

Heartwood and sapwood allometry of seven Chinese temperate tree species

Xingchang WANG, Chuankuan WANG*, Quanzhi ZHANG, Xiankuai QUAN

College of Forestry, Northeast Forestry University, 26 Hexing Road, Harbin 150040, China

(Received 20 May 2009; accepted 9 October 2009)

Keywords:

allometric equation /
heartwood formation /
sapwood area /
wood development

Mots-clés :

équations d'allométrie /
formation du bois de cœur /
surface d'aubier /
développement du bois

Abstract

- Allometry of sapwood/heartwood is essential for understanding tree growth, water transport and carbon allocation, timber production and use, but such an allometry is lacking for Chinese temperate tree species.
- We studied the allometry and development of heartwood and sapwood for seven Chinese temperate tree species: Korean pine (*Pinus koraiensis* Sieb. et Zucc), Dahurian larch (*Larix gmelinii* Rupr.), Japanese elm (*Ulmus davidiana* Planch var. *japonica* (Rehd.) Nakai), Manchurian ash (*Fraxinus mandshurica* Rupr.), Manchurian walnut (*Juglans mandshurica* Maxim.), Amur cork-tree (*Phellodendron amurense* Rupr.), and Mongolian oak (*Quercus mongolica* Fisch.).
- All heartwood parameters investigated, including heartwood radius (*HR*), heartwood formation rate (*HFR*), heartwood ring number (*HRN*), heartwood initiation age (*HIA*), and heartwood volume ratio (*HVR*), were positively correlated with tree cambial age (*CA*). The *HR*, sapwood width (*SW*), sapwood area (*SA*), heartwood and sapwood volumes were significantly related to stem diameter at breast height (*DBH*) or xylem diameter. There was a polynomial relationship between the sapwood ring longevity (*SRL*) and sapwood ring number (*SRN*). However, most of the allometric relationships were species-dependent. The hardwood formation patterns were different between coniferous and broadleaved tree species. A power function was suitable to scale *SA* from *DBH*, but the exponent varied from 1.32 for the larch to 2.19 for the cork-tree.
- Our allometry provided a practical means to assess wood development and related physiology for the temperate tree species.

Résumé – Allométrie du bois de cœur et de l'aubier pour sept espèces d'arbres tempérées chinoises.

- L'allométrie de l'aubier/bois de cœur est essentielle pour comprendre la croissance de l'arbre, le transport de l'eau et l'allocation, la production et l'usage du bois, mais cette allométrie est manquante pour les espèces d'arbres chinoises de milieu tempéré.
- Nous avons étudié l'allométrie et le développement du bois de cœur et de l'aubier pour sept espèces d'arbres tempérés chinois : le pin de Corée (*Pinus koraiensis* Sieb. et Zucc), le mélèze de Dahurie (*Larix gmelinii* Rupr.), l'orme du Japon (*Ulmus davidiana* Planch var. *japonica* (Rehd.) Nakai), le frêne de Mandchourie (*Fraxinus mandshurica* Rupr.), le noyer de Mandchourie (*Juglans mandshurica* Maxim.), le phellodendron de l'Amur (*Phellodendron amurense* Rupr.), et le chêne de Mongolie (*Quercus mongolica* Fisch.).
- Les paramètres du bois de cœur étudiés sont le rayon (*HR*), le taux de formation (*HFR*), l'âge d'initiation (*HIA*) et le ratio du volume (*HVR*) : ils sont corrélés positivement à l'âge cambial (*CA*). Le rayon du bois de cœur (*HR*), la largeur d'aubier (*SW*), la surface d'aubier (*SA*), les volumes de bois de cœur et d'aubier sont significativement liés au diamètre à hauteur de poitrine (*DBH*). Il y a une relation polynomiale entre la durée de vie des cernes d'aubier (*SRL*) et le nombre de cernes (*SRN*). Cependant la plus part des relations allométriques dépendent des espèces. Le patron de formation du bois de cœur diffère entre résineux et feuillus. Une fonction puissance est adaptée pour calibrer les variations de *SA* à partir de *DBH* mais l'exposant varie de 1,32 pour le mélèze à 2,19 pour le phellodendron de l'Amur.
- Pour les essences d'arbres tempérés, notre allométrie fournit un moyen pratique pour estimer le développement du bois en tenant compte de la physiologie qui y est associée.

* Corresponding author: wangck-cf@nefu.edu.cn

1. INTRODUCTION

The xylem of most “mature” trees is composed of heartwood in the inner part and sapwood at the periphery, which are histologically similar but physiologically different (Pinto et al., 2004). Developing allometry of sapwood/heartwood and exploring wood development are essential for understanding tree growth, water transport and carbon allocation, timber production and use (Mäkelä, 2002; Ogle and Pacala, 2009; Pinto et al., 2004), because (1) sapwood contains water conducting pipes (i.e., tracheids and vessels); (2) sapwood stores most carbohydrates for tree survival and growth (Hoch et al., 2003); (3) the living parenchyma cells in sapwood and sapwood growth contribute to most respiration cost of the whole tree (Pruyn et al., 2003); and (4) heartwood contains abundant extractives that improve heartwood natural durability and enhance the crown support (Taylor et al., 2002), although it is physiologically inactive in terms of water conduction and energy reserve materials.

Once heartwood formation begins, heartwood is added every year, and consequently the tracheids or vessels disuse simultaneously. However, there are no conclusive results on sapwood longevity and heartwood formation rate (*HFR*) yet. For instance, Yang and Hazenberg (1991a) reported a constant *HFR* (0.6 ring per year) for *Populus tremuloides* until 90 years old, while Knapic and Pereira (2005) found that the heartwood of *Pinus pinaster* increased 0.5 ring per year before 50 years old and 0.8 ring per year afterwards. The mean sapwood ring longevity varied with tree species, e.g., ~45 y for *Picea abies* (Longuetaud et al., 2006), ~67 y for *Pinus sylvestris* (Mäkelä, 2002). Up to now there are no data on sapwood transformation for Chinese temperate tree species.

Transpiration and stem respiration are tightly correlated to sapwood area (*SA*) for individual trees and stands (e.g., Damesin et al., 2002; Meinzer et al., 2001). A power function model for scaling *SA* from stem diameter has been widely accepted, but the universal exponent of 7/3 of the power function proposed by Enquist (2002) has been challenged. For example, Meinzer et al. (2005) investigated 25 temperate and tropical species, and reported that the exponents varied from 1.42 to 1.90 depending upon species groups. Clearly, more measurements on sapwood allometry for diverse tree species are needed for validating the theoretical model (Enquist, 2002).

