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Spatial variations in non-structural carbohydrates in stems of twelve temperate tree species

Haiyan Zhang · Chuankuan Wang · Xingchang Wang

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Abstract The radial, axial and inter-specific variations in concentrations and contents of non-structural carbohydrates (NSC) in stems were investigated for 12 Chinese temperate tree species. These species had contrasting leaf phenology (evergreen and deciduous) and wood types (non-, ring- and diffuse-porous wood). For each species, we sampled bark (periderm and phloem), outer wood (light-colored) and inner wood (dark-colored) at four heights along the stem (stump, breast height, crown base and mid-crown). Concentrations of total NSC (TNC, sum of sugars and starch), sugars and starch were much higher in bark than those in wood. On average, contents of sugars and starch accounted for 48 and 52 % of the TNC, respectively, and contents of TNC in bark, outer wood, and inner wood accounted for 34, 38, and 28 % of the stem total, respectively. Bark was the major pool of sugars in the stem (accounting for 50 % of the stem total on average), while outer wood was the major pool of starch (41 %). The concentration of sugars varied axially for all the conifers but did not for the broadleaved species. Mean concentrations of TNC, sugars and starch in stem varied by more than twofold among the species. However, there were no significant differences in these values for the species groups with different leaf phenology or wood types. Ignoring the radial, axial and inter-specific variations in NSC in stem would introduce large bias in estimating NSC storage at tree or ecosystem levels.

Keywords Bark · Non-structural carbohydrate · Sugar · Starch · Wood

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H. Zhang · C. Wang (✉) · X. Wang
Center for Ecological Research, Northeast Forestry University, 26 Hexing Road, Harbin 150040, China
e-mail: wangck-cf@nefu.edu.cn

Introduction

Carbohydrates in trees consist of two primary components: structural (an immovable pool with a long life-time, such as cellulose and lignin) and non-structural carbohydrates (NSC, a metabolically active pool with a short life-time, mainly soluble sugars and starch) (Kozlowski 1992; Luo et al. 2006). NSC is considered as a measure of carbon (C) supply for tree growth, and reflects the capital for flushing, reproduction, and buffering capacity of trees to various stresses (Chapin et al. 1990; Körner 2003; Würth et al. 2005). In addition, NSC storage is an important backbone of life strategies of long-living trees (Magel et al. 2000; Myers and Kitajima 2007). Nevertheless, internal C cycling within trees is poorly understood and thus inadequately represented in forest ecosystem models (Le Roux et al. 2001; Génard et al. 2008; Gough et al. 2009). It is, therefore, crucial to explore variations and allocation of NSC to understand growth and survival of trees under environmental changes (Ryan 2011; Sala et al. 2012; Wiley and Helliker 2012; Richardson et al. 2013; Rocha 2013).

Concentrations of NSC vary considerably with species, tissues, site conditions, and stand characteristics (Kozlowski 1992; Magel et al. 2000; Newell et al. 2002; Hoch et al. 2003; Würth et al. 2005). It is often considered that deciduous trees more rely on C reserves than evergreen conifers in temperate climate because the evergreen needles can sequester C concurrently (Epron et al. 2012;

Michelot et al. 2012). The wood growth before leaf expansion in spring for ring-porous species in angiosperms is presumably more dependent on the NSC accumulated during the previous growing season than that for diffuse-porous species (Barbaroux and Bréda 2002; Barbaroux et al. 2003; Palacio et al. 2011; Michelot et al. 2012). This hypothesis, however, needs validating with solid data across a suite of species particularly at a whole stem or tree level (c.f. Hoch et al. 2003).

It is important to distinguish between concentration and content of NSC in different tree tissues (Pallardy 2008), because high concentrations of total NSC (TNC, sum of soluble sugars and starch) occur in tissues that often have a small proportion of biomass (e.g., bark). Stem is the major pool of NSC in mature trees because of its large proportion of biomass (Pallardy 2008). For example, Barbaroux et al. (2003) reported that the stems contain 44 % of the TNC pool in *Quercus petraea* and *Fagus sylvatica* in June and October, and Würth et al. (2005) observed more than 60 % of TNC storage in the stems in a tropical forest. However, few studies quantify contents of NSC for large trees partly because of the difficulty in exploring spatial variations in NSC or lack of data on biomass allocation (Barbaroux et al. 2003).

Anatomically, stem is composed of bark (periderm and phloem), sapwood and heartwood, which have different functions and chemical compositions (Plomion et al. 2001). Most previous studies have only quantified the NSC in the outer part of sapwood (e.g., Barbaroux and Bréda 2002; Gough et al. 2009; Richardson et al. 2013), and pay less attention to the NSC in bark and heartwood probably because bark accounts for a small proportion of the total biomass and heartwood has presumably non-physiological functions (Pallardy 2008). Nevertheless, bark often has much higher concentration of NSC than sapwood (e.g., Barbaroux et al. 2003; Luo et al. 2006). Also, some studies report that a considerable amount of NSC exists in inner wood even close to pith (Piispanen and Saranpää 2001; Hoch et al. 2003; Würth et al. 2005). Clearly, sampling sapwood only is inadequate to determine the content and allocation of NSC in the whole stem, especially for large-sized trees (Gholz and Cropper 1991; Rocha 2013).

Given that the concentration of NSC tends to vary across the stem cross-section (Saranpää and Höll 1989; Fischer and Höll 1992; Magel et al. 1994; Piispanen and Saranpää 2001; Hoch et al. 2003; Würth et al. 2005; Luo et al. 2006; Chantuma et al. 2009), along the stem (Piispanen and Saranpää 2001; Barbaroux et al. 2003; Wong et al. 2003; Silpi et al. 2007), and with species (Barbaroux et al. 2003; Hoch et al. 2003; Würth et al. 2005), inadequate representation of spatial variations in NSC is likely to introduce bias in estimation of the content and allocation of NSC in trees or ecosystems. In this study, we measured concentrations and contents of NSC in the bark, outer wood (light-colored) and inner wood (dark-colored) at four heights (i.e., stump, breast height, crown base and mid-crown) along the stem for 12 co-occurring tree species with contrasting leaf phenology (evergreen and deciduous) and wood types (non-, ring- and diffuse-porous wood) in a temperate forest, Northeast China. Our specific objectives were to: (1) examine radial, axial and inter-specific variations in concentrations and contents of NSC for these tree species, and (2) compare concentrations and contents of NSC in stems of the species groups with different leaf phenology and wood types. We hypothesized that concentrations and contents of NSC vary spatially and ignoring these variations will introduce significant bias in estimating the NSC storage at tree or ecosystem levels.

Materials and methods

Site description and experimental design

The study was conducted at the Maoershan Forest Ecosystem Research Station, Northeast China (45°24′N, 127°40′E, 400 m a.s.l.). The climate is continental monsoon climate. The mean (1989–2009) annual precipitation is 629 mm, and annual, January, and July air temperature are 3.1, −18.5, and 22.0 °C, respectively. The frost-free period is between 120 and 140 days with early frosts in September and late frosts in May. Refer to Wang et al. (2013) for details.

