Trees (2008) 22:205–216
DOI 10.1007/s00468-007-0177-4

ORIGINAL PAPER

Distribution of vessel size, vessel density and xylem conducting efficiency within a crown of silver birch (*Betula pendula*)

Arne Sellin · Andrus Rohejärv · Märt Rahi

Received: 15 March 2007 / Revised: 23 May 2007 / Accepted: 10 September 2007 / Published online: 2 October 2007

Abstract Spatial patterns in vessel diameter, vessel density and xylem conducting efficiency within a crown were examined in closed-canopy trees of silver birch (*Betula pendula*). The variation in anatomical and hydraulic characteristics of branches was considered from three perspectives: vertically within a crown (lower, middle and upper crown), radially along main branches (proximal, middle and distal part), and with respect to branch orders (first-, second- and third-order branches). Hydraulically weighted mean diameter of vessels (D_h) and theoretical specific conductivity of the xylem (k_t) exhibited no vertical trend within the tree crown, whereas leaf-specific conductivity of the xylem (LSC_t) decreased acropetally. Variation in LSC_t was governed by sapwood area to leaf area ratio (Huber value) rather than by changes in xylem anatomy. The acropetal increase in soil-to-leaf conductance (G_T) within the birch canopy is attributable to longer path length within the lower-crown branches and higher hydraulic resistance of the shade leaves. D_h, k_t and LSC_t decreased, while vessel density (VD) and relative area of vessel lumina (VA) increased distally along main branches. A strong negative relationship between vessel diameter and VD implies a trade-off between hydraulic efficiency and mechanical stability of xylem. D_h and VD combined explained 85.4% of the total variation of k_t in the regression model applied to the whole data set. Xylem in fast-growing branches (primary branches) had greater area of vessel lumina per unit cross-sectional area of sapwood, resulting in a positive relationship between branch radial growth rate and k_t. D_h, k_t and LSC_t decreased, whereas VD increased with increasing branch order. This pattern promotes the hydraulic dominance of primary branches over the secondary branches and their dominance over tertiary branches. In this way crown architecture contributes to preferential water flow along the main axes, potentially providing better water supply for the branch apical bud and foliage located in the outer, better-insolated part of the crown.

Keywords Hagen–Poiseuille law · Huber value · Hydraulically weighted diameter · Hydraulic conductivity of xylem · Leaf-specific conductivity · Vessel diameter · Wood anatomy

Introduction

A primary cost for obtaining CO_2 for photosynthesis is the evaporation of water from leaf surfaces. Therefore, plants must continuously optimise their stomatal openness to enable the acquisition of CO_2 on one hand, and to prevent excessive water loss from foliage on the other hand. However, leaf water status depends not only on leaf diffusive conductance and atmospheric evaporative demand but also on leaf water supply. Thus, the ability of plants to supply water to foliage is ultimately associated with their productivity, competitiveness and survival. A number of studies (e.g., Köstner et al. 2002; Macinnis-Ng et al. 2004; Santiago et al. 2004; Renninger et al. 2006) have confirmed a relationship between plant hydraulic properties and

---

Communicated by M. Zwieniecki.

A. Sellin (✉) · A. Rohejärv
Institute of Botany and Ecology, University of Tartu,
Lai 40, 51005 Tartu, Estonia
e-mail: arne.sellin@ut.ee

M. Rahi
Institute of Agricultural and Environmental Sciences,
Estonian University of Life Sciences, Riia 181,
51014 Tartu, Estonia

stomatal conductance, photosynthetic capacity and growth rate. Differences in the competitive capability of conifer and angiosperm species are associated with their respective xylem physiology (Brodribb et al. 2005; Pittermann et al. 2005).

Leaf water supply depends primarily on soil moisture availability, hydraulic conductivity of the vascular tissues, sapwood area to leaf area ratio (Huber value, HV), and driving forces (i.e., water potential gradient) between the soil and leaves. Hydraulic conductivity is not uniform across the whole vascular transport path; we focus on branches that contain a major portion of the stem resistance (Yang and Tyree 1994). Maximum xylem hydraulic conductivity is primarily determined by wood anatomy, particularly on the distribution of conduit inner diameters (Domec et al. 2006; Hacke et al. 2006; Renninger et al. 2006): according to the Hagen–Poiseuille law, conduit hydraulic conductivity is proportional to its diameter raised to the fourth power.

The hydraulic limitation hypothesis (HLH) proposes that the decline of forest productivity with age is a consequence of the loss of whole-plant and leaf-specific hydraulic conductance with tree height resulting from a rise in friction and gravitational potential, and increased investment in non-photosynthetic tissues (Ryan and Yoder 1997; Woodward 2004; Mencuccini et al. 2005). As trees grow taller, their stomatal conductance and photosynthesis wane, and, as a result, the height growth declines. A review of 51 studies confirmed that hydraulic limitation of gas exchange with increasing tree size is a common—but not completely universal—phenomenon (Ryan et al. 2006).

The HLH was proposed to provide a mechanism for gas exchange and growth limitation observable at the whole-tree level. Opposite patterns of hydraulic capacity have often been revealed within crowns of both coniferous and broad-leaved trees: specific hydraulic conductivity of branches (Protz et al. 2000; Lemoine et al. 2002; Jerez et al. 2004; Burgess et al. 2006) or shoot hydraulic conductance increased with branch height in the crown (Aasamaa et al. 2004). Also apparent soil-to-leaf hydraulic conductance (G_T), defined as a current transpiration rate divided by water potential drop from soil to leaves (Meinzer et al. 1995; Wullschleger et al. 1998), has been shown to increase from basal to top branches (Sellin and Kupper 2004, 2005a, 2007a). Thus, qualitatively different phenomena can be observed within a crown. Branch autonomy may promote environmental screening and enhance differential growth by optimising the use of available light resources (Henriksson 2001). Extensive studies on silver birch (*Betula pendula* Roth) suggest that water flow from soil to shade foliage located at the crown base needs to overcome greater resistance than flow to sun foliage at the tree top (Sellin and Kupper 2005a, b). The mean G_T in birch was 1.7 times higher for the upper canopy compared to the lower canopy. In a recent paper, Sellin and Kupper (2006) revealed a pronounced vertical trend in Huber values: at the whole-branch level, HV increased basipetally within the crown. Thus, sapwood to leaf area ratios of the branches cannot account for the differences in G_T at different crown positions in silver birch. On the contrary, the higher HV observed in the lower-crown branches may be considered a means to compensate for differences in xylem conducting capacity between the lower and upper canopy. Hydraulic compensation by adjusting sapwood to leaf area ratio with increasing tree height has been well documented in multiple species (Ryan et al. 2006).

In this paper, we report the results of anatomical studies of branchwood in silver birch and discuss them extensively with respect to data published for other woody species. The main objective of this study was to gain a more detailed understanding of how different parts of crown compare anatomically and hydraulically, and their contribution to the distribution of transpirational fluxes within the canopy. Spatial patterns of anatomical and hydraulic characteristics of xylem within a crown were investigated from three perspectives: vertical variation, variation with distance from trunk, and variation depending on branch order. This paper addresses two specific objectives: first, to establish the variation in vessel diameter and density, the characteristics relevant to both hydraulic and mechanical properties of xylem (Preston et al. 2006), with respect to canopy position, and second, to test the hypothesis that vertical differences in G_T within the crown result from a variation in specific conductivity of xylem. Distribution of hydraulic conductance within the crown is an essential factor driving canopy development during forest maturation. Protz et al. (2000) suggested that reduction in branch sapwood hydraulic conductivity over time limits survival of lower branches, and therefore controls the vertical crown recession in closed-canopy trees. On the other hand, forest management operations may have substantial consequences on plant hydraulics, affecting both growth rate of trees and wood characteristics (Renninger et al. 2006). In addition, this topic concerns the perspectives of our forests; in light of global climate change, hydraulic architecture of trees has considerable implications for forest condition and productivity over longer periods (DeLucia et al. 2000; Maherali and DeLucia 2000).