In this study, we investigated the heartwood and sapwood development for seven temperate tree species in northeastern China. These species were Korean pine (*Pinus koraiensis* Sieb. et Zucc), Dahurian larch (*Larix gmelinii* Rupr.), Japanese elm (*Ulmus davidiana* Planch var. *japonica* (Rehd.) Nakai), Manchurian ash (*Fraxinus mandshurica* Rupr.), Manchurian walnut (*Juglans mandshurica* Maxim.), Amur cork-tree (*Phellodendron amurense* Rupr.), and Mongolian oak (*Quercus mongolica* Fisch.). Our objectives were to (1) develop allometric models of heartwood and sapwood parameters (e.g., heartwood radius, sapwood width, sapwood area, sapwood volume) for the seven tree species; and (2) examine development of sapwood (e.g., sapwood longevity, sapwood ring number) and heartwood (e.g., heartwood formation rate, heartwood initiation age) for the species. We hypothesize that (1) there are

allometric relationships of sapwood/heartwood parameters on tree age or stem diameter, but the relationships are species-dependent; (2) the characteristics of wood development differ significantly between coniferous and broadleaved tree species.

2. MATERIALS AND METHODS

2.1. Study area description

The research site is located at the Maoershan Forest Ecosystem Research Station in Heilongjiang Province (127° 30′–34′ E, 45° 20′–25′ N). The site has an average altitude of 400 m above sea level and an average slope of 10°–15°. The parent material is granite bedrock and the soil is Haplumbrepts or Eutroboralfs. The climate is continental monsoon climate with mean annual values: 700 mm precipitation, 884 mm evaporation, and 2.8 °C air temperature (Wang, 2006).

The primary forest was dominated by Korean pine mixed with such deciduous species as *Betula* spp., *Populus* spp., *Quercus* spp., *Ulmus* spp., etc. Since the turn of the 20th century, the forest was repeatedly harvested by large-scale industrial logging. The current forests are mainly composed of secondary forest types (mainly Mongolian oak, mixed deciduous forest, hardwood forests) and plantations (mainly Korean pine and Dahurian larch plantations). In this study, we sampled trees from stands with 50–60 years old age, 1800–3100 trees ha⁻¹ density, 12–22 cm mean diameter at breast height (*DBH*), and 27–40 m² ha⁻¹ basal area. Refer to Wang (2006) for details.

2.2. Field sampling

We sampled seven tree species, including Korean pine, Dahurian larch, Japanese elm, Manchurian ash, Manchurian walnut, Amur cork-tree, and Mongolian oak. For each species, two dominant, three co-dominant, three intermediate, and two suppressed healthy trees were destructively sampled in August 2004 (the elm trees were sampled in August 2005). Tree height (*H*, m) and *DBH* (cm) were measured after the tree was fallen. Stems were cut into 1 m sections. At the end of each stem section, a 5 cm thick disc was cut and taken to the laboratory for heartwood and sapwood measurements. The characteristics of the sampled trees were summarized in Table I.

2.3. Heartwood and sapwood determination

Each of the discs was planed and polished until the annual rings were clearly determined, and then scanned with a professional scanner equipped for a tree ring analyzer (Windendro2003, Regent Instruments Co., Canada). The heartwood radius (*HR*, cm), sapwood width (*SW*, cm), xylem radius (*XR*, the sum of *HR* and *SW*), annual ring numbers of heartwood (*HRN*) and sapwood (*SRN*), and cambial age (*CA*, the sum of *HRN* and *SRN*) were measured from 4 radial directions of each disc (north, south, east and west) with the Windendro2003, and averaged. The discs whose rings or heartwood could not be determined were excluded.

Table I. Characteristics of the sampled trees for the seven tree species. *DBH* stands for stem diameter at breast height. The sample size for heartwood radius (*HR*), sapwood width (*SW*), heartwood ring number (*HRN*), and sapwood ring number (*SRN*) is provided. The age is the tree age at breast height.

Tree species	DBH (cm)		Height (m)		Age (year)		Sample size		
	Mean	Range	Mean	Range	Mean	Range	HR/SW	HRN	SRN
Korean pine	18.5	6.8–30.0	12.7	7.4–17.3	27	23–31	9	9	9
Dahurian larch	32.5	23.2–41.4	23.7	22.3–22.7	40	39–40	6	6	6
Japanese elm	21.0	4.3–38.2	15.7	7.7–20.1	46	19–95	10	8	8
Manchurian ash	23.1	2.6–45.5	16.4	5.4–21.8	55	11–97	10	9	9
Manchurian walnut	26.1	8.1–40.9	17.3	11.9–21.5	32	20–53	10	4	4
Amur cork-tree	20.6	6.4–37.1	15.2	8.4–18.4	62	61–63	10	2	7
Mongolian oak	23.7	9.7–41.9	15.9	9.7–19.2	59	58–60	6	0	0

2.4. Data analysis

2.4.1. Calculation of heartwood and sapwood parameters

Sapwood area (*SA*, cm²): assuming wood section and heartwood region were circular, we calculated *SA* as:

$$SA = 2 \times \pi \times XR \times SW - \pi \times SW^2. \quad (1)$$

Heartwood volume (*HV*, cm³) and sapwood volume (*SV*, cm³): the *HV* and xylem volume (*XV*, cm³) for each stem segment were calculated as a truncated cone by the Simpson formula (Pinto et al., 2004):

$$V = \frac{h}{3} \times (A_1 + A_2 + \sqrt{A_1 \times A_2}), \quad (2)$$

where *h* was the stem segment length (cm). The *A*₁ and *A*₂ were the area of the two segment ends (cm²). The tree top was only comprised of sapwood, of which the volume was calculated as a cone. The tree-level *HV* and *XV* were calculated by summing all stem segment volumes for the individual tree. The *SV* was computed as the difference between *XV* and *HV*. The Heartwood volume ratio (*HVR*) was defined as the ratio of *HV* to *XV*.

Heartwood formation rate (*HFR*, rings y⁻¹), heartwood initiation age (*HIA*, y) and heartwood initiation xylem radius (*HIXR*, cm): the slope of the function of *HRN* against *CA* represented the *HFR* (the rings transformed from sapwood to heartwood per year). The *HIA* was estimated by extrapolating the regressive curve of *HRN* against *CA* to zero *HRN* (Pinto et al., 2004). Similarly, the slope of the function of *HR* against *XR* represented the radial heartwood formation rate, and the extrapolation was *HIXR*.