The forest is a temperate forest representative in northeastern China (Zhang and Wang 2010). Twelve co-existing tree species were selected to include various leaf phenology and wood types (Table 1). For each species, three healthy dominant mature trees with similar ages (50–60 years old) were randomly sampled to maximize inter-specific comparisons and minimize potential effects of age and social status of trees in a stand on NSC concentration and biomass allocation (c.f. Genet et al. 2010).

Field sampling

Field sampling for the 12 tree species was implemented seven times across the growing seasons in 2010 (for 5 species) and 2011 (for 7 species) based on the phenology, i.e., mid-April (before bud swollen), mid-May (bud breaking for the early leafing species), late-May (bud breaking for the late-leafing species), late-June (foliage fully expanded), mid-August (latewood formation), mid-September (before leaf senescence), late-October (complete defoliation for the deciduous species). Within a specific sampling date, we conducted field sampling between

Table 1 Basic characteristics of the sampled trees for the 12 temperate tree species

Species (code)	Scientific name	Leaf phenology	Wood type	Location	H (m)	DBH (cm)	OWW (cm)
Korean spruce (KS)	*Picea koraiensis*	Evergreen	Non-porous	Valley bottom	18.9 (0.2)	29.9 (1.3)	5.1 (0.1)
Korean pine (KP)	*Pinus koraiensis*	Evergreen	Non-porous	Mid slope	20.4 (0.9)	23.3 (0.4)	2.3 (0.1)
Mongolian pine (MP)	*Pinus sylvestris var. mongolica*	Evergreen	Non-porous	Toe slope	23.2 (0.5)	27.3 (1.0)	6.1 (0.4)
Dahurian larch (DL)	*Larix gmelinii*	Deciduous	Non-porous	Toe slope	26.5 (0.4)	31.6 (1.1)	2.1 (0.1)
Manchurian walnut (MW)	*Juglans mandshurica*	Deciduous	Semi-ring-porous	Toe slope	21.3 (1.0)	33.5 (1.5)	3.1 (0.4)
Japanese elm (JE)	*Ulmus japonica*	Deciduous	Ring-porous	Valley bottom	24.1 (1.2)	40.3 (1.9)	1.8 (0.1)
Manchurian ash (MA)	*Fraxinus mandshurica*	Deciduous	Ring-porous	Toe slope	24.7 (2.0)	33.6 (1.2)	2.4 (0.0)
Mongolian oak (MO)	*Quercus mongolica*	Deciduous	Ring-porous	Upper slope	19.1 (0.3)	32.5 (0.6)	3.2 (0.1)
Amur linden (AL)	*Tilia amurensis*	Deciduous	Diffuse-porous	Mid slope	20.8 (2.0)	46.1 (3.6)	21.2 (1.8)§
Ussuri poplar (UP)	*Populus ussuriensis*	Deciduous	Diffuse-porous	Mid slope	23.4 (0.9)	41.5 (1.5)	5.0 (0.5)
Korean aspen (KA)	*Populus davidiana*	Deciduous	Diffuse-porous	Mid slope	25.4 (0.6)	42.3 (0.9)	6.9 (1.6)
White birch (WB)	*Betula platyphylla*	Deciduous	Diffuse-porous	Upper slope	23.0 (1.0)	33.4 (1.7)	16.2 (1.1)§

The numbers are means (standard deviations) with a sample size $n = 3$. H, DBH, and OWW stand for tree height, diameter at breast height, and outer wood width at breast height, respectively. § White birch and Amur linden are regarded as outer wood-only species because of undistinguishable color of wood. Manchurian walnut is arbitrarily classified as the ring-porous group for the analyses

8:00 and 17:00 because potential diurnal variations in NSC are negligible compared to seasonal variations (Bansal and Germino 2009).

For each sampled tree on each sampling date, stem cores (5-mm diameter from bark to pith) were taken at the south direction at four heights: stump (10 cm above the ground surface, ST), breast height (130 cm above the ground surface, BH), crown base (the height of the lowest live branch, CB) and mid-crown (CM). The locations of sequent-sampling cores were shifted a few centimeters to the left or right of the previous ones (Barbaroux and Bréda 2002). The holes left were filled with lubricant to prevent potential pathogen.

The sampled cores were separated into bark and wood samples. The bark samples were combined for the four heights for each sampled tree due to the small amount of bark biomass. The wood samples for all the species except for white birch and Amur linden were further separated into outer wood (light-colored) and inner wood (dark-colored). For white birch and Amur linden whose wood is visually indistinguishable, the wood cores were divided into 2-cm-wide sub-cores from the outermost wood to pith. All the samples were immediately placed in a cooler (0–5 °C) until they were processed within 5 h after the core collection. The samples were microwaved at 600 W for 90 s to eliminate enzymatic activity (Hoch et al. 2003) and kept air-dried for further laboratory analyses.

Determining concentrations of NSC

A modified phenol–sulfuric method was used to determine concentrations of NSC (Buysse and Merckx 1993; Chow and Landhäusser 2004). All the samples were oven-dried at 65 °C for 2–3 days, and ground to pass a 0.2-mm sieve. Sixty mg of the powdered samples was placed in a 50-mL centrifuge tube and extracted with 10 mL of 80 % v/v ethanol for 24 h, then centrifuged at 4,000 rpm for 10 min. The residuals were re-extracted with 5 mL of 80 % v/v ethanol, and centrifuged once again. The supernatant solution was used for determining the concentration of soluble sugars with a spectrophotometer (UV–VIS, Purkinje General Instrument Co., Beijing, China) at a wavelength of 490 nm (Chow and Landhäusser 2004).

After the ethanol in the ethanol-insoluble residuals evaporated, the residues were boiled for 15 min with 10 mL of distilled water; once they were cooling to room temperatures, fungal α amylase (300 U mg^{-1}) was added, and the residuals were then incubated in water bath at 60 °C for 1 h. The supernatant solution was used for determining the concentration of starch with the same procedure as that for sugars. The concentration of starch was obtained by multiplying a reference concentration of glucose by the conversion factor of 0.9 (Chow and Landhäusser 2004). The concentrations of sugars and starch were presented in a percentage dry matter (% DM). For a

specific sample, the total concentration of NSC (TNC, % DM) was obtained by summing the concentrations of the sugars and starch.