Materials and methods

Study area

The field studies were carried out in Järvselja Experimental Forest (58°16′N, 27°20′E, elevation 38–40 m) in eastern Estonia. The average annual precipitation is 650 mm; the average temperature is 17.0°C in July and –6.7°C in January. The growth season usually extends 175–180 days, from mid-April to October. The annual global short-wave radiation in the region averages 3,518 MJ m^{-2}, and the annual radiation budget is 2,552 MJ m^{-2} (Russak 1990). Detailed climatic data on the study area were presented by Sellin and Kupper (2005b). The soil is a gleyed pseudo-podsol formed on a loamy till with a large water storage capacity (Niinemets and Kull 2001).

The studies were performed in a mixed stand dominated by silver birch (*B. pendula*) and growing in a *Vaccinium myrtillus* site type. The total basal area is 33.2 m^2 ha^{-1}; the stand composition is: *B. pendula* 46%, *Picea abies* (L.) Karst. 44%, *Pinus sylvestris* L. 8%, and *Populus tremula* L. 2% of the total basal area. The mean (±S.E.) height of the birch trees is 18.1 ± 0.26 m, DBH 10.8 ± 0.21 cm, and live crown ratio is 0.40 ± 0.008.

Sampling of trees

We sampled five birch trees, 22.0–26.0 m in height, from which three branches were sawn off—one branch from the basal, middle and upper third of the crown. The diameter at the base and length of each branch were measured in the laboratory. At each primary branch, we selected one II order and one III order branch inserted in the former. The branch was then dissected and sampled at five points avoiding branch junctions:

Pr	the primary branch at $^1/_{10}$ of its total length;
Mi (or I)	the primary branch at ½ of its total length;
Di	the primary branch at ¾ of its total length;
II	the second-order branch in the middle;
III	the third-order branch in the middle.

Exact sample locations were determined with a tape measure. From each sampling location a branch segment 3–4 cm in length was cut, the conducting xylem of which was identified by perfusing an aqueous solution of methylene blue (0.5% w/v) through the specimens by means of a vacuum pump. The sapwood cross-sectional area, foliage area situated acropetally in relation to the wood specimens, and Huber value (sapwood area to leaf area ratio, HV) were determined as described in Sellin and Kupper (2006). The wood specimens were dried at 80°C for at least 48 h and preserved for anatomical studies.

Wood anatomy and xylem conducting efficiency

The dried wood samples were boiled in distilled water for about 2 h to soften the wood and thin slices were cut with a razor blade. Cross-sectional surfaces of the slices were coated with gold in a sputter coating system and examined with a BS-301 scanning electron microscope (Tesla, Czech Republic). Three digital images (one at 300× and two at 500× magnification) covering one to seven outermost growth rings were taken of each wood specimen and the images analysed with a Scion Image (release Beta 4.0.2; Scion Corporation, USA) software. From the 500× images we measured minor and major vessel inner diameters (µm), estimated as lengths of the minor and major axes of the best-fitting ellipse, cross-sectional area of vessel lumina (µm^2), and vessel density (mm^{-2}). For most images the number of measured vessels ranged 120–170. Width of the growth rings (mm) was determined at the 300× magnification. Mean vessel diameter (D) was calculated as follows:

$$D = \frac{\sum_{i=1}^{n} \sqrt{a_i b_i}}{n}, \tag{1}$$

where a_i and b_i are minor and major perpendicular lumen diameters of the ith vessel, and n is the number of the measured vessels. Vessel diameters were analysed for their frequency in 5 µm diameter classes (10.0–14.9, 15.0–19.9 µm, etc.) and for their relative contribution of each diameter class to the sum of all the conduits raised to the fourth power. On the basis of the vessel contribution to hydraulic conductance, we calculated a hydraulically weighted mean diameter (D_h) for each sample (Sperry et al. 1994; Kolb and Sperry 1999):

$$D_h = \frac{\sum_{i=1}^{n} \left(\sqrt{a_i b_i}\right)^5}{\sum_{i=1}^{n} \left(\sqrt{a_i b_i}\right)^4}. \tag{2}$$

To characterise the xylem conducting efficiency expressed per sapwood transverse area, a theoretical specific conductivity of the xylem (k_t, kg m^{-1} s^{-1} MPa^{-1}; sensu Tyree and Ewers 1991) was used. In fact, k_t indicates theoretical lumen conductance, omitting the resistance between vessels. It was computed according to Lewis and Boose (1995):

$$k_t = \frac{\pi \rho}{64 \eta A_x} \sum_{i=1}^{n} \frac{a_i^3 b_i^3}{a_i^2 + b_i^2}, \tag{3}$$

where ρ is the density of water (kg m^{-3}), A_x is the sampled cross-sectional area of xylem (m^2), and η is the dynamic viscosity of water (MPa s). Theoretical leaf-specific conductivity of the xylem (LSC_t; kg m^{-1} s^{-1} MPa^{-1}) was calculated as the product of k_t and HV. The theoretical hydraulic characteristics were calculated for a reference temperature of 20°C.

Data analysis

Data analysis was carried out using Statistica, Version 6.0 (StatSoft, USA). In the analysis with respect to branch orders, we compared samples from middle part of the branches, thus the primary branches were represented by sample location Mi (i.e., Mi = I). To analyse the effects of branch position in the crown (lower, middle and upper crown), sample radial location along main branches (sample locations Pr, Mi and Di), branch order (sample locations I, II and III), as well as other branch variables on anatomical and hydraulic characteristics, an analysis of covariance (ANCOVA) was performed using the general linear models module. Branch position, branch order, and sample location were treated as fixed factors, while branch length, branch diameter measured under the bark (i.e., diameter of the xylem cylinder) at sampling points and mean width of the growth rings were treated as covariates. The covariates were included in the models to reveal possible effects resulting from variation in branch size and growth rate, which may affect the relationships of the categorical independents to the dependent variables. During the analysis, the models were modified by a step-by-step removal of insignificant covariates. Type IV sums of squares were used in the calculations. Normality and homogeneity of variances were checked using the Kolmogorov–Smirnov *D*-statistic and the Levene test, respectively. When appropriate, logarithmic (LSC_t) or square root transformations (k_t, vessel density) were applied to the data. Post hoc mean comparisons were conducted using the Tukey HSD test. Shape and strength of the bivariate relationships between the studied characteristics and independent variables were analysed by applying linear or non-linear regression procedures based on the least-squares method.

Results

Vertical variation

The lower, middle and upper thirds of the crown did not vary in vessel lumen diameters (*D*) in branchwood; *D* for the three canopy layers ranged from 22.6 to 23.3 μm. Diameter of individual vessels varied between 10 and 60 μm, the modal diameter class (23.6–25.3% of all vessels) for all three canopy positions was 15–20 μm. ANCOVA revealed a significant (Table 1, $P = 0.025$) effect of crown position on hydraulically weighted mean diameter (D_h) of vessels. However, the Tukey test revealed no clear vertical trend within the canopy (Fig. 1a). Vessel density (VD) ranged from 122 to 702 mm^{-2} and vessel lumina covered 8.4–26.8% of the sapwood cross-sectional area in the whole data set. Neither VD nor relative area of vessel lumina (VA) depended on branch height within a crown as far as covariates were included in the ANCOVA model (Table 1). After the covariates were discarded, branch position turned out to be a significant ($P < 0.05$) factor: VD increased acropetally within the crown (Fig. 1 b). Judging by the mean squares, mean width of the growth rings (*W*) accounted for 22.6% of the variation in VD. In the analysis of covariance, the influence of branch position had been hidden by effects of *W*, because width of the branch growth rings varied with canopy layers ($P < 0.001$), and *W* and VD were positively correlated (Pearson's correlation coefficient $r = 0.195$, $P < 0.05$). Higher branch radial growth rate was also associated with larger proportion of vessels to the total cross-sectional area of xylem (Pearson $r = 0.479$, $P < 0.001$).