Sapwood ring number (*SRN*) and sapwood ring longevity (*SRL*, y): the age-dependent dynamic model of *SRN* was given by Mäkelä (2002):

$$SRN(k+1) = SRN(k) + 1 - SRN(k)/SRL, \quad (3)$$

where *SRN*(*k*) was the *SRN* at cambial age *k*. *SRN*(*k*) could also be written as equation (4) (Longuetaud et al., 2006). This formula permitted estimation of *SRL* by non-linear regression

$$SRN(k) = \frac{SRL^k - (SRL - 1)^k}{SRL^{(k-1)}}. \quad (4)$$

To examine relationships between tree growth and wood development, we calculated three growth parameters: mean first decade ring width (*MFRW*, cm), mean last decade ring width (*MLRW*, cm), and mean sapwood ring width (*MSRW*, cm).

2.4.2. Statistical analysis

The Pearson's correlation analysis was used to correlate sapwood and heartwood parameters across the seven tree species. A simple linear regression equation was fitted for *HRN* against *CA*, and *HR* against *XR*. The relationship of *SRL* against *SRN* across all species was fitted with a polynomial function.

The allometry of sapwood cross-sectional area at breast height (i.e., sapwood basal area, *SBA*) against *DBH* was often described as a power function in the literature (Prunyn et al., 2003). To linearize the function, a log-log equation was fitted for all species as:

$$\log_{10} SBA = a + b(\log_{10} DBH). \quad (5)$$

To correct for the systematic bias introduced by logarithmic transformation (Sprugel, 1983), a correction factor (*CF*) was computed for all equations. The regressions of *SV*, *HV* and *XV* against *DBH* or *SBA* were also fitted with the same equation form as equation (5). All the statistical analyses were performed with the SPSS 13.0.

3. RESULTS

3.1. Heartwood allometry

All heartwood parameters investigated (i.e. *HR*, *HFR*, *HIA*, and *HVR*) were positively correlated with the cambial age (*CA*) (Tab. II). The heartwood radius (*HR*) and heartwood volume ratio (*HVR*) were also significantly correlated with *DBH*, while heartwood formation rate (*HFR*) and heartwood initiation age (*HIA*) were not. The *HFR* was positively correlated to *HR*.

Pooling the data across all tree species, the heartwood ring number (*HRN*) was linearly related to *CA* ($HRN = 0.967CA - 6.82$, $n = 569$, $R^2 = 0.97$, $P < 0.001$), while *HR* was closely related to xylem radius (*XR*) ($HR = 0.902XR - 0.632$, $n = 894$, $R^2 = 0.97$, $P < 0.001$). However, tree species significantly ($P < 0.05$) affected both intercepts and slopes of the equations. The species-specific linear models of *HRN* against *CA* explained >91% variations in *HRN* (Tab. III), while those of *HR* against *XR* did > 97% variations in *HR* (Tab. IV). The mean heartwood formation rate (*HFR*) varied from 0.68 ring y⁻¹ for the pine to 1.04 ring y⁻¹ for the cork-tree. The *HIA* ranged from 4.2 y for the elm to 8.5 y for the ash. The *HIXR* varied from 0.2 cm for the cork-tree to 2.1 cm for the larch. The

Table II. Correlation coefficients between heartwood and sapwood parameters across the seven tree species. The parameters examined includes cambial age (*CA*, y), stem diameter at breast height (*DBH*, cm), heartwood radius (*HR*, cm), sapwood width (*SW*, cm), heartwood formation rate (*HFR*, rings y^{-1}), heartwood initiation age (*HIA*, y), heartwood volume ratio (*HVR*), sapwood ring number (*SRN*), sapwood ring longevity (*SRL*, y), mean first decadal ring width (*MFRW*, cm), mean last decadal ring width (*MLRW*, cm), and mean sapwood ring width (*MSRW*, cm). The *HR*, *SW*, *SRN*, and ring widths are all at breast height.

Parameter	<i>DBH</i>	<i>HR</i>	<i>SW</i>	<i>HFR</i>	<i>HIA</i>	<i>HVR</i>	<i>SRN</i>	<i>SRL</i>	<i>MFRW</i>	<i>MLRW</i>	<i>MSRW</i>
<i>CA</i>	0.67** (38)	0.71** (38)	NS (38)	0.60** (37)	0.49* (37)	0.73** (38)	NS (38)	NS (37)	NS (38)	NS (38)	NS (38)
<i>DBH</i>		0.98** (63)	0.58** (63)	NS (37)	NS (37)	0.27* (63)	NS (38)	NS (37)	0.32* (38)	0.51** (38)	0.62** (38)
<i>HR</i>			0.49** (63)	0.35* (37)	NS (37)	0.35** (60)	NS (38)	NS (37)	NS (38)	0.47** (38)	0.57** (38)
<i>SW</i>				NS (37)	NS (37)	-0.47** (60)	0.38* (38)	NS (37)	0.67** (38)	0.56** (38)	0.64** (38)
<i>HFR</i>					0.44** (37)	0.65** (37)	-0.69** (37)	-0.73** (37)	-0.57** (37)	NS (37)	NS (37)
<i>HIA</i>						NS (37)	NS (37)	NS (37)	-0.42** (37)	NS (37)	NS (37)
<i>HVR</i>							-0.46** (38)	-0.60** (37)	NS (38)	NS (38)	NS (38)
<i>SRN</i>								0.95** (37)	0.33* (38)	-0.40* (38)	NS (38)
<i>SRL</i>									NS (37)	-0.45** (37)	-0.36* (37)

** , * , and NS stand for highly significant ($\alpha = 0.01$), significant ($\alpha = 0.05$), and insignificant ($\alpha > 0.05$), respectively. The values in the parentheses are sample size.

Table III. Allometric equations of heartwood ring number (*HRN*) against cambial age (*CA*, y) for the six tree species. The heartwood initiation age (*HIA*, y) is extrapolated from the equations. *N* and R^2 are sample size and determination coefficient. The equations are all significant ($P < 0.001$).