Data analysis

Estimating biomass of stem tissues

Biomass of stem tissues was estimated by the following steps: (1) Total stem biomass was mostly estimated from the site-species-specific allometric equations developed by Wang (2006). For the tree species that were absent of the site-specific allometric equations, we applied the equations reported by Dong et al. (2011) for Mongolian pine and Korean spruce, and applied the site-specific allometric equation for Korean aspen to Ussuri poplar. We assumed that these substitutions would not introduce much bias in estimation of stem biomass because these trees are from the same species or genus and stem has the most stable allometry among biomass tissues (Wang 2006). (2) Species-specific proportion of bark biomass to the total stem biomass was used to partition stem biomass into bark and wood. The bark proportion was calculated from the literature [for Korean pine (Yin 2004), Mongolian pine (Zianis et al. 2005), Korean spruce (Mu et al. 1995), Korean aspen and Ussuri poplar (Hu and Guo 2008), Amur linden (Zhan et al. 1990)] or our measurements (for the rest species, data not shown). (3) Biomass proportions of outer wood and inner wood were obtained from the volumes of outer wood and inner wood multiplied by the measured tissue density (Table S1). The volumes of outer wood and inner wood were estimated by the generalized allometric equations developed from the data in Wang et al. (2010) for Mongolian pine, Korean spruce, Korean aspen and Ussuri poplar, and by the site-species-specific allometric equations for the rest species by Wang et al. (2010). Note that the terminologies of outer wood and inner wood in this study were equivalent to those of sapwood and heartwood in Wang et al. (2010). (4) We divided the stem into four segments (from ground surface to BH, BH to CB, CB to CM, and CM to treetop, see "Field sampling") to examine axial variations in concentrations or contents of NSC. For each stem segment, we calculated the volumes of outer wood and inner wood as a truncated cone except for the uppermost segment that was treated as a cone (Wang et al. 2010), and obtained the biomass by multiplying the tissue density (Table S1).

Calculating concentrations and contents of NSC

We normalized all the trees to an identical size (i.e., a DBH of 30 cm) to minimize potential effects of tree size on biomass allocation and thus contents of NSC. The concentration of NSC for bark was the measured value of the four-height combined bark sample, while that for wood was weighted with its biomass. The biomass-weighted concentration of NSC was calculated by the following steps:

For all the species except for white birch and Amur linden, the biomass-weighted concentrations of NSC in the outer wood and inner wood at the i height ($i = 1,\ldots, 4$) (C_i, % DM) were the measured values of the outer wood and inner wood at the i height, respectively. The C_i for white birch and Amur linden was calculated from Eq. (1):

$$C_i = \sum_{j=1}^{n} (A_{ij} \times D_{ij} \times C_{ij}) \Big/ \sum_{j=1}^{n} (A_{ij} \times D_{ij}), \quad (1)$$

where j represents the serial number of the 2-cm-wide sub-core from the outermost wood to pith (c.f., "Field sampling"). A_{ij}, D_{ij}, C_{ij} represent the cross-sectional area (treated as a circle, cm^2), tissue density (mg cm^{-3}), and measured concentration of NSC (% DM) of the j 2-cm-wide sub-core at the i height, respectively.

The biomass-weighted concentration of NSC of the i stem segment ($C_{segment-i}$, % DM) was calculated from Eq. (2):

$$C_{segment-i} = (A_{top-i} \times D_{top-i} \times C_{top-i} + A_{bot-i} \times D_{bot-i} \times C_{bot-i}) \Big/ (A_{top-i} \times D_{top-i} + A_{bot-i} \times D_{bot-i}), \quad (2)$$

where $A_{top\text{-}i}$, $D_{top\text{-}i}$, $C_{top\text{-}i}$, $A_{bot\text{-}i}$, $D_{bot\text{-}i}$, $C_{bot\text{-}i}$ represent the surface area, tissue density, and concentration of NSC at the top end and bottom end of the i truncated-cone segment, respectively.

The biomass-weighted concentration of NSC of the whole stem (C_{stem}, % DM) was calculated from Eq. (3):

$$C_{stem} = \sum_{j=1}^{3} \sum_{i=1}^{4} (M_{ij} \times C_{ij}) \Big/ \sum_{j=1}^{3} \sum_{i=1}^{4} (M_{ij}), \quad (3)$$

where M_{ij} represents the biomass of the j tissue ($j = 1, 2, 3$, standing for bark, outer wood, and inner wood, respectively) of the i stem segment ($i = 1,\ldots, 4$); C_{ij} represents the concentration of NSC of the j tissue of the i stem segment.

The content of NSC for each stem tissue was computed as the product of its biomass and corresponding concentration of NSC. The total content of NSC in the stem was obtained by summing the contents of NSC of all the tissues of the four segments.

Statistical analysis

An ANOVA procedure with repeated measures and the Tukey's Honestly Significant Difference (HSD) test was

used to test the fixed effects of species, tissue, height and their interactions on concentrations of NSC (Hoch et al. 2003) by assigning three replicate sampled trees nested with the seven sampling dates as the random effect. The tissues in this ANOVA included only outer wood and inner wood because the bark sample was combined across the four heights (refer to "Field sampling"). White birch and Amur linden were regarded as outer wood-only species due to the undistinguishable color of wood. Manchurian walnut was the only semi-ring-porous species, and arbitrarily classified as the ring-porous group for the analyses due to their similar phenology. The differences in concentrations and contents of NSC between the species groups with different leaf phenology or wood types were also tested with a one-way ANOVA and HSD procedure.

Results

Variation in concentrations of NSC in stems

Radial variation in concentrations of NSC

Tissue and its interaction with height had significant effects on concentrations of TNC and sugars (both $P < 0.05$) but did not on that of starch ($P > 0.05$; Table 2). On average, bark (9.6 % DM) had 2.6-fold and 3.4-fold higher concentrations of TNC than did outer wood (2.7 % DM) and inner wood (2.2 % DM), respectively (Fig. 1a). The mean concentration of TNC in bark varied from 7.0 % DM in Mongolian oak to 14.7 % DM in Korean spruce, that in the outer wood varied from 1.6 % DM in Korean pine to 3.8 % DM in Japanese elm, and that in the inner wood varied from 1.4 % DM in Manchurian ash to 2.8 % DM in Dahurian larch. There was no significant difference in mean concentrations of TNC between the species groups with different leaf phenology or wood types ($P > 0.05$).

Mean concentrations of sugars in bark, outer wood, and inner wood were 6.7 ± 2.0 % DM (mean $\pm$ SD), 1.2 ± 0.4 % DM, and 0.6 ± 0.2 % DM, respectively (Fig. 1b). The mean concentration of sugars in bark was 4.6-fold and 10.6-fold higher than that in the outer wood and inner wood, respectively. Korean spruce had the highest concentration of sugars in bark (11.0 % DM), while Japanese elm had the lowest (3.9 % DM). Japanese elm had the highest concentration of sugars in outer wood (1.8 % DM), while Korean pine had the lowest (0.63 % DM). The highest concentration of sugars in inner wood occurred in Manchurian walnut (0.94 % DM), while the lowest occurred in Korean spruce (0.32 % DM). On average, the concentration of sugars in bark was significantly higher ($P < 0.05$) for the evergreen (8.6 % DM) or non-porous species (8.2 % DM) than the deciduous (6.0 % DM) or diffuse- and ring-porous species (5.9 % DM), while that in outer wood showed an oppose trend. There was no significant difference in the concentration of sugars in inner wood between the species groups with different leaf phenology or wood types ($P > 0.05$).

