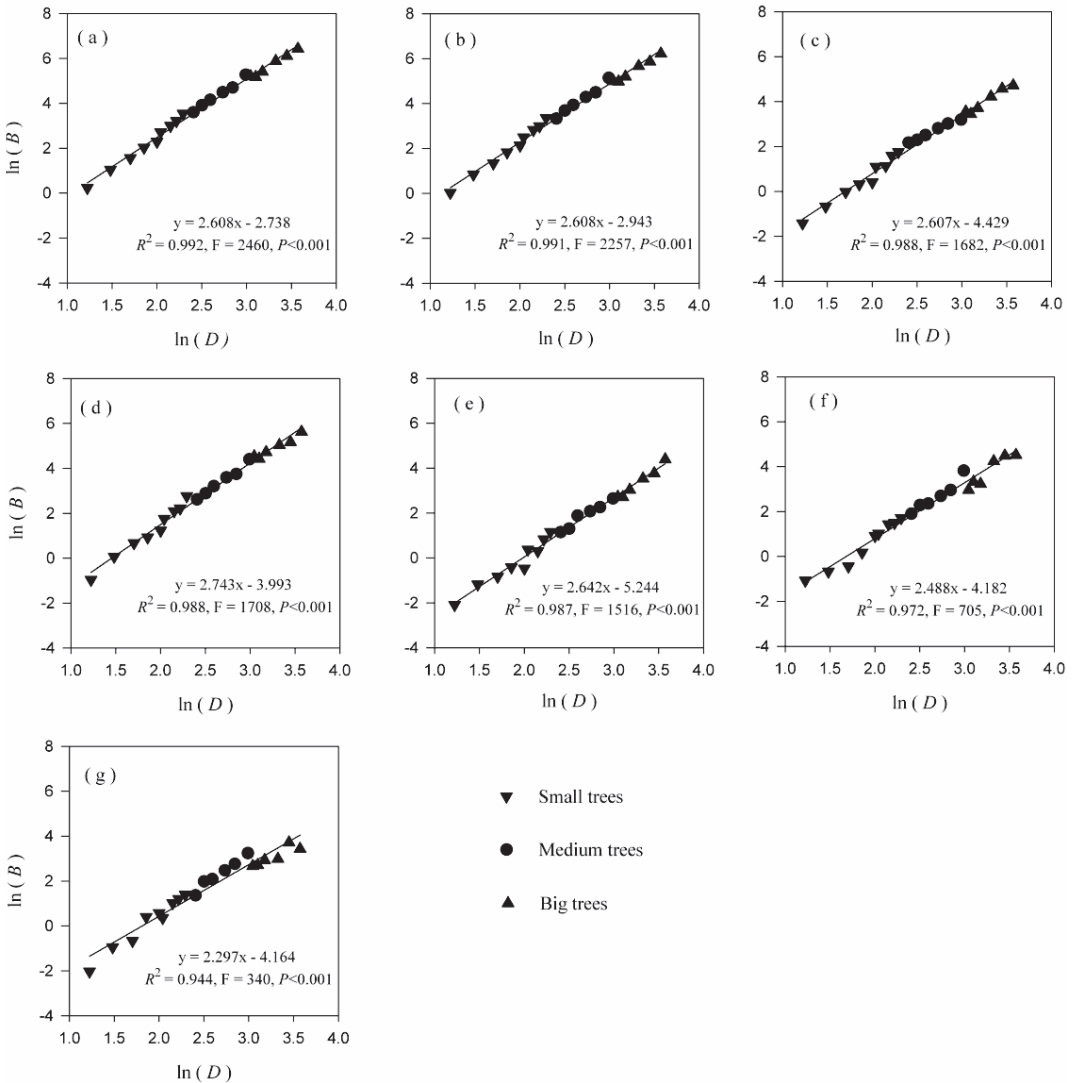


Fig. 5. Relationships between biomass components and the diameter at breast height. Biomass components include total tree (a), total aboveground (b), coarse roots (c), stem wood (d), stem bark (e), live branches (f) and foliage (g).

and foliage) against D exhibited more variability than those of total aboveground, belowground and total tree biomass, which could be confirmed in terms of RMSEs and AIC. The constants a and b in the biomass equations of aboveground components differed among tree sizes. This may be the result of changes in the biomass structure as shown above and thus also confirm the application of the tree size-specific allometry.

