

**HYDRAULIC AND ENVIRONMENTAL
LIMITATIONS TO LEAF WATER RELATIONS
IN TREES WITH RESPECT
TO CANOPY POSITION**

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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following papers which are referred to in the text by Roman numerals:

- I Sellin, A. and 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. *Annals of Forest Science* **61**: 419–429.
- II Sellin, A. and Kupper, P. 2005. Variation in leaf conductance of silver birch: effects of irradiance, vapour pressure deficit, leaf water status and position within a crown. *Forest Ecology and Management* **206**: 153–166.
- III Sellin, A. and Kupper, P. 2005. Effects of light availability versus hydraulic constraints on stomatal responses within a crown of silver birch. *Oecologia* **142**: 388–397.
- IV Kupper, P., Sellin, A., Tenhunen, J., Schmidt, M. and Rahi, M. 2006. Effects of branch position on water relations and gas exchange of European larch trees in an alpine community. *Trees — Structure and Function*. (in press)
- V Sellin, A. and Kupper, P. 2006. Spatial variation in sapwood area to leaf area ratio and specific leaf area within a crown of silver birch. *Trees — Structure and Function*. (in press)
- VI Kupper, P., Sellin, A., Klimankova, Z., Pokorný, R. and Puértolas J. 2006. Water relations in Norway spruce trees growing at ambient and elevated CO₂ concentrations. *Biologia Plantarum*. (in press)

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The author participated in preparing the listed co-authored publications as follows:

- paper I – collecting data (20%), analysing data and preparing the text (20%);
- paper II – collecting data (60%), analysing data and preparing the text (20%);
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- paper IV – collecting data (100%), analysing data and preparing the text (70%);
- paper V – collecting data (50%), analysing data and preparing the text (20%);
- paper VI – collecting data (70%), analysing data and preparing the text (70%)

LIST OF ABBREVIATIONS

AC	ambient CO ₂ concentration (350 μmol CO ₂ mol ⁻¹)
A_l/A_s	leaf area to sapwood area ratio (reciprocal of HV ; m ² cm ⁻²)
b	reference leaf conductance at VPD = 1 kPa (mmol m ⁻² s ⁻¹)
c₁	initial slope of the leaf conductance light-response curve
c₂	leaf conductance in the dark (mmol m ⁻² s ⁻¹)
C_{soil}	soil volumetric water content (%)
D_T	tracheid diameter (μm)
E	transpiration rate (mmol m ⁻² s ⁻¹)
EC	elevated CO ₂ concentration (ambient + 350 μmol CO ₂ mol ⁻¹)
F	sap flux density (mmol cm ⁻² s ⁻¹)
g_L	leaf conductance to water vapour (mmol m ⁻² s ⁻¹)
g_{max}	maximum leaf conductance at infinite Q_p (mmol m ⁻² s ⁻¹)
G_T	total hydraulic conductance of the soil-to-leaf pathway (mmol m ⁻² s ⁻¹ MPa ⁻¹)
HV	Huber value (reciprocal of A_l/A_s ; cm ² m ⁻²)
K_{cap}	hydraulic conductivity of a capillary (m ⁴ s ⁻¹ Pa ⁻¹)
l	length (m)
-m	stomatal sensitivity to VPD (mmol m ⁻² s ⁻¹ kPa ⁻¹)
P	hydrostatic pressure (Pa)
q	empirical parameter (Eq. 4)
Q_p	photosynthetic photon flux density (μmol m ⁻² s ⁻¹)
r	capillary radius (m)
t	time (s)
V	volume of water (m ³)
VPD	vapour pressure difference between the leaf interior and the bulk air (kPa)
η	dynamic viscosity of water (Pa s ⁻¹)
ΔΨ	water potential differences between the soil and leaves/shoots (MPa)
Ψ_L	bulk leaf water potential (MPa)
Ψ_{opt}	optimum water potential for leaf conductance (MPa)
Ψ_S	bulk soil water potential (MPa)
Ψ_X	bulk shoot water potential (MPa)

1. INTRODUCTION

Water transfer from the soil, through vegetation, to the atmosphere, takes place in a soil-plant-atmosphere continuum along a water potential or hydrostatic pressure gradient. Plants are a central component of the continuum, and the biggest drop of water potential occurs on the surface of plant leaves. For trees, the primary water driving force is, most of the time, the transpiration that pulls water from the soil to the leaves and creates and maintains a variable gradient of water potential throughout the whole plant (Cruziat et al., 2002). It has been suggested that over half of the annual precipitation falling on land may be channelled back to the atmosphere through plant vascular systems (Donovan and Sperry, 2000).

Although water transfer in the soil-plant-atmosphere continuum is considered a passive physical process, plants possess several structures and mechanisms allowing them to actively regulate water fluxes. It is well known that aquaporins modify membrane permeability to water at the cellular level wherever water must pass across cell membranes, tuning the whole plant water supply (Eisenbarth and Weig, 2005; Vandeleur et al., 2005). However, a principal regulation mechanism is located in plant leaves, where stomata control the transfer of water vapour out of the leaf and the diffusion of carbon dioxide into the leaf interior. The physiological role of stomatal regulation is to prevent excessive water loss and to facilitate CO₂ diffusion to mesophyll cells, whereas several environmental (irradiance, air humidity, carbon dioxide concentration, soil water availability) and internal factors (intercellular carbon dioxide concentration, leaf water status, turgor of guard cells) control stomatal conductance.