The concentration of starch in bark was significantly higher than that in outer wood or inner wood, with the mean values of 2.9 % DM, 1.6 % DM, and 1.6 % DM, respectively (Fig. 1c). The concentration of starch in bark varied from 1.8 % DM for white birch to 4.8 % DM for Amur linden, that in outer wood varied from 0.8 % DM for white birch to 2.0 % DM for Japanese elm, and that in inner wood varied from 0.7 % DM for Manchurian ash to 2.4 % DM for Dahurian larch. We did not find significant differences in concentration of starch in bark, outer wood and inner wood between the species groups with different leaf phenology or wood types except that the concentration of starch in inner wood for the non-porous tree species (2.0 % DM) was significantly higher than that for the diffuse-porous (1.6 % DM) or ring-porous species (1.2 % DM) ($P < 0.05$).

Axial variation in concentrations of NSC

Height and its interaction with tissue had significant effects on mean concentrations of TNC and sugars (both $P < 0.01$) but did not on that of starch ($P > 0.05$; Table 2). The HSD test showed that the concentrations of TNC at stump were higher than the other three heights. Sampling

Table 2 Analysis of variation (ANOVA) on concentrations of NSC (% DM) in stem with repeated measures for the 12 tree species

Fixed effect	*df*	TNC		Sugars		Starch	
		F	*P*	*F*	*P*	*F*	*P*
Species	11/203	137.3	<0.001	144.8	<0.001	160.0	<0.001
Tissue	1/203	635.2	<0.001	1615.3	<0.001	0.4	0.538
Height	3/203	11.6	<0.001	17.5	<0.001	2.3	0.079
Species × Tissue	9/203	112.6	<0.001	44.0	<0.001	127.4	<0.001
Species × Height	33/203	1.4	0.074	1.6	0.035	1.1	0.309
Tissue × Height	3/203	4.2	0.007	2.8	0.041	2.1	0.097

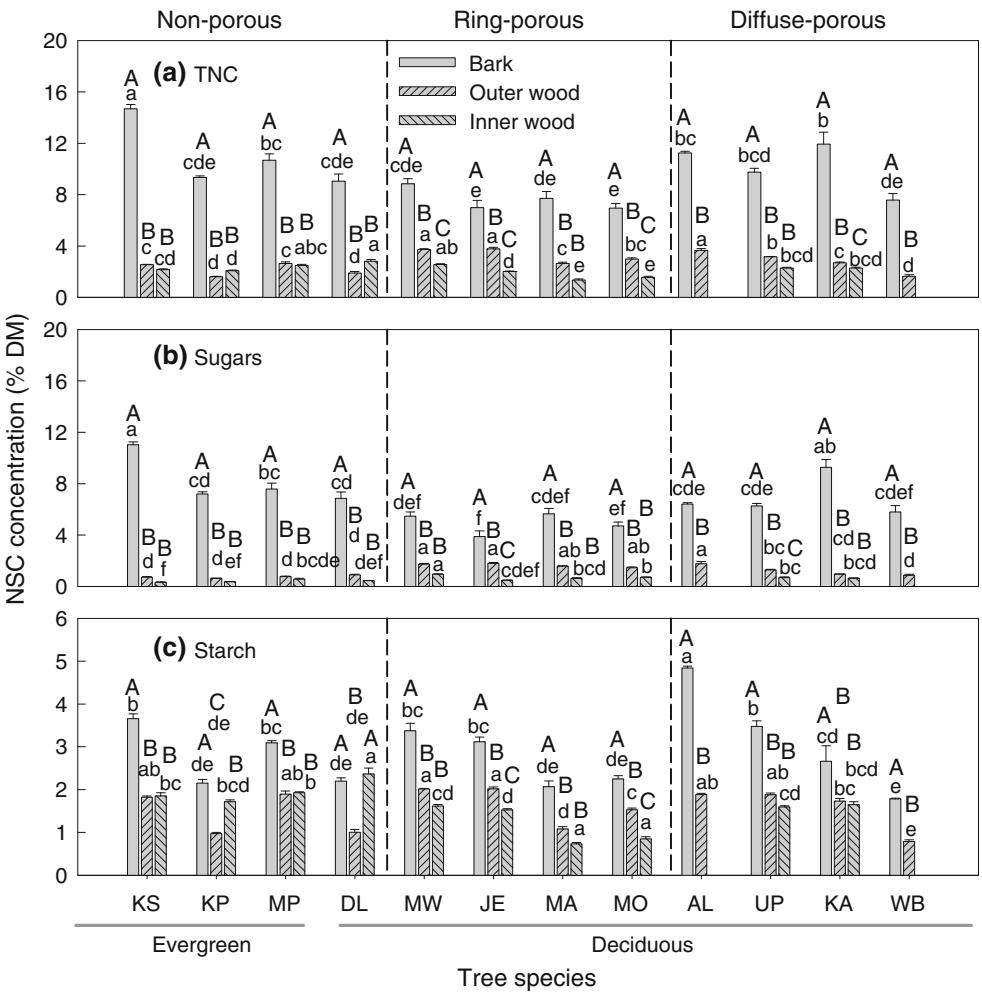

Fig. 1 Mean concentrations of NSC in stem bark, outer wood and inner wood for the 12 tree species. The *error bars* are standard errors ($n = 3$). The different *capital letters* and *lowercase letters* above the *bars* indicate significant differences between tissues and between species, respectively, based on HSD test ($P < 0.05$). Refer to Table 1 for the tree species codes

height significantly (all $P < 0.05$) influenced the concentrations of sugars for all conifers, but did not for the broadleaved species (Fig. 2). TNC and starch axially differed significantly ($P < 0.05$) only for Dahurian larch. These axial variations, however, changed with sampling date and NSC components (Fig. S1). In general, axial variations were lower in May (the depletion period of NSC) for most species, and mainly reflected changes in starch (Fig. S1).

Inter-specific variation in concentrations of NSC

Species and its interaction with tissue had significant effect on concentrations of TNC, sugars and starch (all $P < 0.001$; Table 2). Mean concentrations of TNC, sugars and starch of the whole stem differed significantly among species (all $P < 0.001$, Fig. 3). The highest concentrations of TNC (4.8 % DM), sugars (2.5 % DM) and starch (2.3 % DM) all occurred in Amur linden, while the lowest ones occurred in white birch (2.3 % DM), Japanese elm (0.98 % DM), and white birch (0.89 % DM), respectively. The lowest values were only 48, 40, and 38 % of the highest ones, respectively. There were no significant differences in mean concentrations of NSC between the species groups with different leaf phenology or wood types ($P > 0.05$). However, the concentration of NSC tended to increase as shade tolerance of the tree species increased or its successional stage proceeded within each wood type in spite of no conclusive pattern (Figs. 1, 3).