Tree species	<i>N</i>	<i>CA</i> range	Allometric equation	R^2	<i>HIA</i>
Korean pine	102	5–36	$HRN = 0.68CA - 3.11$	0.910	4.6
Dahurian larch	131	5–43	$HRN = 0.86CA - 4.23$	0.976	4.9
Japanese elm	116	5–112	$HRN = 0.98CA - 4.14$	0.995	4.2
Manchurian ash	132	9–103	$HRN = 0.97CA - 8.22$	0.984	8.5
Manchurian walnut	53	7–58	$HRN = 0.94CA - 5.04$	0.997	5.4
Amur cork-tree	35	9–65	$HRN = 1.04CA - 6.07$	0.999	5.8

Table IV. Allometric equations of heartwood radius (*HR*, cm) against xylem radius (*XR*, cm) for the seven tree species. The heartwood initiation xylem radius (*HIXR*, cm) is extrapolated from the equations. *N* and R^2 are sample size and determination coefficient. The equations are all significant ($P < 0.001$).

Tree species	<i>N</i>	Allometric equation	R^2	<i>HIXR</i>
Korean pine	102	$HR = 0.84XR - 0.97$	0.970	1.5
Dahurian larch	131	$HR = 0.94XR - 2.01$	0.979	2.1
Japanese elm	146	$HR = 0.97XR - 0.54$	0.996	0.6
Manchurian ash	142	$HR = 0.93XR - 0.74$	0.988	0.8
Manchurian walnut	154	$HR = 0.96XR - 0.82$	0.988	0.9
Amur cork-tree	144	$HR = 0.96XR - 0.23$	0.998	0.2
Mongolia oak	73	$HR = 0.89XR - 0.41$	0.987	0.5

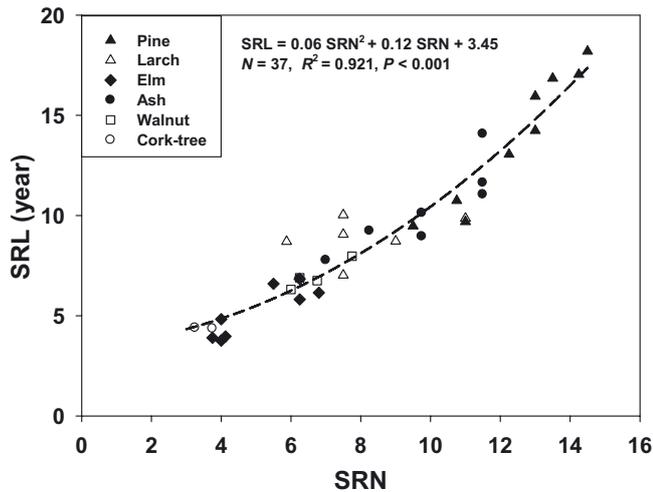


Figure 1. Relationship between sapwood ring longevity (*SRL*) and sapwood ring number at breast height (*SRN*) across the six tree species.

HFR and *HIA* of the conifers tended to be less than those of the angiosperms, whereas the *HIXR* showed a contrary pattern (Tabs. III and IV).

3.2. Sapwood allometry

The sapwood area (*SA*) was positively correlated with *DBH* and *HR* (Tab. II). Combined the data from different heights within a specific tree species, the sapwood width (*SW*) was positively correlated to stem diameter. The correlation coefficients ranked in an order of oak (0.79) > pine (0.75) > ash (0.69) > cork-tree (0.69) > walnut (0.43) > elm (0.43) > larch (0.40) (all $P < 0.001$).

Both sapwood ring number (*SRN*) and sapwood ring longevity (*SRL*) were negatively correlated to *HFR* and *HVR* (Tab. II). The *SW* was positively correlated to *DBH* and *HR*, but was not significantly affected by *CA*.

The *SRL* was ranked as: pine (13.0 ± 0.4 y, mean \pm *SE*) > ash (9.8 ± 0.2 y) > larch (8.9 ± 0.2 y) > walnut (7.3 ± 0.1 y) > elm (5.2 ± 0.1 y) > cork-tree (4.4 ± 0.2 y). The *SRL* of the pine was nearly three times as great as that of the cork-tree. Pooling the data across the six species, we found a highly significant ($P < 0.001$) polynomial relationship between the *SRL* and *SRN* (Fig. 1).

Combining the seven species, sapwood basal area (*SBA*) was significantly correlated to *DBH* on a logarithmic scale ($\log_{10}SBA = -0.733 + 1.852 \log_{10}DBH$, $N = 63$, $R^2 = 0.79$, $P < 0.001$). However, tree species significantly affected the intercepts ($P < 0.001$) but not the slope ($P = 0.181$). The R^2 of the species-specific equations varied from 0.71 to 0.96 (Tab. V).

3.3. Heartwood and sapwood volumes

The heartwood volume ratio (*HVR*) was positively correlated to *CA*, *DBH*, *HR* and *HFR*, but negatively to *SW* (Tab. II). The xylem volumetric components were all significantly correlated with *DBH* on a logarithmic scale when the data for all species were combined (Figs. 2a–2c), among which the sapwood volume (*SV*) equation was the poorest ($R^2 = 0.81$). The regression of $\log_{10}SV$ against $\log_{10}SBA$ substantially improved the fit ($R^2 = 0.97$, Fig. 2d). However, all the relationships above were significantly affected by tree species (all $P < 0.001$).

The species-specific equations provided better fittings than the generalized models for some species (Tab. VI). Overall, the regressions of *SV* against *DBH* had the largest variations among the xylem volumetric components (R^2 : 0.70–0.98), while the larch had the poorest fitting (R^2 : 0.70–0.90) among the seven species. Using *SBA* as the independent variable, instead of *DBH*, improved the species-specific allometric regressions of *SV* (R^2 increased by 0.04–0.21).

To exclude the effect of *DBH* on xylem volume (*XV*), heartwood volume (*HV*) and sapwood volume (*SV*) of the seven species, we standardized the *DBH* to 20 cm (Fig. 3). The greatest *XV*, *HV* and *SV* all occurred in the larch, whereas the least occurred in the cork-tree, the pine, and the cork-tree, respectively. The inter-specific variability in *SV* was the greatest among the wood volumetric components.