4 Discussion

4.1 Biomass Structure

Forest trees usually compete with their neighbours for essential resources, e.g. photosynthetically active radiation, water, and nutrients (Simon and Edmund 2000). Plants always adjust their above- and below-ground biomass structure in

Table 5. Allometric equations for each biomass component (B , kg) against the diameter at breast height (D , cm) in different tree sizes. Equation form is $\ln B = a + b \ln D$, a and b the two coefficients of regression.

Components	a (S.E.)	b (S.E.)	R^2_{adj}	RMSE	AIC	CF
Small trees						
Stem wood	-4.901 (0.360)***	3.233 (0.188)***	0.974***	0.190	-0.62	1.045
Stem bark	-5.535 (0.518)***	2.799 (0.270)***	0.930***	0.273	5.90	1.064
Live branches	-4.850 (0.444)***	2.841 (0.232)***	0.949***	0.234	3.15	1.041
Foliage	-5.751 (0.395)***	3.127 (0.206)***	0.966***	0.208	1.04	1.003
Total aboveground	-3.740 (0.214)***	3.035 (0.112)***	0.989***	0.113	-9.99	1.026
Coarse roots	-5.037 (0.356)***	2.918 (0.186)***	0.968***	0.188	-0.82	1.034
Total tree	-3.503 (0.224)***	3.015 (0.117)***	0.988***	0.118	-9.14	1.026
Medium trees						
Stem wood	-4.426 (0.491)***	2.926 (0.183)***	0.981***	0.089	-8.35	1.008
Stem bark	-4.941 (0.721)**	2.549 (0.269)***	0.947***	0.132	-3.74	0.999
Live branches	-5.263 (1.028)**	2.961 (0.383)**	0.922**	0.188	0.51	1.035
Foliage	-5.593 (0.678)**	2.953 (0.253)***	0.965***	0.124	-4.48	1.000
Total aboveground	-3.616 (0.487)**	2.898 (0.181)***	0.981***	0.089	-8.45	1.008
Coarse roots	-2.294 (0.242)***	1.853 (0.090)***	0.988***	0.044	-16.82	0.999
Total tree	-2.911 (0.375)**	2.713 (0.140)***	0.987***	0.068	-11.58	1.006
Big trees						
Stem wood	-2.035 (0.748) ^{ns}	2.121 (0.228)***	0.945***	0.106	-6.39	1.006
Stem bark	-7.031 (0.747)***	3.169 (0.228)***	0.975***	0.105	-6.41	1.011
Live branches	-6.695 (1.710)*	3.200 (0.521)**	0.880**	0.241	3.53	1.005
Foliage	-2.798 (1.470) ^{ns}	1.791 (0.448)*	0.750*	0.207	1.71	1.018
Total aboveground	-2.553 (0.496)**	2.453 (0.151)***	0.981***	0.070	-11.33	1.002
Coarse roots	-4.379(0.845)**	2.568 (0.257)***	0.952***	0.119	-4.93	1.002
Total tree	-2.417 (0.518)**	2.478 (0.158)***	0.980***	0.073	-10.80	1.001

S.E. is an abbreviation of standard error; ns indicates not significant at the $P=0.05$ probability; RMSE is the root mean square error; AIC is the Akaike's Information Criterion; R^2_{adj} is the adjusted coefficient of determination and CF is the logarithmic correction factor.