Variation in contents of NSC in stems

Radial variation in contents of NSC

The allocation pattern of NSC contents among stem tissues varied with species and NSC components. Surprisingly, we found that inner wood contained a substantial amount of NSC (Fig. 4j–l), and also the proportion of NSC content in inner wood fluctuated seasonally (Fig. S2). On average, inner wood contained 36 % of TNC, 19 % of sugars, and 39 % of starch pools in the whole stem.

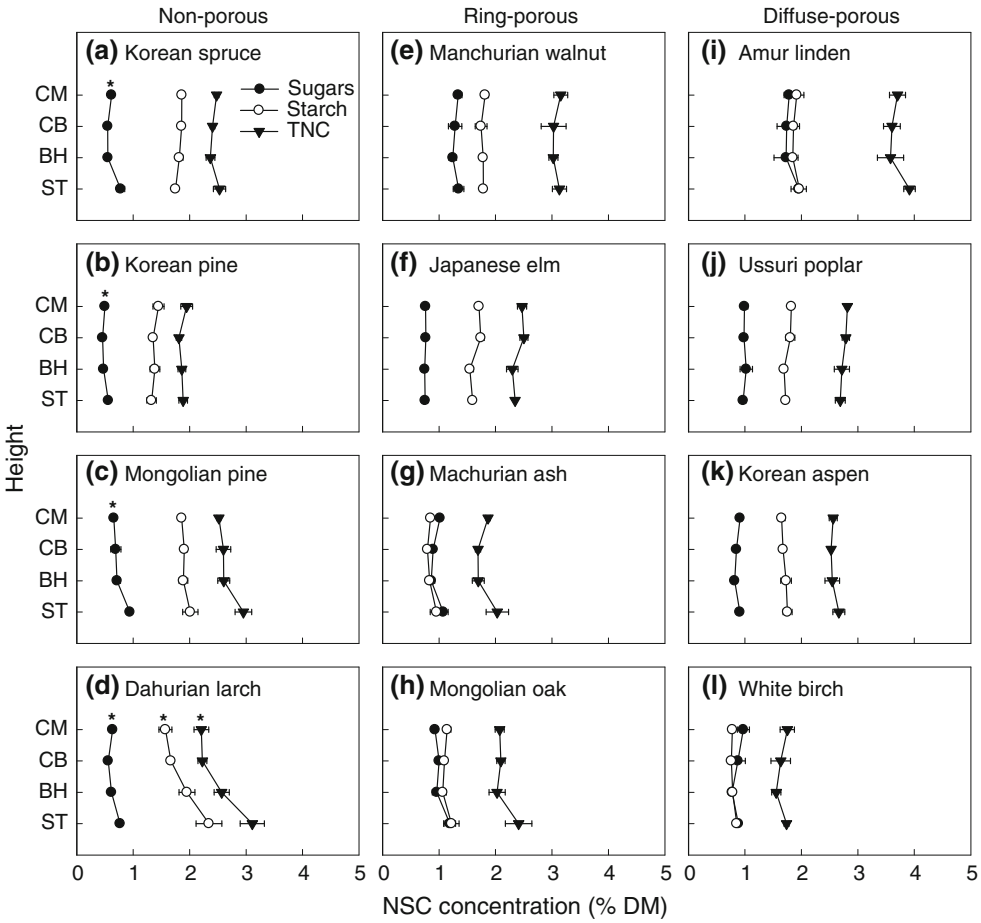

Fig. 2 Axial variations in mean concentrations of NSC for the 12 tree species. The bark is excluded in the axial analysis because of the small amount of biomass sampled at each height. The letters *ST*, *BH*, *CB*, and *CM* stand for stump, breast height, crown base, and mid-crown, respectively (See the text in "Field sampling"). The *error bars* are 95 % confidence intervals. *Asterisk* represents significant difference among the heights ($P < 0.05$)

Overall, bark was the largest pool of sugars, varying from 37 % for Mongolian oak to 72 % for Korean spruce and averaging 50 % of the total content of sugars in the stem (Fig. 4k). The proportion of sugar content in outer wood varied from 17 % for Manchurian walnut to 60 % for Amur linden, while that in inner wood varied from 7 % for Korean spruce to 40 % for Japanese elm.

Outer wood was overall the largest pool of starch, varying from 15 % for Japanese elm to 77 % for white birch and averaging 41 % of the total content of starch in the stem (Fig. 4l). The proportion of starch content in bark varied from 11 % for Mongolian pine to 30 % for Amur linden, while that in inner wood varied from 0 % for the outer wood-only species (i.e., white birch and Amur linden) to 67 % for Japanese elm. On average, the allocation proportions of TNC in bark, outer wood, and inner wood were 34, 36, and 30 %, respectively (Fig. 4j). The maximum proportion of TNC in outer wood to the total stem (65 %) occurred in Amur linden, and that in inner wood occurred in Japanese elm (57 %).

Axial variation in contents of NSC

The axial allocation of contents of TNC, sugars and starch was conservative for all the species (Fig. 5a–c). For the four stem segments from ground surface to treetop (see "Field sampling"), the mean proportions of TNC were 20, 53, 15, and 12 %, respectively, those of sugars were 20, 52, 15, and 13 %, respectively, and those of starch were 19, 54, 15, and 12 %, respectively. Nevertheless, some tree species showed more seasonal variability in the axial allocation of TNC contents than the other species (Fig. S3).

Inter-specific variation in contents of NSC

For each stem tissue, there were significant differences in contents of NSC among species (Fig. 4). In bark, Korean pine had the least contents of TNC, sugars and starch among the species, while Korean aspen had the greatest contents of TNC and sugars, and Amur linden had the greatest content of starch. In outer wood, Japanese elm had the least contents of TNC and starch, and Korean pine had the least content of sugars, while Amur linden had the greatest contents of TNC, sugars and starch among the species. In inner wood, Korean pine had the least contents of TNC, sugars and starch among the species, while Manchurian walnut had the greatest contents of TNC and sugars, and Dahurian larch had the greatest content of starch. The contents of TNC, sugars and starch in outer wood were significantly greater