Leaf water supply is a primary factor regulating stomatal conductance (Buckley, 2005), particularly in trees having a long pathway for water transfer from roots to leaves. Meinzer (2002) suggested, that stomatal regulation of vapour-phase conductance balances transpiration with the efficiency of the vascular system to provide adequate water supply to the leaves, avoiding leaf desiccation at one extreme, and unnecessary restriction of carbon dioxide uptake at the other. Several studies have shown that, beside stomatal conductance, xylem hydraulic capacity also limits the net photosynthesis in many tree species (Hubbard et al., 1999; Santiago et al., 2004; Brodribb et al., 2005) and therefore the growth of higher and older trees (Koch et al., 2004; Woodward, 2004). This accords with the “hydraulic limitation hypothesis”, which proposes that hydraulic resistance will increase as trees grow taller, because water must travel a longer path and because slower-growing trees contain smaller xylem conduits, which are less permeable to water flow (Ryan and Yoder, 1997). Water flow through xylem conduits can be described using the Ohm’s law analogy (Tyree and Zimmermann, 2002): the volume flow rate through a capillary (dV/dt) is proportional to the applied hydrostatic pressure gradient (dP/dl) and the hydraulic conductivity (K_{cap}),

$$\frac{dV}{dt} = -K_{\text{cap}} \frac{dP}{dl} \quad (1)$$

Hagen and Poiseuille (Nobel, 1999) found empirically that

$$K_{\text{cap}} = \frac{\pi \cdot r^4}{8 \eta} \quad (2)$$

where r is a capillary radius and η is the dynamic viscosity of the water. It is important to note that flow rate is proportional to the radius of the capillary to the fourth power. As capillary radius increases, the resistance to water flow caused by friction along the cell wall is rapidly reduced (Tyree and Zimmermann, 2002). However, because xylem conduits (vessels and tracheids) are of finite length and water must move many times from one conduit to the next, the perforation plates and pit areas also represent a considerable resistance to water flow. Thus, water transfer through the sapwood is a function of the anatomy of conduits, depending on both lumen diameter and conduit length, and the length is particularly important in coniferous wood, which contains only tracheids (Sperry et al., 2005). It should be mentioned that, beside vascular resistance to water flow through the xylem conduits, there exists also resistance of the extra-vascular pathway located in living cells; thus, both compartments are concerned when we talk about hydraulic resistance to water transfer through the whole plant. It is presumed that at least 50% of the hydraulic resistance to liquid water flow from the root surface to the leaf evaporative surface is extra-vascular and mediated by aquaporins (Tyree and Zimmermann, 2002).

Numerous studies have demonstrated that variability in stomatal conductance closely associates with variation in the total hydraulic conductance of the soil-to-leaf pathway, G_T (Hubbard et al., 1999; Meinzer et al., 1999; Kolb and Stone, 2000; Addington et al., 2004). The information about G_T is crucial for understanding how the tree's hydraulic design influences the movement of water from soil to leaves (Tyree and Evers, 1991). Spatial variation of G_T has important implications for patterns of transpiration and leaf water potential observed within forest canopies (Wullschleger et al., 1998). If G_T decreases due to changes in xylem structure or in response to xylem embolism, foliage water supply could be limited. For a given G_T , the value of stomatal conductance required to maintain leaf water potential above the threshold value for runaway embolism depends on atmospheric vapour pressure deficit (Meinzer et al., 1999; Addington et al., 2004). Therefore, stomatal responses to atmospheric humidity must always be considered in interpreting co-ordination of vapour and liquid-phase water transport properties (Meinzer, 2002).

Many temperate tree species exhibit isohydric behaviour: a maintenance of nearly constant leaf water potential over a wide range of environmental

conditions, indicating a tight coupling between water loss from foliage and the water transport capacity of the stem. A hypothesis suggests that a homeostatic balance exists between transpiration rate, leaf area, sapwood area, and hydraulic sufficiency of the stem to supply water to leaves (Tyree and Ewers, 1991). Hydraulic capacity of the stems and branches expressed per unit leaf area depends directly on leaf area to sapwood area ratio (A_l/A_s), which is an important adjustable characteristic reflecting aboveground biomass allocation patterns – a tree's investment in photosynthetic tissue (leaves) relative to water-conducting tissue (sapwood). Leaf area to sapwood area ratio must decrease to maintain leaf-specific hydraulic sufficiency if path length, tortuosity, and gravity reduce the whole-plant hydraulic conductance. The decrease in A_l/A_s with increasing tree size observed in many woody species is one of the mechanisms that at least partially compensates for decreased hydraulic conductance as trees grow in height (McDowell et al., 2002; Reid et al., 2003). However, the leaf area to sapwood area ratio may also vary within a crown, allowing the offsetting of increasing hydraulic resistance (Protz et al., 2000; Hubbard et al., 2002).