Table 1 Results of ANCOVA for the effects of branch position and other factors on anatomical and hydraulic characteristics of the branchwood (analyses across all sampling locations and branch orders)

Dependent variable	Factor/covariate	*P*
Vessel density, VD (mm^{-2})	Branch position	0.095
	Sample location	<0.001
	Growth rings' width	<0.001
	Branch length	0.012
Vessel relative area, VA (%)	Branch position	0.452
	Sample location	0.037
	Growth rings' width	<0.001
Mean hydraulic diameter, D_h (μm)	Branch position	0.025
	Sample location	<0.001
	Branch diameter	<0.001
Specific conductivity, k_t (kg m^{-1} s^{-1} MPa^{-1})	Branch position	0.453
	Sample location	<0.001
	Growth rings' width	<0.001
	Branch diameter	<0.001
Leaf-specific conductivity, LSC_t (kg m^{-1} s^{-1} MPa^{-1})	Branch position	<0.001
	Sample location	<0.001
	Branch diameter	<0.001

P statistical significance

Specific conductivity of xylem (k_t) did not vary with branch position (Table 1, Fig. 2a), whereas leaf-specific conductivity (LSC_t) exhibited a decreasing trend with increasing branch height (Fig. 2b). Variation in k_t can be divided into two components—mean hydraulic diameter and vessel density. To estimate combined effects of D_h and VD on k_t, we applied non-linear regression analysis and developed an empirical model. The best fit resulted from the following multiplicative function (Fig. 3):

$$k_t = -12.98 + D_h^{0.580}\mathrm{VD}^{0.143}, \quad n = 150, \quad R^2 = 0.854, \ \mathrm{S.E.} = 0.540, \tag{4}$$

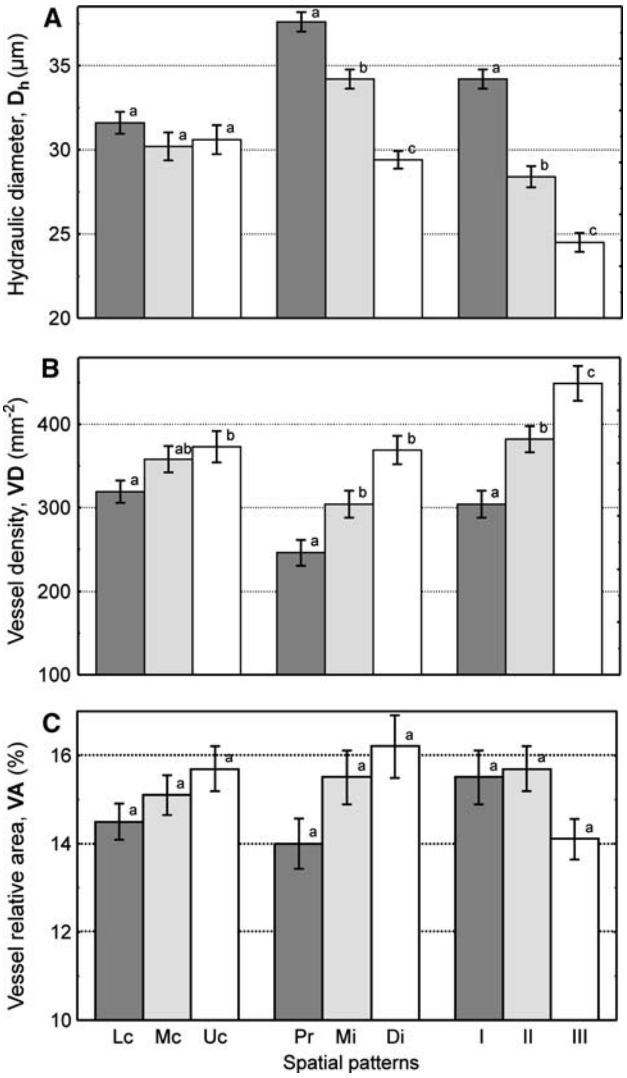

Fig. 1 Spatial variation of mean hydraulic diameter of vessels (**a**), vessel density (**b**) and relative area of vessel lumina (**c**) within a crown: vertical variation (*Lc*, *Mc*, *Uc*—lower, middle and upper crown, respectively); radial variation (*Pr*, *Mi*, *Di*—branch proximal, middle and distal parts, respectively; variation depending on branch order (*I*, *II*, *III*—first-, second- and third-order branches, respectively). The *bars* indicate ±SE of the means; *different letters* at the columns denote statistically significant ($P < 0.05$) differences

where all three parameters were statistically highly significant ($P < 0.001$).

Specific conductivity of xylem also depended significantly (Table 1) on mean width of the growth rings; higher radial growth rate of branches was associated with higher hydraulic conductivity of xylem (Pearson $r = 0.358$, $P < 0.001$). The data analysis revealed a significant effect ($P < 0.001$) of the branch diameter (d_b), measured at sampling points, on VD, VA as well as k_t. D_h, k_t and LSC_t increased, and VD declined with increasing d_b (Fig. 4). Thus, D_h and VD exhibited opposite trends with branch diameter, resulting from a strong negative relationship between vessel size and vessel density (Fig. 5).

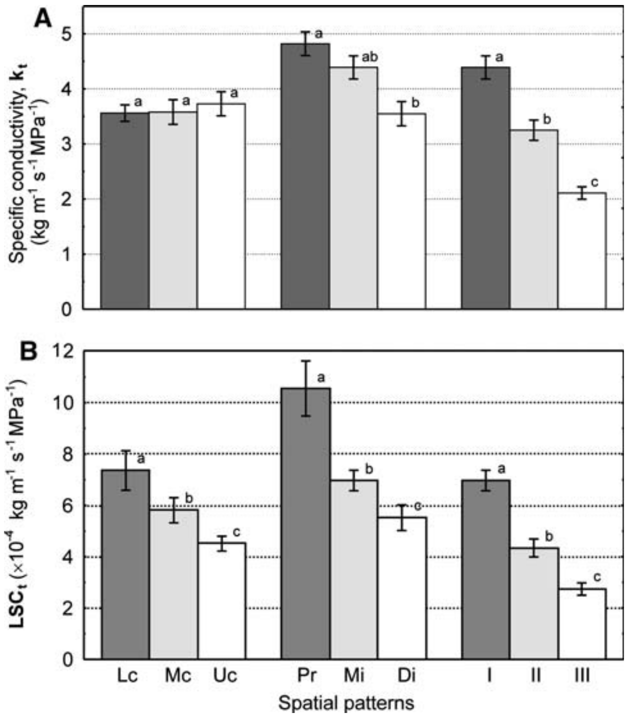

Fig. 2 Spatial variation of theoretical values of specific conductivity (**a**) and leaf-specific conductivity of xylem (**b**) within a crown: vertical variation (*Lc*, *Mc*, *Uc*—lower, middle and upper crown, respectively); radial variation (*Pr*, *Mi*, *Di*—branch proximal, middle and distal parts, respectively; variation depending on branch order (*I*, *II*, *III*—first-, second- and third-order branches, respectively). The *bars* indicate ±SE of the means; *different letters* at the columns denote statistically significant ($P < 0.05$) differences