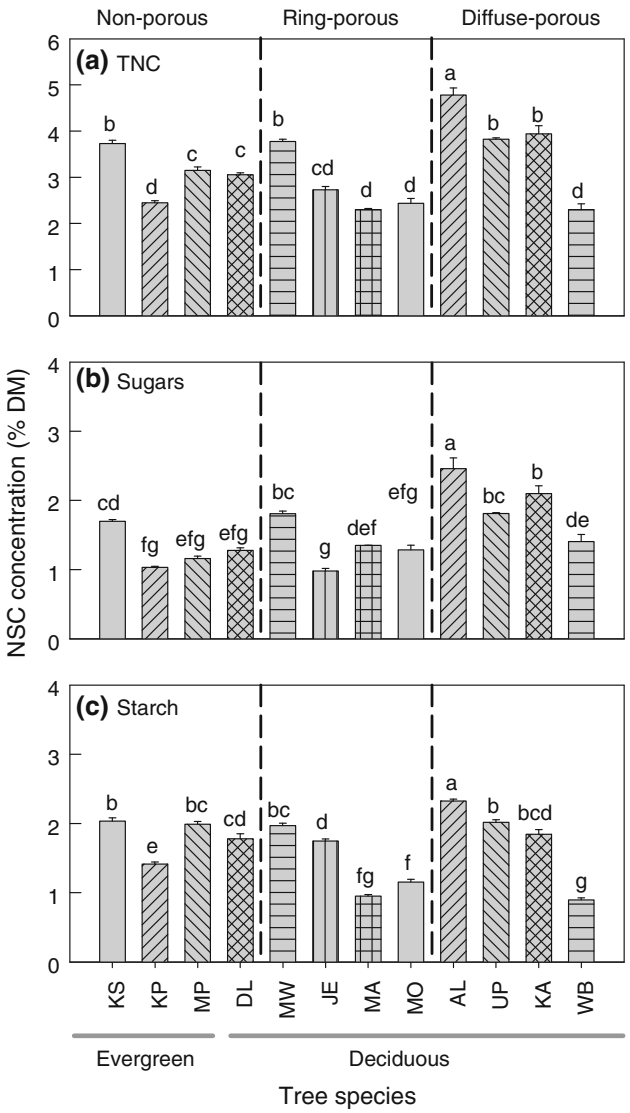

Fig. 3 Mean concentrations of NSC in the whole stem for the 12 tree species. The *error bars* are standard errors ($n = 3$). The *different letters* above the *bars* indicate significant differences among the species based on HSD test ($P < 0.05$). Refer to Table 1 for the tree species codes

for the diffuse-porous species (Fig. 4d–f), while the content of sugars in inner wood was greater for ring-porous species ($P < 0.05$; Fig. 4h). The contents of NSC for each stem tissue did not vary significantly with leaf phenology ($P > 0.05$), and neither did the contents for bark vary with wood types ($P > 0.05$).

For the whole stem, significant differences in contents of NSC among species were found when all the DBHs were normalized to 30 cm (all $P < 0.001$; Fig. 6). Korean pine had the least contents of TNC, sugars and starch, while Amur linden had the greatest contents. There were no significant differences in the contents of NSC between the species groups with different leaf phenology or wood types ($P > 0.05$).

Discussion

Radial variation in concentrations and contents of NSC in stem

Our data showed that outer wood often had high concentrations of NSC for most of the tree species (Fig. 1), in accordance with previous studies (Saranpää and Höll 1989; Fischer and Höll 1992; Magel et al. 1994; Hoch et al. 2003). This may partly explain why many studies often scale the concentration of NSC in the outer wood to estimate NSC storage at a tree or ecosystem level (e.g., Le Roux et al. 2001; Génard et al. 2008; Gough et al. 2009; Richardson et al. 2013).

However, the concentrations of NSC in bark (including periderm and phloem) for all the species were significantly higher than those in wood (Fig. 1). Bark contained 34, 50, and 20 % of the total contents of TNC, sugars and starch in stem, respectively (Fig. 4j–l). This is consistent with most earlier studies (Landhäusser and Lieffers 2003; Luo et al. 2006; Chantuma et al. 2009; Bustan et al. 2011). However, some studies report a lower concentration of starch (but not TNC) in bark (or phloem) than in the outer part of wood, such as *Quercus petraea* (Bazot et al. 2013), *Fagus sylvatica* (Barbaroux et al. 2003), *Olea europaea* and *Hevea brasiliensis* (Chantuma et al. 2009; Bustan et al. 2011). Another unexpected phenomenon in this study was that all tree species contained detectable NSC in inner wood (dark-colored wood close to pith), sometimes even higher than in outer wood (e.g., for Korean pine and Dahurian larch; Fig. 1). This has been rarely reported in the literature. Hoch et al. (2003) also observed NSC even in the innermost core-sections (approximately 80–100 years old) in temperate tree species in Switzerland. These results indicate that bark and inner wood contribute significantly to the NSC reserves in the whole stem (Fig. 4) because the former has high concentration of NSC and the latter constitutes a large proportion of stem biomass. Therefore, we recommend that bark and inner wood should be included in quantifying NSC reserves at stem, tree, or ecosystem levels.

The radial variations in concentrations and contents of NSC among stem tissues discussed above may be related to the physiological functions of each tissue and NSC component. Starch in wood functions as a long-term reserve of NSC in stem, whereas starch in bark acts as a local buffer (Chantuma et al. 2009). Soluble sugars act as an intermediate, ready-to-use compartment of NSC in both wood and bark (Chantuma et al. 2009). Bark (including phloem) is not only a transport pathway but also an important metabolically active pool of NSC in tree stems. Traditionally, heartwood is defined as the inner layers of wood without living cells and reserve materials (e.g., starch) (IAWA 1964). Given that the distinct dark-colored inner wood