4. DISCUSSION

4.1. Heartwood allometry

The generalized allometric models between heartwood ring number (*HRN*) and tree age or between heartwood radius (*HR*) and stem diameter for the Chinese temperate tree species provide an important means to estimate the heartwood formation rate or sapwood mortality. However, the corresponding species-specific models did improve the fitting (Tabs. III and IV). This result was in accordance with previous studies on *Acacia melanoxylon* (Knapic et al., 2006), *Populus tremuloides* (Yang and Hazenberg, 1991a), and *Eucalyptus globules* (Miranda et al., 2006). Synthesizing the model forms of *HRN* against cambial age (*CA*) in the literature (Fig. 4), we found that the five angiosperms had an excellent linear fit of *HRN* against *CA* ($R^2 > 0.98$) (Tab. III; Yang and Hazenberg, 1991a), whereas the seven conifers had divergent fits. In addition to the Korean pine and Dahurian larch in this study, the Norway spruce also had a linear relationship between *HRN* and *CA* (Longuetaud et al. 2006). The rest four coniferous species had a polynomial function (Fig. 4). We tried a quadratic equation of *HRN* against *CA* for the Korean pine and Dahurian larch, and slightly improved the fitting (the R^2 increased by 0.01 compared to the linear model for both species). Longuetaud et al. (2006) also showed a better fitting of an age-dependent *HRN* curvilinear model for the Norway spruce, although the authors did not provide comparative statistics for the linear

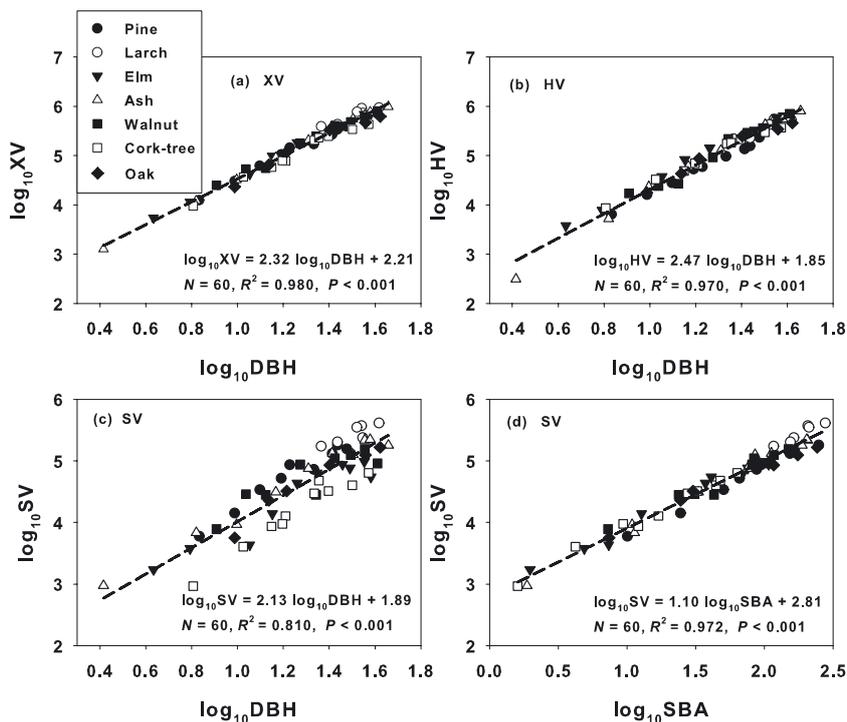


Figure 2. Xylem volume (XV , cm^3) (a), heartwood volume (HV , cm^3) (b) and sapwood volume (SV , cm^3) (c) relating to stem diameter at breast height (DBH , cm), and SV relating to sapwood basal area (SBA , cm^2) (d) on a 10-based logarithmic scale across the seven tree species.

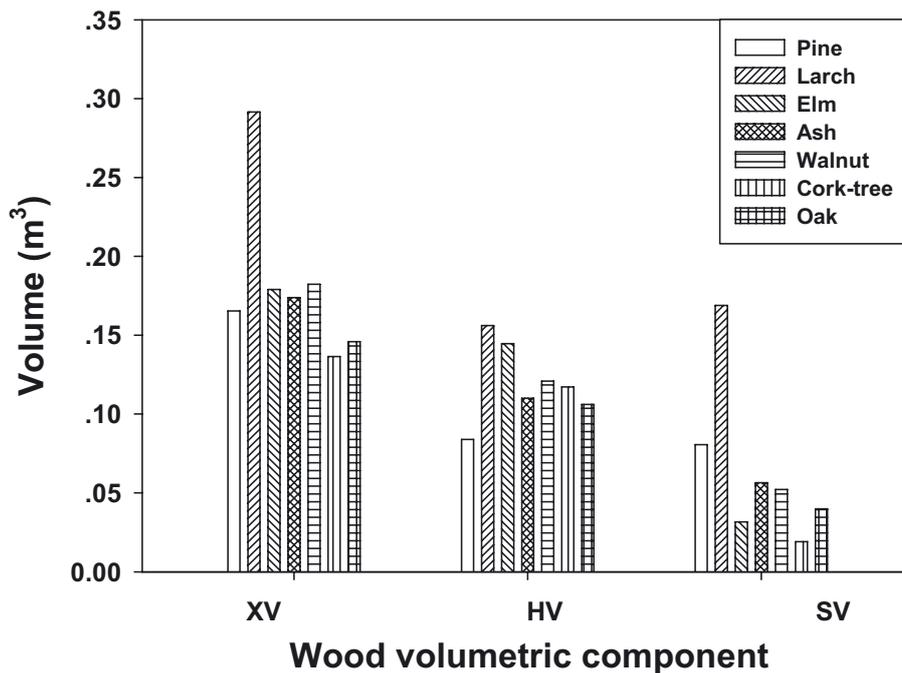


Figure 3. Comparison of the xylem volume (XV), heartwood volume (HV) and sapwood volume (SV) among the seven tree species when standardizing the DBH to 20 cm.

Table V. Allometric equations of sapwood basal area (SBA , cm^2) against stem diameter at breast height (DBH , cm) for the seven tree species. The equations are of the form $\log_{10}SBA = a(\log_{10}DBH) + b$. The sample size (N), coefficients (a and b), determination coefficient (R^2), standard error of the regression (SEE), P values, and the logarithmic correction factor (CF) are given.

Species	N	a	b	SEE	R^2	P	CF
Korean pine	9	-0.53	1.94	0.10	0.944	< 0.001	1.005
Dahurian larch	6	0.27	1.32	0.06	0.776	0.013	1.002
Japanese elm	10	-0.78	1.76	0.21	0.879	< 0.001	1.022
Manchurian ash	10	-0.43	1.69	0.13	0.964	< 0.001	1.008
Manchurian walnut	10	-0.15	1.42	0.22	0.707	0.001	1.025
Amur cork-tree	10	-1.53	2.19	0.13	0.932	< 0.001	1.009
Mongolia oak	8	-1.05	2.10	0.13	0.951	< 0.001	1.008

Table VI. Allometric equations relating xylem volume (XV , cm^3), heartwood volume (HV , cm^3), or sapwood volume (SV , cm^3) to stem diameter at breast height (DBH , cm) or sapwood basal area (SBA , cm^2) for the seven tree species. All slope coefficients are significant ($P < 0.05$). The sample sizes are 9, 6, 10, 10, 9, 10, and 6 for the pine, larch, elm, ash, walnut, cork-tree, and oak, respectively. The coefficients (a and b), determination coefficient (R^2), standard error of the regression (SEE), P values, and the logarithmic correction factor (CF) are given.