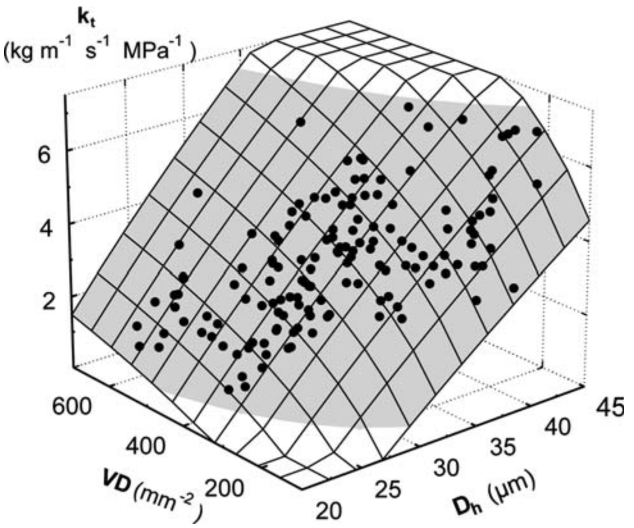

Fig. 3 Theoretical specific conductivity of xylem (k_t) as a function of mean hydraulic diameter of vessels (D_h) and vessel density (VD)

The stronger relationship between d_b and LSC_t compared to k_t (Fig. 4b) resulted from Huber values largely

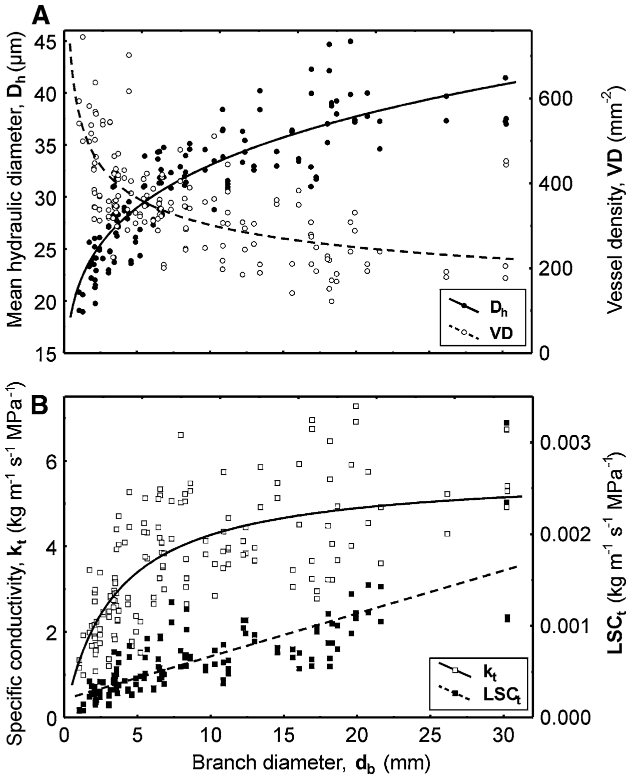

Fig. 4 Branch diameter measured at sampling point versus (**a**) mean hydraulic diameter of vessels ($R^2 = 0.765$, $P < 0.001$) and vessel density ($R^2 = 0.467$, $P < 0.001$), (**b**) theoretical specific conductivity ($R^2 = 0.513$, $P < 0.001$) and leaf-specific conductivity of xylem ($R^2 = 0.618$, $P < 0.001$)

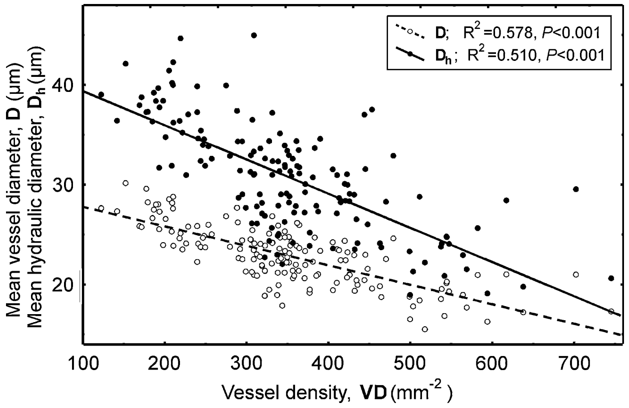

Fig. 5 Reverse relationship between vessel diameter and vessel density

determined by branch diameter (Sellin and Kupper 2006). The branches of silver birch sampled in the present study contained heartwood in marginal quantities, the non-functional region in the centre of branches mostly comprised up to 4% of their total cross-sectional area (Fig. 6). Only in very thin distal parts of the branches, the non-functional area extended up to 8% due to relatively big proportion of the pith.

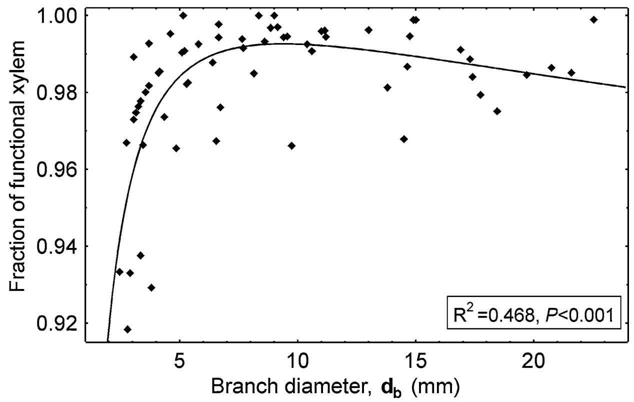

Fig. 6 Branch diameter versus fraction of functional xylem of the branch cross-sectional area measured under bark

Variation with distance from trunk

The distribution of inner diameters of the vessels varied in main branches with distance from the trunk (Fig. 7). In the proximal and middle parts of the branches, the frequency of vessels decreased smoothly from the 10–15 to 55–60 µm diameter class. However, the largest contribution to water transport in the branch base were from the 35–45 µm vessels and in the branch centre from the 30–40 µm diameter vessels. In the distal part of the branch, the modal size class (24.0% of all vessels) was unexpectedly wider, 20–25 µm, while the vessel frequency decreased steeply with increasing diameter (Fig. 7c); most of the xylem water transfer was attributable to the vessels 25–35 µm in diameter.

Distance from the trunk had a significant effect on vessel hydraulic diameter, vessel density and vessel relative area (Table 2). D_h decreased from an average of 37.6 µm at the branch base to 29.4 µm in the distal part of the branches, while VD and VA, in contrast, increased in branch distal direction (Fig. 1). However, according to the Tukey test, the differences in the mean VA along the main branches were insignificant. Neither k_t nor LSC_t depended on distance from the trunk when covariates were included in the ANCOVA model (Table 2). After the covariates had been removed, the effect of sample location on the theoretical hydraulic characteristics of xylem became highly significant ($P < 0.001$). The covariates, d_b in particular, explained the major part of the variation in both characteristics (Table 2, Fig. 4b), accounted for the factors included in the final models. Thus, the decrease in k_t and LSC_t in the branch distal direction (Fig. 2) is primarily associated with the branch taper.