Due to the great size of trees and remarkable environmental gradients within forest canopies, branches located at various positions in the crown are exposed to different environmental conditions. Thus, trees have to develop foliage acclimatised both physiologically and morphologically to heterogenous conditions within a canopy (Niinemets et al., 1998; Sellin, 2001), permitting more efficient utilisation of the existing microenvironment. Both stomatal conductance and light-saturated photosynthetic capacity exhibit a declining trend with decreasing light availability toward the base of the canopy (Bond et al., 1999; Rijkers et al., 2000), and it is generally accepted that branch and foliage growth at the base of the crown is limited by low irradiance. If branch growth rate declines with decreasing light availability, the diameter of xylem conduits is expected to decrease too. Thus, according to Hagen-Poiseuille equation, the shaded lower-crown branches should be hydraulically less efficient than the exposed upper-crown branches that receive more sunlight. Several studies performed in different tree species support this concept (Cochard et al., 1999; Lemoine et al., 2002a; Mayr et al., 2003). In lodgepole pine, the hydraulic permeability was smaller in the lower branches than in the upper branches, due to narrower tracheids in the sapwood of lower branches (Protz et al. 2000). High resistance to water flow through the xylem may also be caused by the development of short shoot internodes, mostly located in secondary axes (Rust and Hüttel, 1999; Tyree and Zimmermann, 2002), or twig abscission zones (Rust et al., 2004). Also formation of compression wood and opposite wood at different sides of conifer branches may remarkably vary their xylem hydraulic efficiency and safety (Mayr and Cochard, 2003). Therefore, within a tree crown, the length of the water transport pathway does not necessarily determine the resistance to water flow, as sapwood permeability to water plays a substantial role too.

Recent studies have demonstrated that resistance of the leaf vascular and extra-vascular pathways may also substantially vary with crown positions. In general, leaves account for approximately one quarter of the whole-plant hydraulic resistance (Sack et al., 2003), whereas 60–90% of the resistance is located in the extra-vascular pathway (Cochard et al., 2004; Gasco et al., 2004; Sack et al., 2004). Sack et al. (2003) showed that sun leaves had 15–67% higher leaf hydraulic conductance compared to shade leaves in six temperate woody species. The sensitivity of hydraulic conductance to irradiance suggests that light availability may affect the functioning of aquaporins in membranes of the leaf cells (Tyree et al., 2005; Nardini et al., 2005) and could modify hydraulic resistance of the leaf extra-vascular compartment. Cochard et al. (1997) studied the distribution of the resistances to water flow in branches of *Fraxinus excelsior* L. trees and found that leaf resistance represented 90% and 10% of the whole-branch hydraulic resistance in the upper and lower-crown branches respectively. Probably, proportions of the vascular and extra-vascular resistances may also change depending on crown positions.

An important internal factor regulating stomatal behaviour is CO₂ concentration in the guard cells, which reflects their own carbohydrate metabolism as well as the CO₂ level in the air within the leaf (Nobel, 1999), depending at the same time on the CO₂ concentration of the surrounding atmosphere. During recent decades, effects of increased atmospheric CO₂ concentration on plant performance and metabolism have been demonstrated in the light of global changes. Several studies both in herbaceous and woody species have confirmed that elevated CO₂ concentration could significantly reduce the stomatal conductance and transpiration of plants (Saxe et al., 1998; Medlyn et al., 2001; Bunce et al., 2004), allowing more economical water use in some forest stands (Schäfer et al., 2002). A meta-analysis performed across a number of species indicated that the response to elevated CO₂ is significantly stronger in young than in old trees, in deciduous compared to coniferous species, and in water-stressed compared to nutrient-stressed trees (Medlyn et al., 2001).

Some papers have indicated that elevated atmospheric CO₂ concentration could offset the effect of low light availability on photosynthesis in shaded canopy parts of the trees (Marek et al., 2001; 2002) and in forest floor species (Osborne et al., 1997). Moreover, one may suppose that improved photosynthesis in the shaded foliage could mitigate the effect of larger resistance to water flow in the vascular system through increased growth rate and conduit size. Nevertheless, there is no explicit conception, how xylem conduit diameters and hydraulic efficiency could change at elevated CO₂ (Ceulemans et al., 2002; Atwell et al., 2003), particularly with respect to the canopy position in trees.

Overall, the relationships between leaf functioning within an individual crown and traits of the plant hydraulic architecture are still poorly understood (Cruziat et al., 2002; Hubbard et al., 2002; Tyree and Zimmermann, 2002; Burgess et al., 2005). It is a widely accepted idea that low light availability is

responsible for decreased stomatal conductance and gas exchange rate in shaded canopy parts of forest trees. However, the plant hydraulic capacity to supply leaves with a sufficient amount of water also contributes to stomatal regulation, particularly in trees, the plants with large dimensions. In this thesis, the leaf conductance to water vapour and foliage water relations were studied in the upper and lower canopy positions of three temperate woody species (Norway spruce, silver birch, European larch). A central hypothesis of the thesis was that lower-canopy foliage attached to the branches at the base of the live crown is hydraulically more limited than upper-canopy foliage located at the treetop. On the other hand, certain compensatory mechanisms related to changes in the leaf to sapwood area ratio or triggered by elevated atmospheric carbon dioxide concentration could offset the effect of increased hydraulic resistance in the shaded lower-canopy foliage of the trees. An advanced understanding of how canopy position could influence the leaf conductance and foliage water relations of trees exposed to an array of environmental conditions may improve mechanistic models describing tree growth and functioning in our changeable world.

The objectives of the thesis are as follows:

1. To study the effects of environmental (irradiance, vapour pressure deficit) and hydraulic factors (leaf or shoot water potential, soil-to-leaf hydraulic conductance) on leaf conductance and foliage water relations of trees depending on the position within a canopy (I–IV).
2. To investigate how structural characteristic (xylem conduit diameter, leaf area to sapwood area ratio) contribute to branch and foliage water relations in different crown positions (IV–V).
3. To estimate the effect of elevated atmospheric CO₂ concentration on xylem sap flow and foliage water relations with respect to canopy position (VI).