response to environmental changes. The samples from this study showed that the relative proportion of the stem biomass in the big trees is the greatest among different tree sizes, whereas the canopy biomass in the big trees is smaller than those in the small and medium trees. An increase in the stem biomass along with a decrease in live branch and foliage biomass has also been found in previous studies. For example, a study based on an age-sequence of white pine (*Pinus strobus* L.) forests indicated that the stem wood biomass relative to total tree biomass increased from 25% in the 2-year-old stand to 36, 49, and 69% in the 15-, 30- and 65-year-old stands. While the relative proportion of live branch biomass decreased from 17% to 7%, in the 15-, 30-, and 65-year-old stands, respectively, and foliage biomass decreased from 34% to 12, 6, and 1.5% as forests mature (Peichl and Arain 2007). The likely

explanation for these findings is that biomass structure is adjusted for trees survival. To achieve a greater height, a bigger crown may be crucial for nutrient uptake and photosynthesis during early development (small trees) in response to intensive competition. The increase of stem and coarse roots may be more important at a later stage (big trees) in order to ensure tree stability. This could be confirmed from the changes of H/D and stem/foliage in the study. The small trees had the highest H/D and lower stem/foliage while the big trees the lowest H/D and the highest stem/foliage among the three size classes.

It was reported that 70% of solar radiation was intercepted by the forest canopy and only 3–10% reached the forest surface (Leverens 1996). However, the amount and distribution of intercepted radiation largely depends on crown structure (Stenberg et al. 1994). Vertical foliage

distribution determines the utilization of light and photosynthetic efficiency, and affects individual tree growth (Brix 1981, Teskey et al. 1987, McCrady and Jokela 1996). In our study, the largest live branches were located in the medium and bottom layers of the crown and foliage was mostly laid in the medium layer. Xiao and Ceulemans (2004) explained the phenomena as foliage growth is strongly stimulated by reduced available light with increasing crown depth while live branch biomass is less affected by this reduced light availability because the cumulative time for branch biomass accumulation is longer with increasing crown depth.

The relative proportion of coarse roots to total tree biomass rarely exceeds about 30% for many coniferous species (Karizumi 1974, Santantonio et al. 1977, Cairns et al. 1997). Previous studies reported a linear relationship between aboveground and belowground biomass at both tree- and stand-level (Vanninen et al. 1996, Brown 2002, Kajimoto et al. 2006). The root to shoot mass ratio (averaged 0.23) in our study is within the range reported for pine and other coniferous species (0.18–0.35) (Cairns et al. 1997). In addition, our finding is well in agreement with a previous study in which the relationship between the biomass of aboveground and coarse roots was approximated by a linear equation with a slope of 0.23 (Kurz et al. 1996). Thus, the use of this coarse root to aboveground biomass ratio may be helpful for estimating belowground biomass from aboveground biomass.

As expected, aboveground competition intensity was generally correlated with tree dimensions (e.g., H and D) that are essential for intercepting solar radiation. Numerous studies generally support the idea that resource availability influences biomass structure in the absence of plant-plant interactions (Wilson 1988). Root/shoot often increases under limited nutrients and decrease under low irradiance. However, our data suggested that *A. nephrolepis* did not change root/shoot in response to aboveground competition. The result corresponds with findings in earlier studies of Douglas-fir (Newton and Cole 1991) and *Pinus radiata* (Watt et al. 2003) but differs clearly from other reports (Chang et al. 1996, Bolte et al. 2004). For example, Bolte et al. (2004) concluded that interspecific competition reduced

root/shoot in the study of above- and belowground biomass in mixed stands of European beech and Norway spruce. The dominant spruce trees had the highest root/shoot and the suppressed beeches the lowest.

Root/shoot would be expected to decrease with aboveground competition intensity because of the disproportionate advantage of aboveground size in competing for light (Weiner 1990). However, individuals under severe aboveground competition intensity allocated relatively more photosynthate to live branches and foliage, but the increase in canopy mass was apparently at the expense of stems rather than roots (Fig. 2). This result confirmed the earlier finding that the competition did not significantly alter biomass allocated to the roots of *Pinus radiata* (Watt et al. 2003). *A. nephrolepis* may not exhibit the trade-offs between aboveground and belowground biomass in their ability to compete for light and belowground resources.