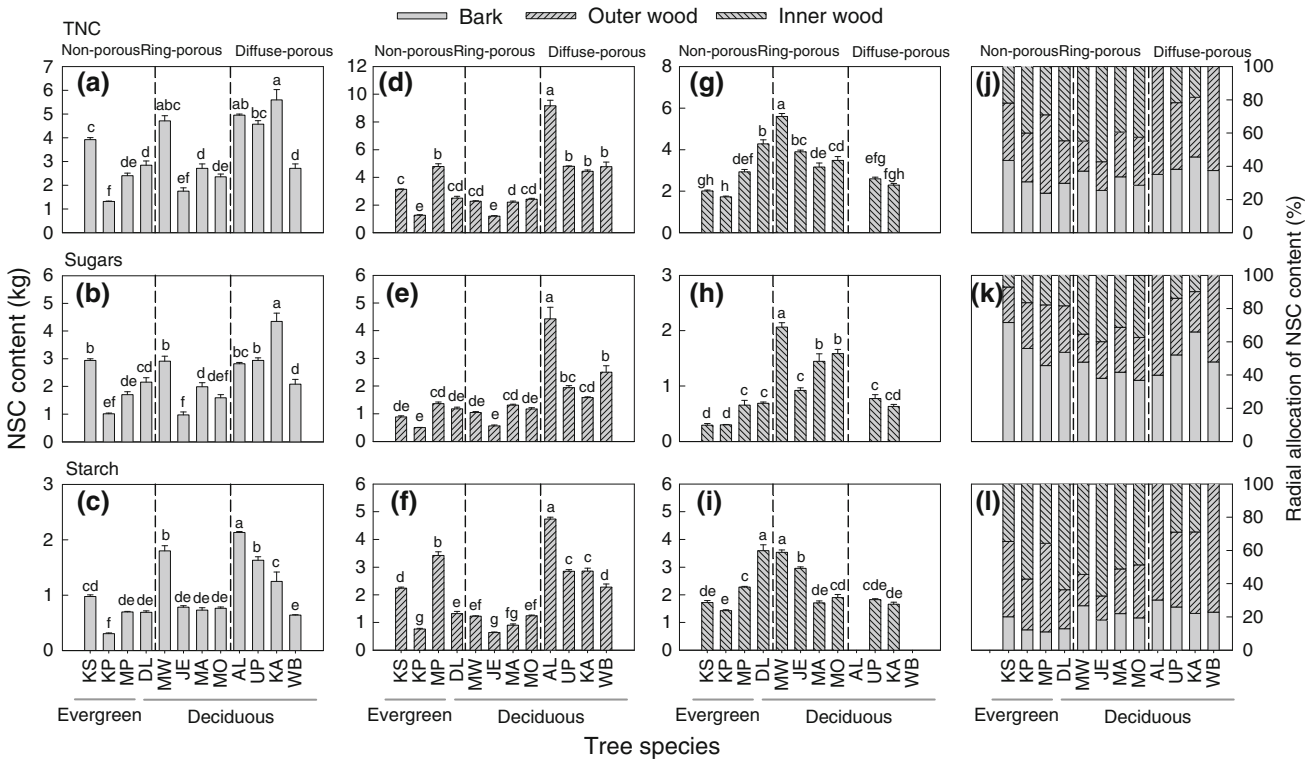

Fig. 4 Contents of NSC in stem bark, outer wood and inner wood for the 12 tree species. The trees for each species have been normalized to a diameter at breast height of 30 cm. The *error bars* are standard errors ($n = 3$). The *different letters* above the *bars* indicate significant differences among the species based on HSD test ($P < 0.05$). Refer to Table 1 for the tree species codes

particularly for the ring-porous tree species in this study is equivalent to heartwood morphologically, our results contradict the conventional notation on the NSC radial allocation and thus physiological function of heartwood (Figs. 1, 4). Gérard and Bréda (2012) suggested that European beech (*Fagus sylvatica*) might use the NSC in inner wood to sustain its C balance in case of multi-year carbon limitation. We have no data about whether there are living cells in inner wood (c.f., Piispanen and Saranpää 2001). However, our temporal data (not the focus of this paper) also support a dynamic feature of NSC in inner wood because the content of NSC in inner wood was changing seasonally for some tree species (Fig. S2). More research on radial profiles of NSC, water content, extractives, and living cell in stems would improve our understanding of physiological functions of NSC in wood (Bamber 1976; Pruyn 2002; Spicer 2005).

Axial variation in concentrations and contents of NSC in stem

There were significant axial differences in concentrations of TNC and sugars (Table 2), in agreement with previous studies (Barbaroux et al. 2003; Wong et al. 2003; Silpi et al. 2007). However, there is discrepancy in axial pattern of concentration of NSC in the literature. Overall, the concentrations of NSC in this study were highest at stump (Table 2; Fig. 2). This partly agrees with the results of Barbaroux et al. (2003) for *Quercus petraea* and *Fagus sylvatica* where the bottom swell has a higher concentration, but contradicts the increasing trend in concentration of TNC with height increasing.

The axial pattern of concentrations of NSC varied with tree species, stem tissues, NSC components (Table 2; Fig. 2), and sampling date (i.e., the status of NSC supply and demand; Fig. S3). The axial changes in sugars for the coniferous species especially Dahurian larch were more dramatic than those in starch for the broadleaved species (Fig. 2). Similarly, Piispanen and Saranpää (2001) found an increasing concentration of sugars but decreasing concentration of starch along the stem of *Betula pendula* in July. Wong et al. (2003) reported that an axial increasing trend in starch in Mid-July (the accumulation period of NSC) was much stronger than in early May and October for *Acer saccharum*. Conversely, Barbaroux et al. (2003) found that an axial increasing concentration of NSC (except for the swell near the stump) in *Quercus petraea* and *Fagus sylvatica* was more dramatic in October than in June. Silpi et al. (2007) reported that a

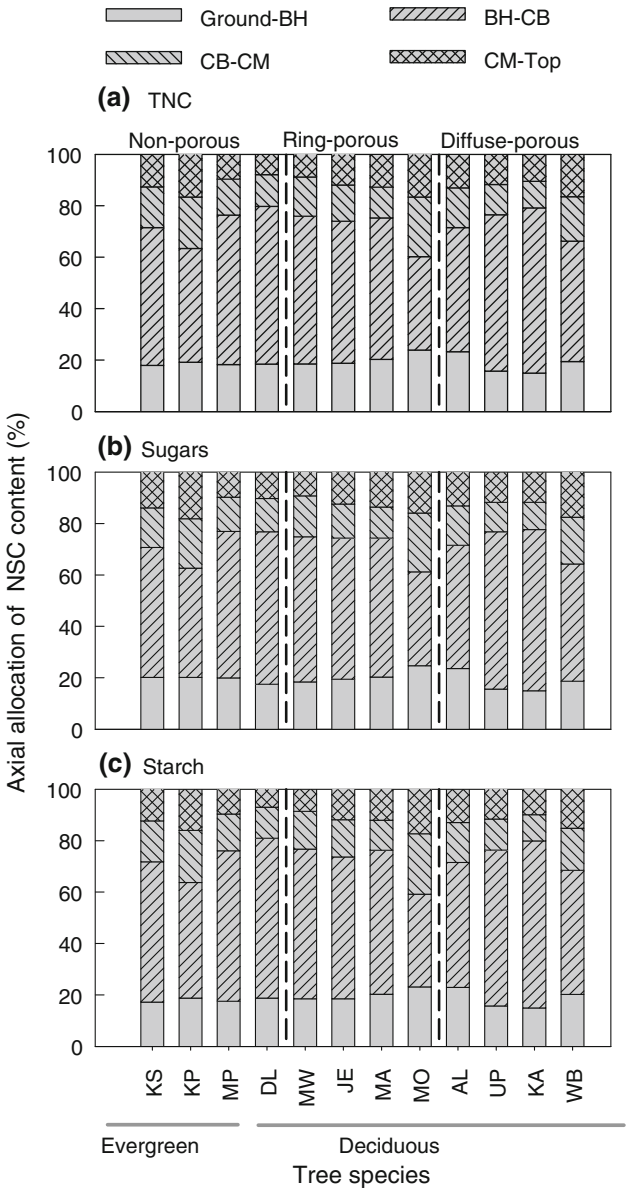

Fig. 5 Axial allocation of contents of NSC for the 12 tree species. Bark is excluded in the axial analysis because of the small amount of biomass sampled at each height. The four stem wood segments are from ground surface to breast height (*BH*), BH to crown base (*CB*), CB to mid-crown (*CM*), and CM to treetop, respectively (See the text "Field sampling"). Refer to Table 1 for the tree species codes

decreasing bottom-up starch gradient along the trunk of *Hevea brasiliensis* was more pronounced in May (the end of dry season). We did not explore the seasonality of NSC in this paper due to its focus of the spatial variability, but our data showed that the weakest axial gradient often occurred in the early growing seasons (i.e., late-May, the depletion period of NSC, Fig. S1). All these results emphasize that species, tissue and sampling date should be taken into account when one estimates NSC storage and allocation in tree stems.