Species	a	b	SEE	R^2	P	CF
$\log_{10}XV = a(\log_{10}DBH) + b$						
Korean pine	2.28	2.26	0.06	0.984	< 0.001	1.002
Dahurian larch	1.74	3.20	0.06	0.865	0.005	1.002
Japanese elm	2.27	2.30	0.06	0.992	< 0.001	1.002
Manchurian ash	2.38	2.15	0.06	0.997	< 0.001	1.002
Manchurian walnut	2.19	2.41	0.07	0.984	< 0.001	1.002
Amur cork-tree	2.22	2.24	0.08	0.979	< 0.001	1.003
Mongolian oak	2.18	2.33	0.11	0.959	< 0.001	1.006
$\log_{10}HV = a + b(\log_{10}DBH) + b$						
Korean pine	2.31	1.92	0.04	0.994	< 0.001	1.001
Dahurian larch	1.90	2.72	0.08	0.833	0.007	1.003
Japanese elm	2.36	2.09	0.07	0.993	< 0.001	1.002
Manchurian ash	2.72	1.50	0.10	0.991	< 0.001	1.005
Manchurian walnut	2.48	1.85	0.12	0.963	< 0.001	1.007
Amur cork-tree	2.19	2.22	0.07	0.981	< 0.001	1.002
Mongolian oak	2.20	2.17	0.11	0.960	< 0.001	1.006
$\log_{10}SV = a(\log_{10}DBH) + b$						
Korean pine	2.23	2.00	0.11	0.951	< 0.001	1.006
Dahurian larch	1.59	3.16	0.09	0.699	< 0.001	1.004
Japanese elm	1.92	1.99	0.21	0.895	< 0.001	1.023
Manchurian ash	1.99	2.15	0.12	0.976	< 0.001	1.008
Manchurian walnut	1.55	2.69	0.22	0.737	0.002	1.024
Amur cork-tree	2.43	1.11	0.14	0.943	< 0.001	1.009
Mongolian oak	2.15	1.80	0.14	0.940	< 0.001	1.009
$\log_{10}SV = a(\log_{10}SBA) + b$						
Korean pine	1.14	2.62	0.05	0.989	< 0.001	1.001
Dahurian larch	1.15	2.85	0.50	0.899	0.003	1.133
Japanese elm	1.07	2.88	0.10	0.978	< 0.001	1.005
Manchurian ash	1.17	2.69	0.08	0.990	< 0.001	1.003
Manchurian walnut	1.00	3.01	0.10	0.950	< 0.001	1.005
Amur cork-tree	1.11	2.81	0.07	0.984	< 0.001	1.003
Mongolian oak	0.93	3.02	0.07	0.982	< 0.001	1.003

and curvilinear models. However, we found that the curvilinear model failed to extrapolate the heartwood initiation age (HIA) for the Korean pine, Dahurian larch and Norway spruce (i.e. negative HIA), perhaps because of their relatively young age (< 45 y). These results suggested that angiosperms and gymnosperms may have different heartwood formation patterns, which are related to the mean first decadal ring width ($MFRW$) (Tab. II). The heartwood rings of the angiosperms

increased with a constant rate as trees age (e.g. Hazenberg and Yang, 1991; Tab. III), whereas those of some conifers increased slower (Tab. III) but progressively (e.g. Björklund, 1999; Fig. 4).

The heartwood formation rates (HFR) in this study were within the range reported in the literature (0.5–1.0 ring y^{-1}) (Björklund, 1999; Hazenberg and Yang, 1991; Knapic and Pereira, 2005; Pinto et al., 2004; Yang and Hazenberg, 1991a).

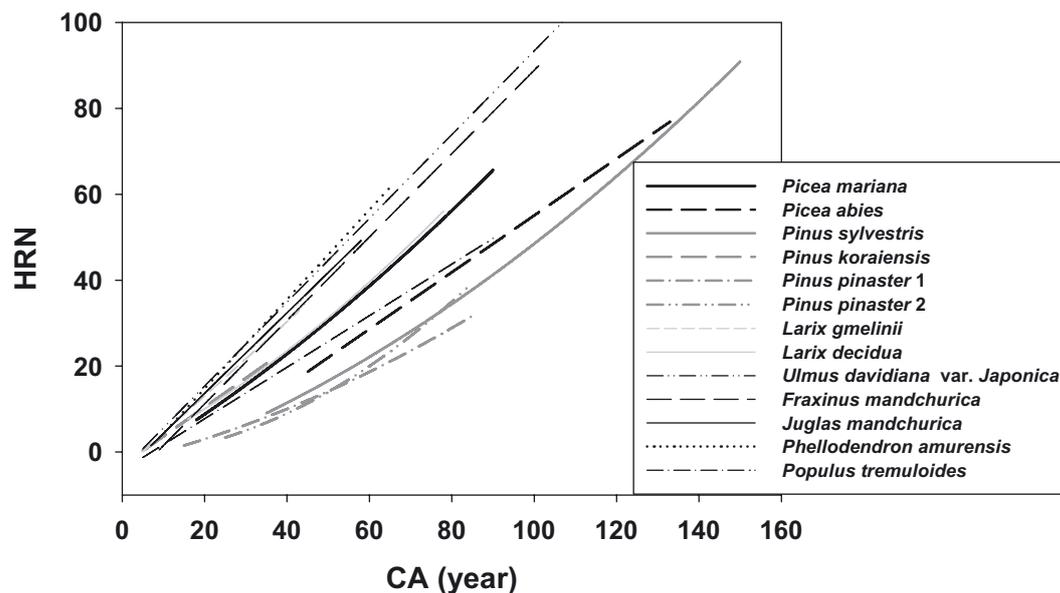


Figure 4. Comparison of allometric model forms of heartwood ring number (*HRN*) against cambial age (*CA*) for diverse tree species. The models for *Picea mariana*, *Picea abies*, *Pinus sylvestris*, *Pinus pinaster* 1, *Pinus pinaster* 2, *Larix decidua*, *Populus tremuloides* are from Hazenberg and Yang (1991b), Longuetaud et al. (2006); Björklund (1999); Pinto et al. (2004); Knapic and Pereira (2005); Nawrot et al. (2008); Yang and Hazengerg (1991a), respectively, whereas the others are from this study.