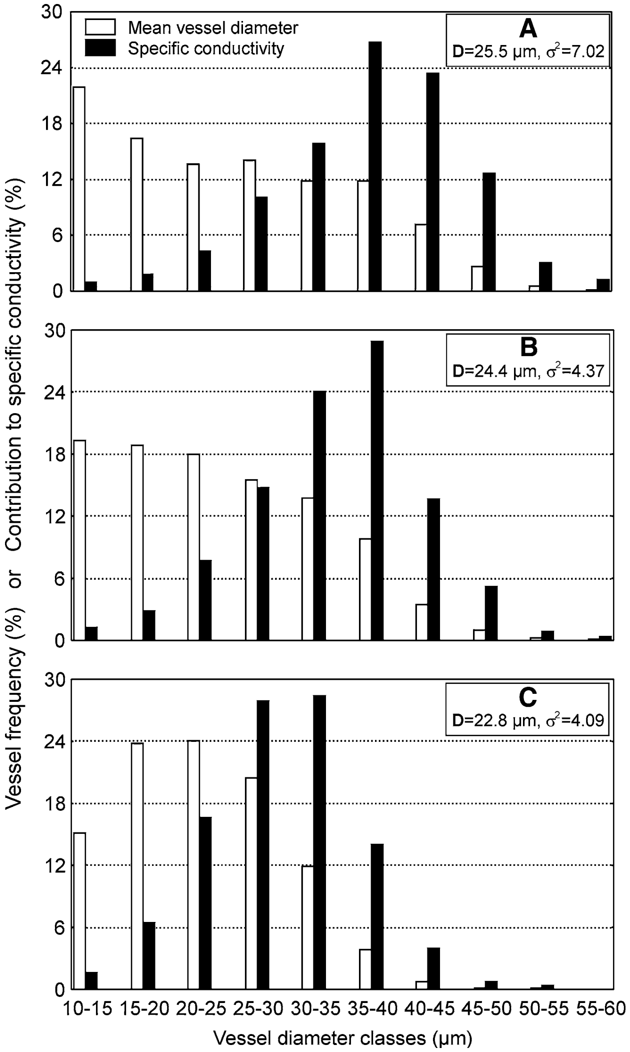

Fig. 7 Frequency distributions of vessel lumen diameters and the contribution of each diameter class to hydraulic conductivity of xylem in the proximal (**a**), middle (**b**) and distal (**c**) parts of the branches. Mean vessel diameter (*D*) in the distal part differed from that both in the middle ($P < 0.05$) and proximal parts ($P < 0.001$) of the branch; the proximal and middle parts did not differ in *D*. σ^2, variance

Variation with branch order

Maximum lumen diameter of vessels extended up to 60, 50 and 45 µm in the first-, second- and third-order branches, respectively (Fig. 8). The modal diameter class was 10–15 µm for the main branches and 15–20 µm for higher-order branches. The largest contribution to hydraulic conductivity was made by vessels of 35–40, 25–30 and 20–25 µm in the I, II and III order branches, respectively. D_h depended significantly ($P = 0.011$) on branching hierarchy, declining steeply with increasing branch order (Fig. 1a). Vessel density and vessel relative area were independent of branch order when covariates were included in the ANCOVA model (Table 3). The effect of branch order on VD became highly significant ($P < 0.001$) after the removal of the covariates. Both k_t and LSC_t decreased significantly ($P < 0.01$) with increasing branch order (Fig. 2). The highest specific conductivity of xylem (5.15 ± 0.405 kg m^{-1} s^{-1} MPa^{-1}; mean ± SE) was observed in the proximal part of the main branches situated in the midcrown and the highest leaf-specific conductivity ($1.36 \times 10^{-3} \pm 0.26 \times 10^{-3}$ kg m^{-1} s^{-1} MPa^{-1}) in the proximal part of the main branches situated in the lower crown. Both hydraulic characteristics were lowest in the tertiary branches: $k_t = 2.11 \pm 0.112$ kg m^{-1} s^{-1} MPa^{-1}; $LSC_t = 2.74 \times 10^{-4} \pm 0.24 \times 10^{-4}$ kg m^{-1} s^{-1} MPa^{-1}.

Table 2 Results of ANCOVA for the effects of the distance from trunk and other factors on anatomical and hydraulic characteristics in main branches (sampling locations Pr, Mi and Di)

Dependent variable	Factor/covariate	*P*
Vessel density, VD (mm^{-2})	Branch position	0.258
	Distance from trunk	<0.001
	Growth rings' width	<0.001
Vessel relative area, VA (%)	Branch position	0.166
	Distance from trunk	0.039
	Growth rings' width	<0.001
Mean hydraulic diameter, D_h (µm)	Branch position	0.639
	Distance from trunk	0.008
	Branch diameter	0.003
Specific conductivity, k_t (kg m^{-1} s^{-1} MPa^{-1})	Branch position	0.383
	Distance from trunk	0.541
	Growth rings' width	0.005
	Branch diameter	0.005
Leaf-specific conductivity, LSC_t (kg m^{-1} s^{-1} MPa^{-1})	Branch position	0.015
	Distance from trunk	0.288
	Branch diameter	<0.001

P statistical significance

Discussion

Vertical patterns within a crown

Mean diameter of vessel lumina in branchwood of *B. pendula* for three canopy layers was uniform, varying merely from 22.6 to 23.3 µm, coinciding with the mean value (23.0 µm) based on both branch- and stemwood samples analysed by Hellberg and Carcaillet (2003). As a consequence of the lack of variation in *D*, neither D_h nor k_t exhibited a vertical trend within the crown of silver birch (Figs. 1a, 2a). Thus, the substantial differences in the apparent soil-to-leaf conductance (G_T) observed between different crown layers (Sellin and Kupper 2005a, b) cannot result from variation of conducting efficiency of the

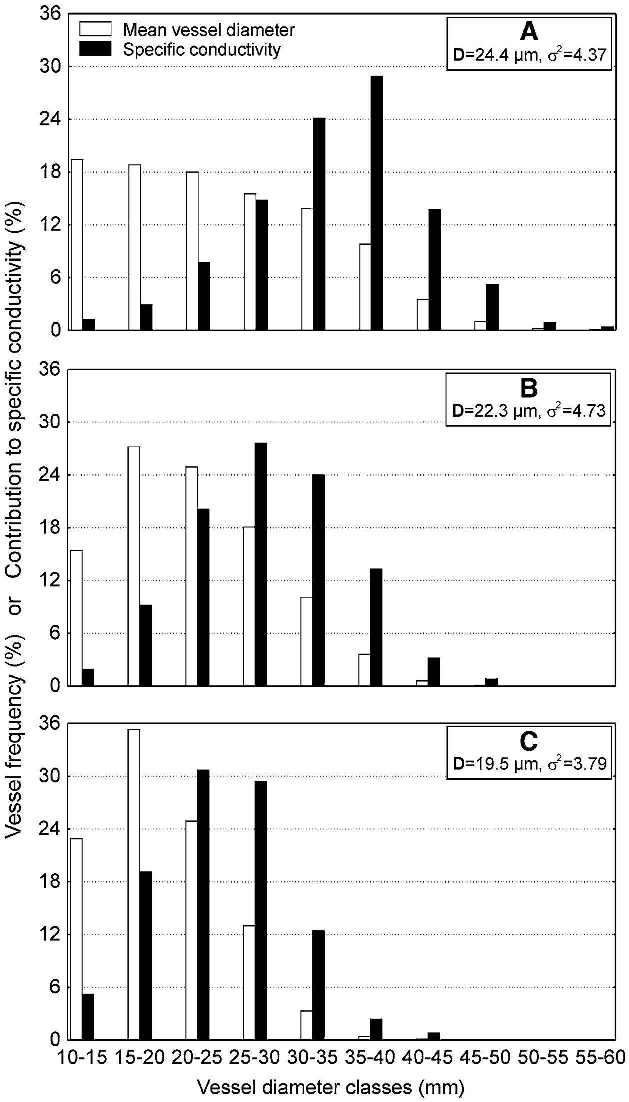

Fig. 8 Frequency distributions of vessel lumen diameters and the contribution of each diameter class to hydraulic conductivity of xylem in the first- (**a**), second- (**b**) and third-order branches (**c**). All three branch orders differed ($P < 0.01$) from each other in mean vessel diameter (D). σ^2, variance

branchwood (i.e., vessel size distribution). As Huber values decreased acropetally within a birch canopy (Sellin and Kupper 2006), $\mathrm{LSC_t}$ even increased in the direction of crown base (Fig. 2b). Hence, $\mathrm{LSC_t}$ is governed mainly by HV (Pearson $r = 0.829$, $P < 0.001$), suggesting that changes in carbon allocation patterns, rather than changes in xylem anatomy, drive the adjustment of leaf-specific hydraulic efficiency within crowns of silver birches. This is not surprising, as both intra- and interspecific studies have shown that regulation of HV is a primary means for maintaining a balance between gas- and liquid-phase conductances in response to environmental variation (Mencuccini and Grace 1995; DeLucia et al. 2000; Maherali and DeLucia 2000; Bucci et al. 2005; Edwards 2006). However, Protz et al. (2000) published contrary results on *Pinus contorta* Dougl. ex Loud., suggesting that the principle hydraulic adjustment within a crown involves changes in sapwood conductivity rather than in HV.