2. MATERIAL AND METHODS

2.1. Study sites and experimental set-up

The field studies were carried out on four different study sites (located in Estonia, Germany and Czech Republic) in three tree species: Norway spruce (*Picea abies* [L.] Karst.), silver birch (*Betula pendula* Roth) and European larch (*Larix decidua* Mill.).

Paper I

The study was carried out at Vooremaa Ecology Station (58°44' N, 26°45' E), eastern Estonia, in the summer months of 1997 and 2000. The effects of irradiance, atmospheric vapour pressure deficit, leaf water status and plant hydraulic constraints on leaf conductance were studied in the basal and top thirds of the crowns of Norway spruce trees (20 years old, 11.2–12.0 m in height) growing in a dense forest plantation of the *Oxalis* site type (Lõhmus, 2004). For physiological measurements a wooden tower provided with two platforms was erected between three neighbouring sample trees. Leaf conductance and transpiration rate were measured with a LI-1600M steady-state diffusion porometer (LI-COR, USA) equipped with a cylindrical leaf chamber. Bulk water potential of shoots (Ψ_x) was measured by the balancing pressure technique using a Scholander-type pressure chamber.

Papers II, III and V

The experiments were performed in Järvselja Experimental Forest (58°22' N, 27°20' E), eastern Estonia, in the summers of 2001 to 2003. Foliage water relations were studied in silver birch trees (40–50 years old, 16.0–17.0 m height) growing in a mixed forest stand of the *Myrtillus* site type (Lõhmus, 2004). Leaf conductance and transpiration rate were measured with a LI-1600M porometer. In Paper II, the effects of irradiance, vapour pressure deficit, leaf water status and plant hydraulic constraints on leaf conductance were studied in intact foliage of three neighbouring trees accessible from a scaffolding tower. In Paper III, the effects of light availability versus hydraulic constraints on stomatal responses were studied both in intact and detached shoots, manipulating experimentally light availability and leaf water supply. Altogether, water relations of foliage subjected to five treatments differing in hydraulic supply (H) and level of irradiance (I) were studied:

- Lc H-I– intact branches in the lower canopy;
- Lc H+I– shoots cut from the lower canopy, saturated with water on the lower platform;
- Lc H+I+ shoots cut from the lower canopy, transported to the upper platform and saturated with water;
- Uc H-I– intact branches in the upper canopy;

Uc H+I+ shoots cut from the upper canopy, saturated with water on the upper platform.

In Paper V, the spatial variation in sapwood area to leaf area ratio (Huber value, **HV**) was studied within crowns of silver birch trees. Altogether, 14 trees were sampled, from which, as a rule, three branches were sawn off – one branch from the basal, middle and upper third of the crown. At the primary branch, we selected one II order and one III order branch inserted in the former. Then the branch was dissected and sampled at five points to estimate **HV**.

Paper IV

The experimental work was accomplished in Berchtesgaden National Park, Bavarian Alps, Germany, at an elevation of 610 m ASL in August 2002. The effect of branch position on water relations and gas exchange was studied in the basal and top thirds of the crowns of small (17–21 years old, up to 6.4 m height) trees of European larch growing in a sparse stand of a mountainous community. Branch sap flux was observed in the crown of four sample trees with gauges operating on the heat balance method, described by Sakuratani (1981). Altogether, eight branches (one in the upper and one in the lower third of the crown) approximately 1.2 cm in diameter were equipped with the sap flux gauges. Leaf conductance and net photosynthesis were measured with a LI-6400 infrared gas analyser (LI-COR, USA) equipped with a conifer chamber. For anatomical investigations, wood samples were examined with a BS-301 scanning electron microscope (Tesla, Czech Republic).

Paper VI

The field studies were carried out on the research site at Bílý Kříž (49°33'N, 18°32'E, 908 m ASL) in the Beskydy Mountains, the Czech Republic, in August 2003. 14-year-old and 4.1–5.0 m-high trees of Norway spruce were grown at ambient CO₂ (350 μmol CO₂ mol⁻¹) and at elevated CO₂ concentrations (ambient + 350 μmol CO₂ mol⁻¹) in two separate glass domes with adjustable windows (for details see Urban et al. 2001). Water relations were studied in the crowns of five sample trees growing at ambient and elevated CO₂ concentrations. Xylem sap flow was measured using SF 300 sap flux gauges (Greenspan Technology, Australia) operating on the heat pulse velocity technique (Köstner et al., 1998). Five sample trees were equipped with two pairs of sap flow gauges, ten sensor pairs altogether. The first pair was installed just under the live crown in sapwood at depths of 20% and 60% of the stem radius. The second sensor pair was installed about 1.2 m above the first pair at the same relative depths in the sapwood. Leaf conductance and net photosynthesis were measured with a CIRAS-1 infrared gas analyser (PP Systems, UK) equipped with a conifer chamber.

2.2. Data processing

The light-saturation point of leaf conductance (g_L) to water vapour (Papers I–III) was taken as the level of photosynthetic photon flux density corresponding to the value of 95% of the maximum leaf conductance calculated from the following equation (Sellin, 2001) by using the boundary line technique (Strachan and McCaughey, 2002):

$$g_L = \frac{g_{\max} \cdot c_1 \cdot (Q_p + q)}{g_{\max} + c_1 \cdot (Q_p + q)} \quad (3)$$

Q_p is the incident photosynthetic photon flux density, g_{\max} is the maximum value of g_L at infinite Q_p , and c_1 is dg_L / dQ_p at $Q_p = 0$.

$$q = \frac{c_2}{c_1} \quad , \quad (4)$$

if it is assumed that the initial slope of the response curve is nearly linear. c_2 is the value of g_L in the dark, and is given by the intercept on the ordinate. c_2 was computed as an absolute term and c_1 as a slope of the regression of g_L from photon flux density at low irradiance ($Q_p < 30 \mu\text{mol m}^{-2} \text{s}^{-1}$) in the morning and evening.