The *HFR* was positively correlated to heartwood volume ratio (*HVR*) but negatively to sapwood ring longevity (*SRL*) (Tab. II), illustrated that the faster the heartwood formed, the more the heartwood contributed to the trunk volume, and the shorter the sapwood ring longevity was.

All trees start heartwood formation once the trees reach certain size or age, but the *HIA* or heartwood initiation xylem radius (*HIXR*) was species-dependent (Tabs. III and IV). The estimated *HIA* varied substantially among species (from 4 y for the Japanese elm in this study to 21 y for maritime pine, Knapic & Pereira, 2005). However, few studies validated the extrapolated *HIA*. We measured the *HIA* of Japanese elm and Manchurian ash saplings (~10 years old) in a natural forest in this region, and found that the measured *HIA* was consistent with the estimated.

4.2. Sapwood allometry

Unlike *HRN*, the sapwood ring number (*SRN*) was not significantly correlated with tree age or *DBH*, but strongly with heartwood formation rate (*HFR*) and sapwood ring longevity (*SRL*) (Tab. II). The significant polynomial relationship between *SRL* and *SRN* across the six species (Fig. 1) illustrated that the more sapwood rings were associated with the greater sapwood longevity. This model provided a simple and practical way to estimate the longevity of parenchyma cell and conducting time of vessel included in the sapwood. The Korean pine had the greatest *SRL* (~13 y) among the six tree species in this study (Fig. 1), which was still considerable less than that of *Picea abies* (45 y, Longuetaud et al., 2006) and *Pinus sylvestris* (67 y, Mäkelä, 2002).

The *SRN* was positively correlated with the mean first decadal ring width (*MFRW*), but negatively with the mean last decadal ring width (*MLRW*) (Tab. II). This non-monotonic curve between *SRN* and the ring growth rate helped trees to maintain relatively constant development of sapwood with tree aging. Nevertheless, the sapwood width (*SW*) was monotonically increasing with the radial growth rate for all the species (Tab. II); it was also more closely correlated with the radial growth rate than the *SRN*. This result suggested that the amount of transformed sapwood should be expressed with the *SW* or *SA* in tree physiology, better than with the *SRN*. Similar relationship has been observed in *Pinus pinaster* (Knapic and Pereira, 2005) and *Picea abies* (Longuetaud et al., 2006; Sellin, 1994).

Allometry of *SA* attracts many scientists in tree physiology and forestry, because *SA* is an important parameter for estimating tree transpiration, stem respiration and leaf area (e.g., Wullschlegel et al., 1998). The *SW* was positively related to the *DBH* but not to *CA* probably because of the positive correlation between *SW* and radial growth rates across the seven species, which varied with trees development (Tab. II). This result is in agreement with previous studies on *Pinus pinaster* (Knapic and Pereira, 2005), *Pinus ridiata* (Carrodus, 1972), *Picea abies* (Sellin, 1994), and *Eucalyptus globules* (Morais and Pereira, 2007).

Commonly, power functions or log-transformed linear models (e.g. Meinzer et al., 2001) have been used for *SA* allometry against stem diameter. Enquist (2002) proposed a power function for scaling *SA* from stem diameter with a universal exponent of 7/3 (i.e. 2.33). However, Meinzer et al. (2005) found that the exponents could be divided into at least three distinct species groupings, varying from 1.42 to 1.90 for

the 25 temperate and tropical species investigated. Our data showed the exponents varied from 1.32 for the Dahurian larch to 2.19 for the cork-tree (Tab. V), supporting the notion proposed by Meinzer et al. (2005) but with a wider exponent range. This conclusion seems plausible because there are divergences in morphological and physiological properties of water conducting system for diverse species (Hacke et al., 2006). For example, conifer tracheids and angiosperm vessels can be substantial different in water conducting capacity (Hacke and Sperry, 2001).

4.3. Heartwood and sapwood volumes

Log-transformed linear models of xylem volume (XV), heartwood volume (HV) and sapwood volume (SV) against DBH fitted well with our data (Tab. VI), in agreement with previous studies (Pérez Cordero and Kanninen, 2003; Climent et al., 2003). However, Pruyn et al. (2003) reported that a log-transformed polynomial model provided a good fit for four coniferous species in the central Cascade Range, Oregon, USA. The discrepancy may result from their much greater DBH range (cf. Tab. I vs. 11–157 cm).

Heartwood is preferred to sapwood for carpentry and wood use mostly because of its natural durability (Taylor et al., 2002), whereas sapwood is physiologically functional because it stores and conducts labile carbon (Ogle and Pacala, 2009) and water (Wullschleger et al., 1998) in trees. Thus, quantifying HV or SV is necessary for selecting silvicultural practices and understanding carbon metabolisms of various tree species. Standardizing the DBH to 20 cm, we found that the Korean pine had only half HV as much as the Dahurian larch (Fig. 3). This result implies that the silvicultural practice for timber production should aim at planting larger size pine trees than the larch trees, because the two species are the dominant conifers for timber production in this region and HVR was positively correlated to CA and DBH (Tab. II).

The SV is often used to scale up stem respiration and transpiration from chamber-based or sapflow measurements to stand level (e.g., Damesin et al., 2002; Pruyn et al., 2003; Wullschleger et al., 1998). The largest variations in the regression of $\log_{10}SV$ on $\log_{10}DBH$ among the wood volumetric components showed the greatest inter-specific difference in SV (Fig. 2). For trees with 20 cm DBH , the SV of the larch was considerably greater than the others in this study (2–8 times larger, Fig. 3), and more than twice of that of *Thuja plicata* (Pruyn et al., 2003), but similar to that of *Pinus canariensis* (Climent et al., 2003), *Abies amabilis*, *Pseudotsuga menziesii* and *Tsuga heterophylla* (Pruyn et al., 2003). Using sapwood basal area (SBA) as the independent variable substantially reduced the variability in the regression of SV (Fig. 2d and Tab. VI), suggesting that the inter-specific variations in SV mainly come from cross-sectional variation in sapwood. The great inter-specific differences in SV may reflect divergent strategies of trees for carbon metabolism and storage of labile carbon (Ogle and Pacala) and water (Wullschleger et al., 1998).