The results do not support our hypothesis on reasons for vertical variation of G_T in silver birch, and contradict several other studies (e.g., Lemoine et al. 2002; Aasamaa et al. 2004; Jerez et al. 2004; Burgess et al. 2006) establishing acropetal increase in both specific and leaf-specific hydraulic conductivity of branchwood within tree crowns. The differences in G_T with respect to crown position in silver birch probably ensued from two factors. First, the length of the water transport path within branches was not even throughout the crown. In fact, the lower-crown main branches were on average 10.5% longer than the upper-crown branches, although the difference was statistically insignificant because of the high variation in branch length within the crown layer (Sellin and Kupper 2006). Warren and Adams (2000) confirmed a strong ($R^2 = 0.842$) negative exponential relationship between branch length and G_T in *Pinus pinaster* Ait. In *Pinus sylvestris*, whole-branch hydraulic conductance (G_B) was related positively to branch diameter and negatively to branch vertical position (Mencuccini and Grace 1996). This resulted in lower G_B for the branches at the crown bottom than branches of the same diameter at the treetop.

One must take into account that the older and longer branches situated at the base of the crown bear considerably longer side branches and contain more nodes/branch junctions, i.e., regions with low xylem conductivity (Rust and Hüttl 1999; Tyree and Zimmermann 2002; Schulte and Brooks 2003). In *Fraxinus excelsior* L., both whole-branch hydraulic resistance ($R_\mathrm{B} = 1/G_\mathrm{B}$) and leaf-specific resistance increased with increasing distance from the branch to the treetop (see Fig. 7 in Cochard et al. 1997). The development of secondary axes containing short internodes was primarily responsible for the increase in R_B. Growing hydraulic constraints on leaf water supply resulting from longer path length within branches have been proved in several tree species using a carbon isotope discrimination analysis (Warren and Adams 2000; Brendel et al. 2003; Samuelson et al. 2003).

The second reason for the spatial patterns of G_T within a crown of silver birch might be leaf hydraulic conductance, which depends largely on light availability. Leaves account for a majority (50–90%) of the hydraulic resistance to water flow through shoots of trees (Yang and Tyree 1994; Nardini and Salleo 2000; Nardini 2001), and thus form a substantial part of the whole resistance of the water transport pathway from soil to leaves (Sack et al. 2003; Sack and Holbrook 2006; Sellin and Kupper 2007a). However, not in all cases, majority of the total hydraulic resistance occurs at the leaf level (Gyenge et al. 2005).

Hydraulic conductance of sun leaves in a number of temperate woody species has been found to be significantly higher than that of shade leaves (Sack et al. 2003; Sellin and Kupper 2007a, b). The same trend holds true for interspecific comparisons: maximum leaf hydraulic conductance in both shade-growing pteridophytes and angiosperms was much lower than that in the sun-dwelling species (Brodribb and Holbrook 2004).

Patterns with respect to the distance from trunk

The anatomical as well as hydraulic characteristics exhibited pronounced trends with respect to the distance from the trunk: D_h, k_t and LSC_t decreased, whereas VD and VA increased in the branch distal direction (Figs. 1, 2). A similar trend has been described for other woody species: contribution of the branch segments to the whole-branch resistance increased exponentially from the base to the tip of the branch (Yang and Tyree 1993; Mencuccini and Grace 1996). As both hydraulic characteristics in silver birch depended on the branch diameter measured under bark (Fig. 4b), their trends with distance from the trunk were related largely to the branch taper (Table 2). To provide adequate water supply to foliage, xylem conductivity must increase with increasing d_b, because branches of bigger diameter were longer and sustained larger transpiring area. Therefore, a positive relationship between stem or branch diameter and hydraulic conductivity is a universal principle recognised in dozens of species from different systematic groups (Coyea and Margolis 1992; Yang and Tyree 1994; Mencuccini and Grace 1996; Maherali and DeLucia 2000; Tyree and Zimmermann 2002).

However, the spatial patterns observed in this study cannot be explained merely with long-distance water transport, because crown architecture needs to satisfy both hydraulic and mechanical demands. The increase in VD and VA in the branch distal direction (i.e., increasing proportion of fibres in the proximal direction) provides greater mechanical strength to resist the greater physical load befalling to the branch base due to the longer force arm and its greater weight including the cumulative weight of laterals and leaves. The low vessel density in the branch bases is functionally balanced by their high conducting efficiency, i.e., by large D_h (Figs. 1a, b). Thus, the strong negative relationship revealed between vessel diameter and density (Fig. 5) probably implies a basic trade-off between hydraulic efficiency and mechanical stability of xylem. A study in congeneric chaparral species (Wagner et al. 1998) has confirmed substantial impact of the size and frequency of vessels within stems on their mechanical properties. Vessel lumen relative area could even override the importance of variation in fibre anatomy and lignification.

In silver birch, D_h and VD combined explained 85.4% of the total variation in specific conductivity of xylem in the whole data set. The negative relationship between vessel diameter and density seems to be a more general feature of xylem anatomy, reflecting optimisation of wood structure to meet diverse functional demands (mechanical support, water transport, respiration of living tissues, etc.) at both ecological and evolutionary scales. The numerical data published by Hellberg and Carcaillet (2003) manifest a close correlation ($R^2 = 0.974$, $P < 0.05$) between D and VD across four European species of *Betula*. The opposite trends in D and VD have also been observed in other studies both within (Mokany et al. 2003) and across species (Vander Willigen et al. 2000; Preston et al. 2006). As a result of this negative relationship, mean VA varied within a narrow range (14.0–16.2%) along main branches of silver birch. VA was determined by VD rather than by D, unlike that published by Wagner et al. (1998) for chaparral shrubs. In *Eucalyptus camaldulensis* (Dehn.), shifts in both VD and D were responsible for the variation in VA as a result of environmental changes (Thomas et al. 2004).

Patterns with branch orders

Four of the five variables depended significantly on branch ranking: D_h, k_t and LSC_t decreased, whereas VD increased with increasing branch orders (Figs. 1, 2). Primary branches had on average 2.1-fold higher k_t compared with third-order branches, primarily due to differences in the frequency distribution of vessel diameter (Fig. 8). Thus, the water transport capacity declined from main branches to branches of higher orders. The pronounced hydraulic hierarchy revealed among the branches may have strong implications on distribution of the transpiration stream within a crown. This pattern promotes the hydraulic dominance of primary branches over secondary branches and their dominance over the tertiary branches; these results are consistent with the hydraulic segmentation hypothesis (Tyree and Zimmermann 2002). Thus, differentiation of branches by hydraulic capacity with branch orders may be interpreted as a mechanism by which crown architecture contributes to preferential water flow along the main axes, potentially providing better water supply to the branch apical bud and foliage located in the outer, better-insolated part of the crown.

Specific conductivity of xylem in silver birch depended significantly (Tables 1, 2, 3) on growth ring width (W): the greater the branch radial growth rate, the higher the water conducting efficiency of the xylem to be formed. Positive correlation between xylem hydraulic conductivity or conduit diameter and stem growth rate has been proved both in gymnosperm and in angiosperm species (Pothier et al.