The changes in daily maximum leaf conductance depending on the vapour pressure difference (**VPD**) between the leaf interior and the bulk air were analysed according to Oren et al. (1999):

$$g_L = -\mathbf{m} \cdot \ln \mathbf{VPD} + \mathbf{b} \quad , \quad (5)$$

where \mathbf{m} and \mathbf{b} are parameters generated in a least-squares regression analysis. The parameter \mathbf{b} is a reference conductance at $\mathbf{VPD} = 1$ kPa; the parameter $-\mathbf{m}$ quantifies the stomatal sensitivity to **VPD**.

$$-\mathbf{m} = -dg_L / d \ln \mathbf{VPD} \quad , \quad (6)$$

while \mathbf{m} is constant over the entire range of **VPD** and thus permits comparisons independent of a specific **VPD** range.

To determine apparent optimum water potential (Ψ_{opt}) for leaf conductance, data on g_L was plotted against those of shoot (Ψ_X) or leaf water potential (Ψ_L) and was smoothed using a polynomial of the third order. As the dependence of g_L on water potential was assumed to have one maximum, the Ψ_X or Ψ_L at

which the first derivative of the equation equals zero was taken as the optimum water potential.

In Papers I–III, the mean total hydraulic conductance (G_T ; $\text{mmol m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$) was estimated from the slope of the regression of transpiration rate (E) from water potential differences ($\Delta\Psi$) between the soil (or deionised water in case of the cut shoots) and shoots/leaves (Meinzer et al. 1995; Wullschleger et al. 1998). G_T was expressed per unit leaf area, and the boundary layer conductance was assumed to approach infinity. In Papers IV and VI, the G_T was calculated on the basis of sap flux (F) and water potential differences between the soil (Ψ_s) and shoot (Ψ_x), and was expressed per total leaf area ($\text{mmol m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$) and sapwood transverse area ($\text{mmol cm}^{-2} \text{s}^{-1} \text{MPa}^{-1}$) using a simple formula:

$$G_T = \frac{F}{\Psi_s - \Psi_x}. \quad (7)$$

3. RESULTS AND DISCUSSION

3.1. Responses to light availability

Leaf conductance (g_L) varied remarkably within the canopy for all studied tree species, depending on leaf position and foliage age (Table 1; see also Table 3 in IV and Table 2 in VI). The upper-canopy foliage (sun leaves) demonstrated 1.6–2.4 times higher daily maximum g_L as compared to the lower-canopy foliage (shade leaves), while the differences in g_L between the canopy positions persisted during the whole day (Fig. 1; see also Fig. 2 in II and III). The sap flux data obtained in European larch and Norway spruce also showed significantly smaller values in the lower branches compared to the upper crown (Fig. 2 in IV; Fig. 1 in VI).

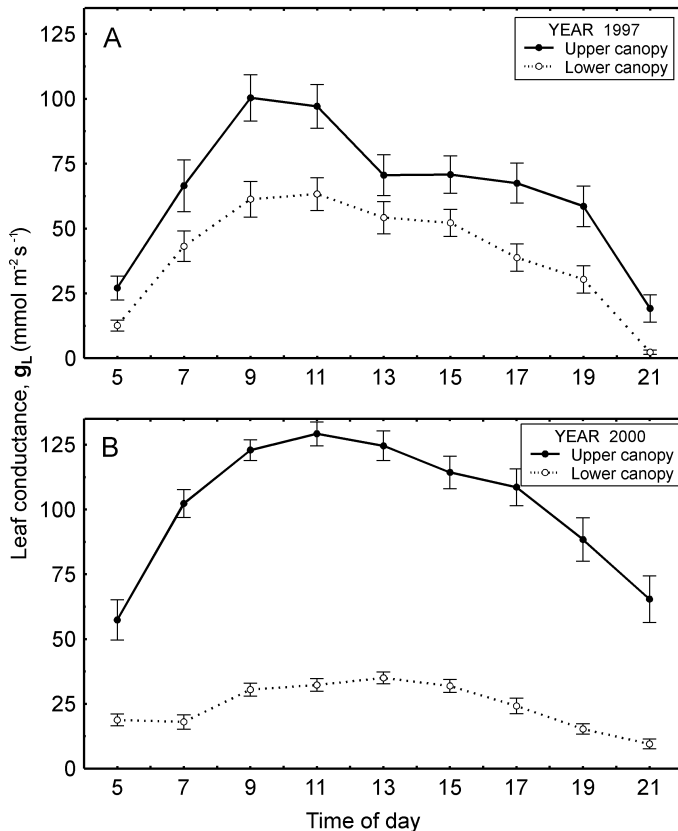


Figure 1. Spatial and temporal variation in leaf conductance in the current-year and older (lower canopy in 2000) foliage of Norway spruce. The bars indicate \pm SE of the means.