5. CONCLUSIONS

The allometry of sapwood and heartwood for the Chinese temperate tree species was species-dependent. Transformation of sapwood to heartwood was closely correlated with tree age, but angiosperms and gymnosperms may have different heartwood formation patterns. Sapwood ring number provided a practical proxy to estimate sapwood longevity, while sapwood width or area provided more robust physiological assessment. Power function was suitable to scale sapwood area from DBH , but the exponent varied with species. The great inter-specific variation in sapwood volume, mainly attributed to cross-sectional variation in sapwood, may reflect divergent strategies of trees for carbon metabolism and storage of labile carbon and water.

Acknowledgements: This research was supported by grants from the National Natural Science Foundation of China (No. 30625010), the Ministry of Science and Technology of China (No. 2006BAD03A0703), and Special Research Program for Public-welfare Forestry (No. 200804001) to C.K. Wang. We thank Dr. Jean-Michel Leban and two anonymous reviewers for their comments.

REFERENCES

- Björklund L., 1999. Identifying heartwood-rich stands or stems of *Pinus sylvestris* by using inventory data. *Silva Fenn.* 33: 119–129.
- Carrodus B.B., 1972. Variability in proportion of heartwood formed in woody stems. *New Phytol.* 71: 713–718.
- Climent J., Chambel M.R., Gil L., and Pardos J.A., 2003. Vertical heartwood variation patterns and prediction of heartwood volume in *Pinus canariensis* Sm. *For. Ecol. Manage.* 174: 203–211.
- Damesin C., Ceschia E., Le Goff N., Ottorini J.M., and Dufrene E., 2002. Stem and branch respiration of beech: from tree measurements to estimations at the stand level. *New Phytol.* 153: 159–172.
- Enquist B.J., 2002. Universal scaling in tree and vascular plant allometry: toward a general quantitative theory linking plant form and function from cells to ecosystems. *Tree Physiol.* 22: 1045–1064.
- Hacke U.G. and Sperry J.S., 2001. Functional and ecological xylem anatomy. *Perspect. Plant Ecol. Evol. Syst.* 4: 97–115.
- Hacke U.G., Sperry J.S., Wheeler J.K., and Castro L., 2006. Scaling of angiosperm xylem structure with safety and efficiency. *Tree Physiol.* 26: 689–701.
- Hazenber G. and Yang K.C., 1991. The relationship of tree age with sapwood and heartwood width in black spruce, *Picea mariana* (Mill) B.S.P. *Holzforchung* 45: 317–320.
- Hoch G., Richter A., and Körner C., 2003. Non-structural carbon compounds in temperate forest trees. *Plant Cell Environ.* 26: 1067–1081.
- Knapic S. and Pereira H., 2005. Within-tree variation of heartwood and ring width in maritime pine (*Pinus pinaster* Ait.). *For. Ecol. Manage.* 210: 81–89.
- Knapic S., Tavares F., and Pereira H., 2006. Heartwood and sapwood variation in *Acacia melanoxylon* R. Br. trees in Portugal. *Forestry* 79: 371–380.
- Longuetaud F., Mothe F., Leban J.-M., and Mäkelä A., 2006. *Picea abies* sapwood width: Variations within and between trees. *Scand. J. For. Res.* 21: 41–53.
- Mäkelä A., 2002. Derivation of stem taper from the pipe theory in a carbon balance framework. *Tree Physiol.* 22: 891–905.

- Meinzer F.C., Bond B.J., Warren J.M., and Woodruff D.R., 2005. Does water transport scale universally with tree size? *Funct. Ecol.* 19: 558–565.
- Meinzer F.C., Clearwater M.J., and Goldstein G., 2001. Water transport in trees: current perspectives, new insights and some controversies. *Environ. Exp. Bot.* 45: 239–262.
- Miranda I., Gominho J., Lourenço A., and Pereira H., 2006. The influence of irrigation and fertilization on heartwood and sapwood contents in 18-year-old *Eucalyptus globulus* trees. *Can. J. For. Res.* 36: 2675–2683.
- Morais M.C. and Pereira H., 2007. Heartwood and sapwood variation in *Eucalyptus globulus* Labill. trees at the end of rotation for pulpwood production. *Ann. For. Sci.* 64: 665–671.
- Nawrot M., Pazdrowski W., and Szymański M., 2008. Dynamics of heartwood formation and axial and radial distribution of sapwood and heartwood in stems of European larch (*Larix decidua* Mill.). *J. For. Sci.* 54: 409–417.
- Ogle K. and Pacala S.W., 2009. A modeling framework for inferring tree growth and allocation from physiological, morphological and allometric traits. *Tree Physiol.* 29: 587–605.
- Pérez Cordero L.D. and Kanninen M., 2003. Heartwood, sapwood and bark content, and wood dry density of young and mature teak (*Tectona grandis*) trees grown in Costa Rica. *Silva. Fenn.* 37: 45–54.
- Pinto I., Pereira H., and Usenius A., 2004. Heartwood and sapwood development within maritime pine (*Pinus pinaster* Ait.) stems. *Trees – Struct. Funct.* 18: 284–294.
- Pruyn M.L., Harmon M.E., and Gartner B.L., 2003. Stem respiratory potential in six softwood and four hardwood tree species in the central cascades of Oregon. *Oecologia* 137: 10–21.
- Sellin A., 1994. Sapwood-heartwood proportion related to tree diameter, age, and growth rate in *Picea abies*. *Can. J. For. Res.* 24: 1022–1028.
- Sprugel D.G., 1983. Correcting for bias in log-transformed allometric equations. *Ecology* 64: 209–210.
- Taylor A.M., Gartner B.L., and Morrell J.J., 2002. Heartwood formation and natural durability – A review. *Wood Fiber Sci.* 34: 587–611.
- Wang C.K., 2006. Biomass allometric equations for 10 co-occurring tree species in Chinese temperate forests. *For. Ecol. Manage.* 222: 9–16.
- Wullschlegel S.D., Meinzer F.C., and Vertessy R.A., 1998. A review of whole-plant water use studies in trees. *Tree Physiol.* 18: 499–512.
- Yang K.C. and Hazenberg G., 1991a. Relationship between tree age and sapwood/heartwood width in *Populus tremuloides* Michx. *Wood Fiber Sci.* 23: 247–252.
- Yang K.C. and Hazenberg G., 1991b. Sapwood and heartwood width relationship to tree age in *Pinus banksiana*. *Can. J. For. Res.* 21: 521–525.