Table 3 Results of ANCOVA for the effects of branch order and other factors on anatomical and hydraulic characteristics of the branchwood (sampling locations I, II and III)

Dependent variable	Factor/covariate	*P*
Vessel density, VD (mm^{-2})	Branch position	0.260
	Branch order	0.157
	Branch diameter	<0.001
Vessel relative area, VA (%)	Branch position	0.863
	Branch order	0.153
	Growth rings' width	0.007
Mean hydraulic diameter, D_h (μm)	Branch position	0.016
	Branch order	0.011
	Growth rings' width	0.035
	Branch diameter	<0.001
Specific conductivity, k_t (kg m^{-1} s^{-1} MPa^{-1})	Branch position	0.161
	Branch order	0.002
	Growth rings' width	<0.001
	Branch diameter	<0.001
Leaf-specific conductivity, LSC$_t$ (kg m^{-1} s^{-1} MPa^{-1})	Branch position	0.005
	Branch order	0.006
	Branch diameter	<0.001

P statistical significance

1989a; Medhurst and Beadle 2002; Reich et al. 2003; Cochard et al. 2005). Because neither *D* nor D_h was correlated with *W* in silver birch, higher k_t observed in the faster-growing branches/zones (primary branches, branch middle parts) is rather attributable to larger relative area of vessel lumina. In the analysis across different species with diverse wood anatomy (coniferous, diffuse- and ring-porous trees) an opposite trend has been observed (McCulloh and Sperry 2005). According to the results of McCulloh and Sperry (2005), the trend toward greater hydraulic efficiency in trees is associated with a decrease in sapwood area occupied by xylem conduits. In the case of *B. pendula*, a heteroxylous angiosperm species, VA was statistically independent of vessel diameter (Pearson $r = 0.098$, n.s.), in contrast with homoxylous wood of conifers, in which the percentage of sapwood area occupied by tracheid lumina is proportional to tracheids' mean diameter (Pothier et al. 1989b).

In terms of the mean LSC$_t$, the primary and third-order branches differed by a factor of 2.5, attributable to the variation in both HV and k_t. As HV in silver birch also exhibited a trend to decrease with increasing branch orders (see Fig. 1b in Sellin and Kupper 2006), a positive correlation was revealed between k_t and HV. This is contrary to the data on hydraulic properties across multiple tree species, different growth conditions or seasons (Vander Willigen et al. 2000; Macinnis-Ng et al. 2004), demonstrating reverse trends in the two characteristics. In this way, low specific conductivity of xylem is balanced by higher Huber values. This is regarded as homeostatic response to increasing hydraulic constrictions to maintain a reasonable stomatal opening across diverse habitats by adjusting sapwood area to leaf area ratio. The apparent contradiction between our data and those referred to above likely results from differences in plant requirements to meet various environments, in species growth strategies or sampling schemes. Hence, the relation of the trends in xylem specific conductivity and Huber value depends on scale (i.e., intra- vs. interspecific study, single versus multiple contrasting habitats, single vs. multiple sampling points within individuals).

To summarise, the differences in soil-to-leaf hydraulic conductance in *B. pendula* between the upper- and lower-canopy foliage did not result from the vertical variation in hydraulic efficiency of branchwood. The acropetal increase in G_T within a birch canopy is rather attributable to the longer path length within the lower-crown branches and higher hydraulic resistance of the shade leaves.

Acknowledgments This study was supported by grant No. 6617 from the Estonian Science Foundation. We are grateful to Tiit Teder for assistance at statistical data analysis and to Robert Szava-Kovats for language correction.

References

Aasamaa K, Sõber A, Hartung W, Niinemets Ü (2004) Drought acclimation of two deciduous tree species of different layers in a temperate forest canopy. Trees 18:93–101

Brendel O, Handley L, Griffiths H (2003) The δ^{13}C of Scots pine (*Pinus sylvestris* L.) needles: spatial and temporal variations. Ann For Sci 60:97–104

Brodribb TJ, Holbrook NM (2004) Stomatal protection against hydraulic failure: a comparison of coexisting ferns and angiosperms. New Phytol 162:663–670

Brodribb TJ, Holbrook NM, Hill RS (2005) Seedling growth in conifers and angiosperms: impacts of contrasting xylem structure. Austr J Bot 53:749–755

Bucci SJ, Goldstein G, Meinzer FC, Franco AC, Campanello P, Scholz FG (2005) Mechanisms contributing to seasonal homeostasis of minimum leaf water potential and predawn disequilibrium between soil and plant water potential in Neotropical savanna trees. Trees 19:296–304

Burgess SSO, Pittermann J, Dawson TE (2006) Hydraulic efficiency and safety of branch xylem increases with height in *Sequoia sempervirens* (D. Don) crowns. Plant Cell Environ 29:229–239

Cochard H, Peiffer M, Le Gall K, Granier A (1997) Developmental control of xylem hydraulic resistances and vulnerability to embolism in *Fraxinus excelsior* L.: impacts on water relations. J Exp Bot 48:655–663

Cochard H, Coste S, Chanson B, Guehl JM, Nicolini E (2005) Hydraulic architecture correlates with bud organogenesis and primary shoot growth in beech (*Fagus sylvatica*). Tree Physiol 25:1545–1552

Coyea MR, Margolis HA (1992) Factors affecting the relationship between sapwood area and leaf area of balsam fir. Can J For Res 22:1684–1693

DeLucia EH, Maherali H, Carey EV (2000) Climate-driven changes in biomass allocation in pines. Global Change Biol 6:587–593

Domec J-C, Meinzer FC, Gartner BL, Woodruff D (2006) Transpiration-induced axial and radial tension gradients in trunks of Douglas-fir trees. Tree Physiol 26:275–284

Edwards EJ (2006) Correlated evolution of stem and leaf hydraulic traits in *Pereskia* (Cactaceae). New Phytol 172:479–489

Gyenge JE, Fernández ME, Dalla Salda G, Schlichter T (2005) Leaf and whole-plant water relations of the Patagonian conifer *Austrocedrus chilensis* (D. Don) Pic. Ser. et Bizzarri: implications on its drought resistance capacity. Ann For Sci 62:297–302

Hacke UG, Sperry JS, Wheeler JK, Castro L (2006) Scaling of angiosperm xylem structure with safety and efficiency. Tree Physiol 26:689–701

Hellberg E, Carcaillet C (2003) Wood anatomy of West European *Betula*: Quantitative descriptions and applications for routine identification in paleoecological studies. Ecoscience 10:370–379

Henriksson J (2001) Differential shading of branches or whole trees: survival, growth, and reproduction. Oecologia 126:482–486

Jerez M, Dean TJ, Roberts SD, Evans DL (2004) Patterns of branch permeability with crown depth among loblolly pine families differing in growth rate and crown size. Trees 18:145–150

Kolb KJ, Sperry JS (1999) Differences in drought adaptation between subspecies of sagebrush (*Artemisia tridentata*). Ecology 80:2373–2384

Köstner B, Falge E, Tenhunen JD (2002) Age-related effects on leaf area/sapwood area relationships, canopy transpiration and carbon gain of Norway spruce stands (*Picea abies*) in the Fichtelgebirge, Germany. Tree Physiol 22:567–574

Lemoine D, Cochard H, Granier A (2002) Within crown variation in hydraulic architecture in beech (*Fagus sylvatica* L): evidence for a stomatal control of xylem embolism. Ann For Sci 59:19–27

Lewis AM, Boose ER (1995) Estimating volume flow rates through xylem conduits. Amer J Bot 82:1112–1116

Macinnis-Ng C, McClenahan K, Eamus D (2004) Convergence in hydraulic architecture, water relations and primary productivity amongst habitats and across seasons in Sydney. Funct Plant Biol 31: 429–439

Maherali H, DeLucia EH (2000) Interactive effects of elevated CO_2 and temperature on water transport in ponderosa pine. Am J Bot 87:243–249