In spruce, there were no significant differences between the current-year up to 2-year-old shoots, while the older foliage exhibited substantially lower daily maxima of g_L (Table 1). The reduction of maximum stomatal conductance with foliage age is a general trend in coniferous species (Day, 2000; Sellin, 2001). Higher leaf conductance observable at higher light availability is also a universal regularity, common for both temperate (Morecroft and Roberts, 1999; Lemoine et al., 2002b) and tropical tree species with different shade tolerance (Rijkers et al., 2000). The primary reason for the difference in g_L between the crown positions could be a limited light availability in the lower canopy layers (Bond et al., 1999). However, our results suggested that the decreased leaf conductance in the lower-canopy foliage could not merely be attributed to the limited light availability. Both in silver birch (II) and Norway spruce (Table 2 in VI), shade leaves showed substantially lower g_L than sun leaves in light saturated conditions as well. Thus, beside light availability, other factors should be responsible for the substantial differences observed in g_L between different canopy layers.

The functional acclimation of the lower-canopy foliage to shade conditions occurred in the form of higher stomatal sensitivity to changes in irradiance. Shade leaves demonstrated a much steeper initial slope of the light-response curve as compared to the sun leaves (Table 1). The light-saturation point of leaf conductance in lower-canopy foliage was achieved at a Q_P several times smaller than in the upper canopy. The steeper initial slope of the light-response curve and the lower light-saturation point together enable prolongation of the daily period of stomatal opening in shade leaves, and thus permit the efficient utilisation of the heterogeneous microenvironment existing within a canopy. Shade acclimation of trees is a complex process including both physiological and morphological adjustments at different levels of organisation, allowing leaves to photosynthesise efficiently despite the very biased distribution of light within the canopy (Terashima and Hikosaka, 1995; Kull, 2002). The experiments in silver birch (Table 1 in III) indicated that stomata are able to quickly respond to changes in the light environment. The improved water supply combined with higher level of irradiance caused a significantly smaller initial slope of the light-response curve in manipulated shoots compared to intact control shoots. However, the abrupt change in the radiation regime was not accompanied by immediate adjustment of the light-saturation point of leaf conductance in detached shoots.

Stomatal responses to irradiance observed in Norway spruce varied between the study years as well (Table 1). In summer 2000, under darker conditions due to denser canopy and cloudy weather the foliage exhibited a considerably lower light-saturation point of g_L . Also the initial slope of the light-response curve was smaller because the stomata were more open at zero irradiance in summer 2000 compared to summer 1997. In contrast to Norway spruce, the stomatal behaviour in silver birch did not significantly vary between the study years, except for daily maximum g_L (Table 1). Thus, the results provided evidence of the effects of specific meteorological conditions on stomatal regulation, including other factors beside irradiance.

Table 1. Main parameters characterising the daily patterns of leaf conductance for shade and sun foliage of different ages (zero denotes the current-year foliage) depending on irradiance. ^aArithmetic mean of the 10 largest records during the study period; ^bmean of the records at 0900 h; ^cmean of the records at 1000 h; ^dmean of the records at 1100 h; ^emean of the records at 1200 h; ^fmean of the records at 1300 h; *ns*, the difference is statistically not significant.

Species	Foliage age (yr)	Year	Mean leaf conductance if $Q_{P=0}$ ($\text{mmol m}^{-2} \text{s}^{-1}$)		Mean initial slope of the light-response		Light-saturation point of leaf conductance ($\mu\text{mol m}^{-2} \text{s}^{-1}$)		Maximum leaf conductance \pm SE ($\text{mmol m}^{-2} \text{s}^{-1}$)					
			Shade	Sun	<i>P</i>	Shade	Sun	<i>P</i>	Shade	Sun	Overall maximum ^a		Mean of daily maxima	
											Shade	Sun	Shade	Sun
Spruce	0	1997	5.4	17.5	<i>ns</i>	1.65	0.48	<0.05	82	131	151 \pm 5.4	198 \pm 5.6	63 ^d \pm 6.3	100 ^b \pm 8.9
		2000	—	68.6	—	—	0.39	—	—	57	—	—	193 \pm 4.8	—
	1	1997	12.1	20.6	<i>ns</i>	1.59	0.75	<i>ns</i>	26	138	137 \pm 5.9	188 \pm 10.3	56 ^d \pm 5.4	90 ^b \pm 8.1
		2000	—	70.3	—	—	0.51	—	—	53	—	—	170 \pm 1.1	—
	2	1997	18.5	34.0	<i>ns</i>	1.85	1.14	<i>ns</i>	27	146	149 \pm 7.1	194 \pm 7.4	58 ^d \pm 5.4	91 ^d \pm 7.7
		2000	—	102.5	—	—	0.32	—	—	26	—	—	219 \pm 3.3	—
2000	17.1	67.6	<0.001	0.84	0.63	<i>ns</i>	6	17	74 \pm 1.9	153 \pm 2.0	35 ^d \pm 2.3	88 ^d \pm 3.7		
Birch	0	2001	9.8	45.1	<0.001	0.505	0.133	<0.001	67	617	166 \pm 6.9	353 \pm 5.5	76 ^e \pm 4.5	186 ^e \pm 7.0
		2002	11.4	47.4	<0.001	0.512	0.150	<i>ns</i>	57	560	143 \pm 6.3	262 \pm 8.4	79 ^e \pm 5.2	161 ^e \pm 8.4

3.2. Effects of vapour pressure deficit and leaf water status

Sun leaves turned out to be more sensitive to changes in atmospheric evaporative demand (here vapour pressure difference between the leaf interior and the bulk air, **VPD**) than shade leaves of silver birch (Table 3 in II). Stomatal sensitivity to **VPD** was positively related to the overall maximum g_L ; thus, the higher the leaf conductance, the more sensitively stomata respond to increasing **VPD**. This is in accordance with the prediction made by Oren et al. (1999), that stomatal sensitivity to vapour pressure deficit is proportional to stomatal conductance at low atmospheric evaporative demand.