Inter-specific variation in concentrations and contents of NSC in stem

The mean concentrations of TNC in stems of the 12 temperate tree species (2.3–4.8 % DM; Fig. 1a) were within the range of previous results for the stem tissues of temperate trees (0.2–9 % DM, Barbaroux and Bréda 2002; Barbaroux et al. 2003; Hoch et al. 2003; Gough et al. 2009), and mostly lower than those of tropical trees (2–30 % DM, most species around 10 % DM; Newell et al. 2002; Würth et al. 2005).

The concentrations of NSC varied more than twofold among the 12 species and tended to increase as their shade tolerance increased or successional stage proceeded within each wood type (Table 2; Figs. 1, 3). However, there were almost no significant differences in concentrations and contents of NSC between the species groups with different leaf phenology or wood types. This result agrees with Hoch et al. (2003) for the ten species in a European temperate forest, but contradicts some other studies (e.g., Palacio et al. 2007; Michelot et al. 2012). Several reasons may contribute to this disparity. First, our study included all tissues of stem (i.e., bark, outer wood and inner wood), while some studies that reported significant differences between functional types only measured the concentration in outer wood (e.g., Barbaroux and Bréda 2002; Michelot et al. 2012). Second, the current study averaged the measurements across the growing season, while some previous comparisons took less than three times measurement across the year (Barbaroux et al. 2003; Genet et al. 2010; Michelot et al. 2012). Third, our inter-specific comparisons were implemented by sampling dominant mature trees and normalizing with tree size and tissue biomass (See "Materials and methods"), which minimized potential effects of tree age, size and social status in the stands on NSC allocation and maximized the comparability. Therefore, we suggest that the variability in concentration of NSC among biomass tissues, seasonality and tree characteristics be considered in such inter-specific comparisons.

Potential errors in estimates of NSC storage at tree or ecosystem levels

Ignoring the radial, axial and inter-specific variations in concentrations and contents of NSC discussed above would likely introduce large errors in estimation of NSC storage at tree or ecosystem levels. Radial variation in NSC is one source of error in tree-level estimation of NSC storage. If we applied the concentration of NSC only in outer wood and ignored that in bark, the relative errors in estimates of NSC storage in the whole stem would be 24 % for TNC, 40 % for sugars, and 9 % for starch. Ignoring the TNC in inner wood would underestimate the total content of NSC

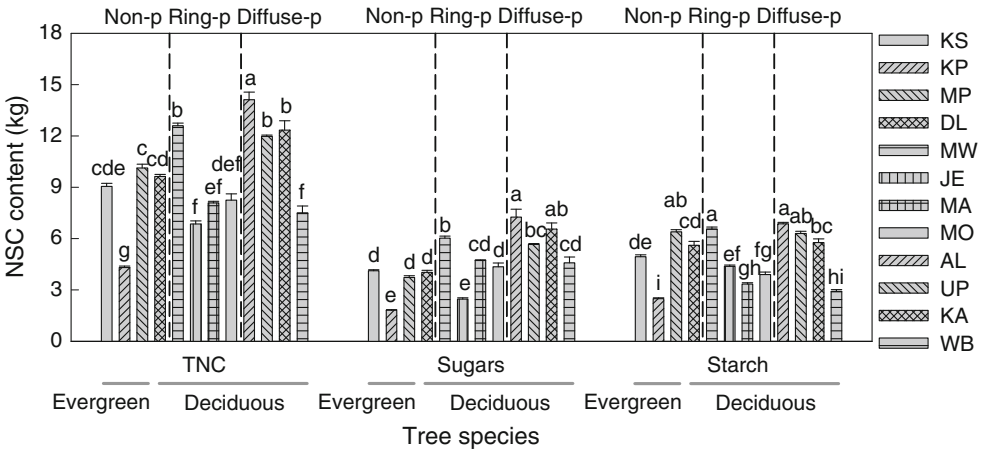

Fig. 6 Contents of NSC of the whole stem for the 12 tree species. The trees for each species have been normalized to a diameter at breast height of 30 cm. Non-p, Ring-p, and Diffuse-p stand for non-porous, ring-porous, and diffuse-porous species, respectively. The *different letters* above the *bars* indicate significant differences among the species based on HSD test ($P < 0.05$). Refer to Table 1 for the tree species codes

in stem by 36 % (c.f., Saranpää and Höll 1989; Fischer and Höll 1992; Magel et al. 1994, 2000).

Many investigators use a simplified sampling scheme, not including the axial variation in NSC, in which a stem core is only taken at breast height to scale up to estimate NSC storage in the whole stem (Ludovici et al. 2002; Gough et al. 2009; Genet et al. 2010; Richardson et al. 2013). We found that the total content of NSC in stem could be biased up to ±31 % at our site using such a simplified sampling scheme (data not shown). Given that there was no generalized axial pattern of NSC for all species (Fig. 2, see "Field sampling"), multiple axial samplings along the stem should be taken if one aims at estimating the NSC pool of the whole tree.

Inter-specific variation in NSC is another source of error in ecosystem-level estimation of NSC storage. For example, Manchurian ash, the dominant tree species in the hardwood forest at the toe slope site (Table 1), had 39 % lower concentration of TNC than the subdominant Manchurian walnut (2.3 % DM vs. 3.8 % DM). Given that the biomass of Manchurian walnut accounted for 20 % of the total biomass in this stand (Zhang and Wang 2010), then using the concentration of TNC of Manchurian ash to estimate the TNC storage of the whole ecosystem (i.e., ignoring the inter-specific variation in NSC) would introduce a relative error of −14 %. Collectively, a comprehensive sampling protocol that accounts for the axial, radial and inter-specific variations in NSC should be adopted for accurately estimating NSC storage at tree or ecosystem levels (Barbaroux et al. 2003; Würth et al. 2005).

Conclusion

Outer wood often has high concentration and content of NSC, but bark and inner wood contribute significantly to the NSC reserves in the whole stem because bark has high concentration of NSC and inner wood constitutes a large proportion of stem biomass. Concentrations of TNC and sugars also change axially for the conifers but do not significantly for the broadleaved trees. Mean concentrations of TNC, sugars and starch of the whole stem vary by more than twofold among the 12 tree species. These radial, axial and inter-specific variations are the major sources of error in estimating NSC storage at tree or ecosystem levels. This study provides a quantitative assessment of spatial variability in concentration and content of NSC in stem for the Chinese temperate tree species, but the physiological function of stem tissues associated with the spatial distribution of NSC deserves further studies.

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