McCulloh KA, Sperry JS (2005) Patterns in hydraulic architecture and their implications for transport efficiency. Tree Physiol 25:257–267

Medhurst JL, Beadle CL (2002) Sapwood hydraulic conductivity and leaf area – sapwood area relationships following thinning of a *Eucalyptus nitens* plantation. Plant Cell Environ 25:1011–1019

Meinzer FC, Goldstein G, Jackson P, Holbrook NM, Gutiérrez MV, Cavelier J (1995) Environmental and physiological regulation of transpiration in tropical forest gap species: the influence of boundary layer and hydraulic properties. Oecologia 101:514–522

Mencuccini M, Grace J (1995) Climate influences the leaf area/sapwood area ratio in Scots pine. Tree Physiol 15:1–10

Mencuccini M, Grace J (1996) Developmental patterns of aboveground hydraulic conductance in a Scots pine (*Pinus sylvestris* L.) age sequence. Plant Cell Environ 19:939–948

Mencuccini M, Martinez-Vilalta J, Vanderklein D, Hamid HA, Korakaki E, Lee S, Michiels B (2005) Size-mediated ageing reduces vigour in trees. Ecol Lett 8:1183–1190

Mokany K, McMurtrie RE, Atwell BJ, Keith H (2003) Interaction between sapwood and foliage area in alpine ash (*Eucalyptus delegatensis*) trees of different heights. Tree Physiol 23:949–958

Nardini A (2001) Are sclerophylls and malacophylls hydraulically different? Biol Plant 44:239–245

Nardini A. Salleo S (2000) Limitation of stomatal conductance by hydraulic traits: sensing or preventing xylem cavitation? Trees 15:14–24

Niinemets Ü, Kull O (2001) Sensitivity of photosynthetic electron transport to photoinhibition in a temperate deciduous forest canopy: photosystem II center openness, non-radiative energy dissipation and excess irradiance under field conditions. Tree Physiol 21:899–914

Pittermann J, Sperry JS, Hacke UG, Wheeler JK, Sikkema EH (2005) Torus-margo pits help conifers compete with angiosperms. Science 310:1924

Pothier D, Margolis HA, Waring RH (1989a) Patterns of change of saturated sapwood permeability and sapwood conductance with stand development. Can J For Res 19:432–439

Pothier D, Margolis HA, Poliquin J, Waring RH (1989b) Relation between the permeability and the anatomy of jack pine sapwood with stand development. Can J For Res 19:1564–1570

Preston KA, Cornwell WK, DeNoyer JL (2006) Wood density and vessel traits as distinct correlates of ecological strategy in 51 California coast range angiosperms. New Phytol 170:807–818

Protz CG, Silins U, Lieffers VJ (2000) Reduction in branch sapwood hydraulic permeability as a factor limiting survival of lower branches of lodgepole pine. Can J For Res 30:1088–1095

Reich PB, Wright IJ, Cavender-Bares J, Craine JM, Oleksyn J, Westoby M, Walters MB (2003) The evolution of plant functional variation: traits, spectra, and strategies. Int J Plant Sci 164:S143–S164

Renninger HJ, Gartner BL, Meinzer FC (2006) Effects of release from suppression on wood functional characteristics in young Douglas-fir and western hemlock. Can J For Res 36:2038–2046

Russak V (1990) Päikesekiirgus. In: Ross J (ed) Tartu kliima ja selle muutumine viimastel kümnenditel. Eesti TA Astrofüüsika ja Atmosfäärifüüsika Instituut, Tartu, pp 51–78

Rust S, Hüttl RF (1999) The effect of shoot architecture on hydraulic conductance in beech (*Fagus sylvatica* L.). Trees 14:39–42

Ryan MG, Yoder BJ (1997) Hydraulic limits to tree height and tree growth. BioScience 47:235–242

Ryan MG, Phillips N, Bond BJ (2006) The hydraulic limitation hypothesis revisited. Plant Cell Environ 29:367–381

Sack L, Holbrook NM (2006) Leaf hydraulics. Annu Rev Plant Biol 57:361–381

Sack L, Cowan PD, Jaikumar N, Holbrook NM (2003) The 'hydrology' of leaves: co-ordination of structure and function in temperate woody species. Plant Cell Environ 26:1343–1356

Samuelson LJ, McLemore III PC, Somers GL (2003) Relationships between foliar δ^{13}C and hydraulic pathway length in *Pinus palustris*. For Sci 49:790–798

Santiago LS, Goldstein G, Meinzer FC, Fisher JB, Machado K, Woodruff D, Jones T (2004) Leaf photosynthetic traits scale with hydraulic conductivity and wood density in Panamanian forest canopy trees. Oecologia 140:543–550

Schulte PJ, Brooks JR (2003) Branch junctions and the flow of water through xylem in Douglas-fir and ponderosa pine stems. J Exp Bot 54:1597–1605

Sellin A, Kupper P (2004) Within-crown variation in leaf conductance of Norway spruce: effects of irradiance, vapour pressure deficit, leaf water status and plant hydraulic constraints. Ann For Sci 61:419–429

Sellin A, Kupper P (2005a) Effects of light availability versus hydraulic constraints on stomatal responses within a crown of silver birch. Oecologia 142:388–397

Sellin A, Kupper P (2005b) Variation in leaf conductance of silver birch: effects of irradiance, vapour pressure deficit, leaf water status and position within a crown. For Ecol Manage 206:153–166

Sellin A, Kupper P (2006) Spatial variation in sapwood area to leaf area ratio and specific leaf area within a crown of silver birch. Trees 20:311–319

Sellin A, Kupper P (2007a) Effects of enhanced hydraulic supply for foliage on stomatal responses in little-leaf linden (*Tilia cordata* Mill.). Eur J For Res 126:241–251

Sellin A, Kupper P (2007b) Temperature, light and leaf hydraulic conductance of little-leaf linden (*Tilia cordata*) in a mixed forest canopy. Tree Physiol 27:679–688

Sperry JS, Nichols KL, Sullivan JEM, Eastlack SE (1994) Xylem embolism in ring-porous, diffuse-porous, and coniferous trees of northern Utah and interior Alaska. Ecology 75:1736–1752

Thomas DS, Montagu KD, Conroy JP (2004) Changes in wood density of *Eucalyptus camaldulensis* due to temperature: the physiological link between water viscosity and wood anatomy. For Ecol Manage 193:157–165

Tyree MT, Ewers FW (1991) The hydraulic architecture of trees and other woody plants. New Phytol 119:345–360

Tyree MT, Zimmermann MH (2002) Xylem structure and the ascent of sap. Springer, Berlin

Vander Willigen C, Sherwin HW, Pammenter NW (2000) Xylem hydraulic characteristics of subtropical trees from contrasting habitats grown under identical environmental conditions. New Phytol 145:51–59

Wagner KR, Ewers FW, Davis SD (1998) Tradeoffs between hydraulic efficiency and mechanical strength in the stems of four co-occurring species of chaparral shrubs. Oecologia 117:53–62

Warren CR, Adams MA (2000) Water availability and branch length determine δ^{13}C in foliage of *Pinus pinaster*. Tree Physiol 20:637–643

Woodward I (2004) Tall storeys. Nature 428:807–808

Wullschleger SD, Meinzer FC, Vertessy RA (1998) A review of whole-plant water use studies in trees. Tree Physiol 18:499–512

Yang S, Tyree MT (1993) Hydraulic resistance in *Acer saccharum* shoots and its influence on leaf water potential and transpiration. Tree Physiol 12:231–242

Yang S, Tyree MT (1994) Hydraulic architecture of *Acer saccharum* and *A. r*ubrum: comparison of branches to whole trees and the contribution of leaves to hydraulic resistance. J Exp Bot 45:179–186