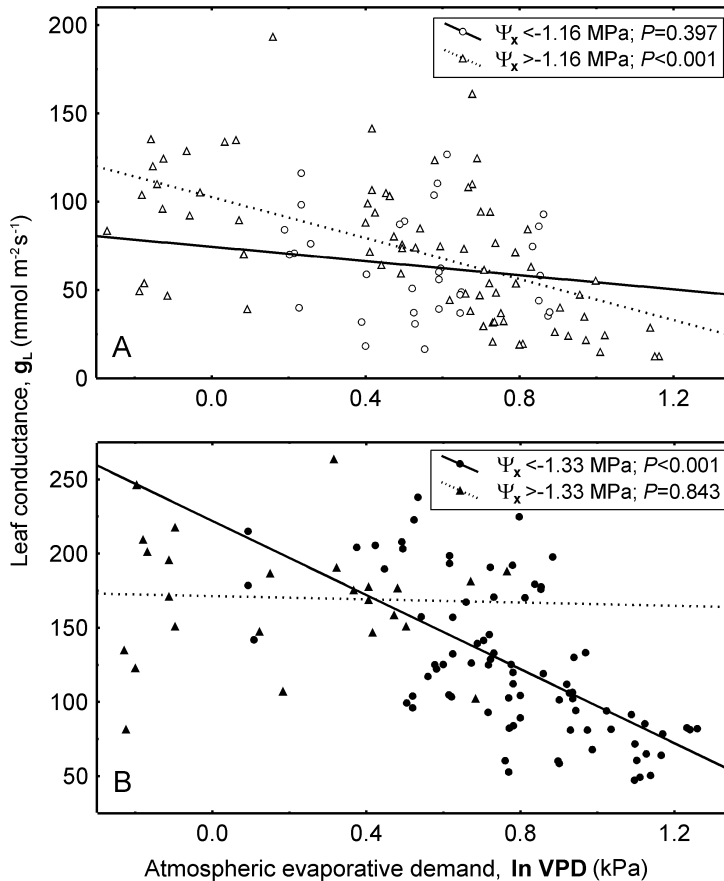


Figure 2. Leaf conductance (g_L) versus atmospheric evaporative demand at leaf water status above and below optimum water potentials (Ψ_{opt}) in the lower (A) and upper-canopy foliage (B) of silver birch.

In Norway spruce (I), the leaf conductance tended to respond more sensitively to changes in **VPD** at lower values of shoot water potential. The results in silver birch also indicated that stomatal sensitivity to **VPD** was modified by leaf water potential (Ψ_L); however, the responses varied remarkably with respect to canopy positions (Fig. 2). Leaf conductance in the lower-canopy foliage seemed to be more strictly controlled by water status: at high leaf water potentials (above Ψ_{opt}) g_L declined unequivocally with the **VPD** increase. At low Ψ_L , there was no statistically significant relationship between g_L and **VPD** in the lower canopy position. Low leaf water potential caused stomatal pores to narrow, thus making stomata insensitive to further changes in atmospheric vapour pressure deficit (Fig 2A). The upper-canopy foliage behaved in an opposite manner: at high Ψ_L , leaf conductance did not depend on **VPD** at all, implying that sufficient/redundant water supply has been provided for leaves. Only at more negative water potentials (below Ψ_{opt}) did the influence of **VPD** on g_L become significant (Fig 2B). Thus, low leaf water potential around midday modified, through negative feedback, the effects of atmospheric demand on g_L . An analogous result has been published for European beech (*Fagus sylvatica* L.), in which a drop in leaf water potential elicited the decrease in stomatal conductance earlier and faster in shaded branches (Lemoine et al., 2002b). The experiments in silver birch indicated that artificially improved water supply made leaf conductance totally insensitive to changes in **VPD** in the lower canopy position, while in the upper canopy, the stomatal sensitivity decreased more than two fold in comparison with intact control shoots (Table 2 in III).

In all studied species, the upper-canopy foliage experienced lower water potentials as compared to the lower-canopy foliage. Both in spruce (I) and birch (II) trees, the effect of leaf water potential on g_L in the midday was relatively stronger in the upper canopy layer as compared to the lower canopy. The leaf conductance decreased if water potential fell below certain threshold values, however, on a diurnal scale the influence of leaf water potential on leaf conductance was rather weak in silver birch (Table 4 in II). Even at midday, the leaf water potential explained merely 3 to 9% of the variation in g_L depending on the study year and canopy layer (Table 6 in II). The actual influence of leaf water potential on g_L could be more substantial, but it was probably hidden by effects of the vapour pressure difference, because Ψ_L and **VPD** were interrelated. In hybrid poplar trees, Hinckley et al. (1994) found that the leaf water status played no role at all in controlling stomatal conductance. The experimental reduction of hydraulic limitations in birch caused leaf water status to increase to the extent that daily minimum Ψ_L remained far above Ψ_{opt} in all treatments with manipulated shoots. The improved water supply to the foliage made leaf conductance more independent from the leaf water status: g_L even increased with decreasing Ψ_L in the lower foliage position, while remaining insensitive in the upper foliage (Table 3 in III).