Though aboveground competition intensity apparently affects the biomass structure of aboveground components, it may be insufficient to explain the complex belowground competition, which is mainly for limited supplies of soil water and nutrients (Casper and Jackson 1997). Due to technical problems of sampling and measurements, belowground competition has been given little attention compared with aboveground competition in mature multi-species forests (Bauhus et al. 2000, Curt and Prévosto 2003, Bolte et al. 2004). Belowground competition is mainly restricted to the fine roots which compete for soil water, nutrients and temperature. So it is necessary to know architecture, nutrient concentrations and vertical distribution of fine roots of *A. nephrolepis* in addition to root biomass in the mixed stand.

4.2 Allometric Relationships

The correlations of most D -based tree size-specific regressions were higher than corresponding regressions using other stem diameters (D_{30} , D_B , D_C). For coarse roots, the regressions based on D showed similar correlations as those using D_{30} , which is in agreement with previous studies on red pine (*Pinus resinosa* Ait.) (Haynes and

Gower 1995) and Norway spruce (*Picea abies* L. Karst) (Drexhage and Gruber 1999). For live branches and foliage, the correlations did not improve significantly if using D_B or D_C , although these two variables had been proved to be better predictors for many coniferous species (Waring et al. 1980, Comeau and Kimmins 1989, Osawa 1990). Thus, D -base allometry proved to be a simple and reliable model for biomass estimation when compared to the other three variables in this study.

The tree size-independent allometric equations using D as an independent variable that ignores individual discrepancy worked very well for different biomass components, which is consistent with previous studies for various tree species (Ter-Mikaelian and Korzukhin 1997, Zianis and Menuccini 2004). Although the tree size-independent equations given here worked well for total aboveground, belowground and total tree biomass, biomass estimation of stem wood, stem bark, live branches and foliage is vulnerable to errors arising from the tree size-independent allometry. Thus, more precise estimation of aboveground components requires the tree size-specific equations, particularly for the foliage biomass. Such D -based tree size-specific allometry is also suggested from previous studies for other coniferous and broad-leaved species. For example, Bond-Lamberty et al. (2002) found that a breakpoint occurred at a D of ca. 3 cm in the allometric relationship, where both slope and intercept changed markedly, and that biomass estimation using D -based allometry with such a breakpoint would potentially underestimate both small and large tree biomass and overestimate medium tree biomass for six boreal tree species in northern Manitoba, Canada.

The size-specific correlations of tree biomass components to D for the big trees were somewhat lower than those for the small and medium trees. This is consistent with the report that the correlations of tree biomass components to D were slightly weaker in a 65-year-old stand compared to 2-, 15-, and 30-year-old stands (Peichl and Arain 2007). The equations describing biomass of aboveground components, especially live branches and foliage, produced consistently higher RMSEs and lower R^2_{adj} values than those for the coarse roots, total aboveground or total

tree biomass for various tree size classes. This has been noted in other species (Cienciala et al. 2006, Wang 2006). Larger discrepancy between sampled and estimated foliage production using the equations may be caused without considering the dynamics of environmental conditions. It was reported that foliage production is highly sensitive to light, water, nutrient, and soil conditions (Bond-Lamberty et al. 2002) and the foliage biomass is highly affected by the position of branches and crown density (Liu 2009). All of these factors probably contribute to reduced allometric precision for canopy biomass components.

5 Conclusion

This study presented new findings for an important tree species in China: a) the greatest amount of living branch biomass was located in the middle and bottom layers of the crown, while the largest foliage biomass was found in the middle layer in each tree size category; b) the relative proportion of stem biomass increased while that of canopy biomass decreased with tree size; c) aboveground competition intensity did not influence crown ratio, height to breast-height diameter ratio and root to shoot mass ratio among tree sizes but apparently regulated the biomass structure of aboveground components; d) individuals under severe aboveground competition intensity had higher proportions of live branches and foliage, but the increase in canopy mass was at the expense of stems rather than roots; e) the correlations between biomass components and D were higher than those using other variables; f) the more precise biomass estimation of aboveground components requires size-specific allometry, particularly for the foliage biomass.

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