3.3. Effects of soil-to-leaf hydraulic conductance

Among various environmental and plant inner factors, the liquid-phase conductance accounted for the largest part (28–82% in spruce and 50–69% in birch, depending on canopy position and study year) of the total variation in leaf gaseous-phase conductance during the midday period. The results indicated that stomatal responsiveness to **VPD** was closely related to stomatal sensitivity to changes in liquid-phase conductance (Fig. 8 in II), whereas the improved water supply made g_L less sensitive to changes in the whole-plant hydraulic conductance, G_T (Table 3 in III). This supports the finding of Meinzer et al. (1995), that stomatal adjustments to G_T coordinate transpiration with liquid-phase transport efficiency rather than with bulk leaf water status. In anisohydric species, however, the stomatal behaviour with respect to G_T involves changes in leaf water potential, resulting in a curvilinear relationship between stomatal conductance and G_T (Hubbard et al., 2001). Recent studies have confirmed that, in addition to maintaining a long-term balance between vapour and liquid-phase water conductances in plants, stomata are exquisitely sensitive to short-term, dynamic perturbations of liquid water transport as well (Buckley and Mott, 2002; Meinzer, 2002).

The mean hydraulic conductance of the soil-to-leaf transport pathway was 1.4–2.6 times higher for the upper than for the lower-canopy foliage in all studied species (Fig. 3; see also Fig. 4 in I, Fig. 5 in III, Table 4 in IV and Table 2 in VI). The same conclusion could be drawn based on the analysis of both porometric (Norway spruce, silver birch) and sap flow data (Norway spruce, European larch). Thus, the water flow to the shade foliage has to overcome a bigger resistance than to the sun foliage. One may conclude that the path length from bulk soil to leaf cannot be the term responsible for the variation in G_T within crowns of the studied tree species, because the distance for water transfer was always longer for the upper-canopy foliage than for the lower-canopy foliage. The results obtained on spruce and larch trees suggested that smaller G_T for the lower-crown branches resulted from greater reductions in sap flow, while there were no statistically significant differences in $\Delta\Psi$ between the lower and upper canopy (Fig. 5 in I; Table 4 in IV).

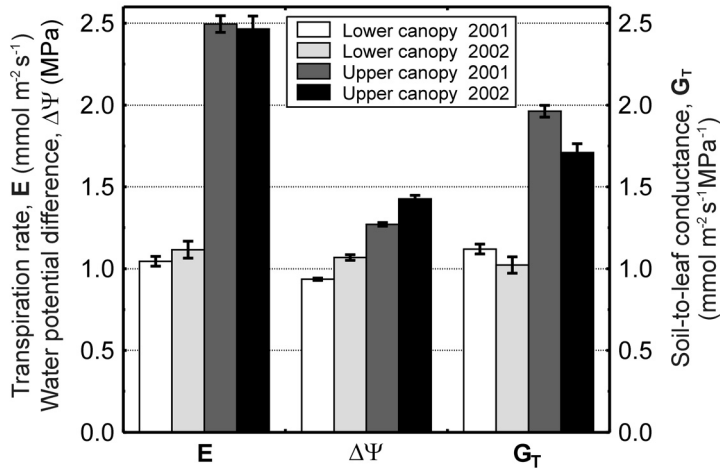


Figure 3. Mean transpiration rate (E), water potential difference ($\Delta\Psi$) between the soil and foliage, and soil-to-leaf conductance (G_T) around midday in silver birch. The bars indicate \pm SE of the means.

Smaller G_T revealed for the lower-canopy foliage is associated with more conservative water economy if compared to the upper canopy. Our results are analogous to the data on grape cultivars with different water-use behaviour published by Schulz (2003). The differential stomatal control allows a tree to conserve water, reserving it for upper and photosynthetically more effective foliage. Conservative water use might be advantageous for the lower canopy if low xylem transport efficiency is related to higher vulnerability to cavitation. Studies performed in different tree species have indicated that sun or leader branches are hydraulically more efficient and less vulnerable to xylem embolism than shaded branches or side shoots (Cochard et al., 1999; Lemoine et al., 2002a; Mayr et al., 2003; Burgess et al., 2005).

The experiments in silver birch indicated that both hydraulic capacity of the vascular system and light availability are involved in regulation of the leaf water relations depending on canopy positions and time of day. In the morning, leaf conductance in the lower-canopy foliage was limited primarily by light availability (Fig. 4B); in the afternoon, the birch shoots situated in shade but artificially provided with enhanced water supply (Lc H+I-) demonstrated the highest g_L among the shade foliage treatments. By this time the trees' internal water reserves had been depleted, long-distance water transport became critical, and g_L was primarily being limited by the hydraulic capacity of the water-conducting system. It has been shown that stem water storage could play a significant role in water and carbon economy of tall trees, the contribution of which increases with tree size (Goldstein et al., 1998; Phillips et al., 2003b).

Stratton et al. (2000) indicated that species with higher wood-saturated water content were more efficient in terms of long-distance water transport, exhibiting smaller diurnal variation in Ψ_L and higher maximum photosynthetic rates. In the upper canopy of silver birch, the reduction of hydraulic constraints resulted in neither higher leaf conductance nor transpiration rate (Fig. 4A; see also Fig. 3A in III). Thus, the long-distance water transport and hydraulic constraints were not limiting for the upper-canopy foliage.

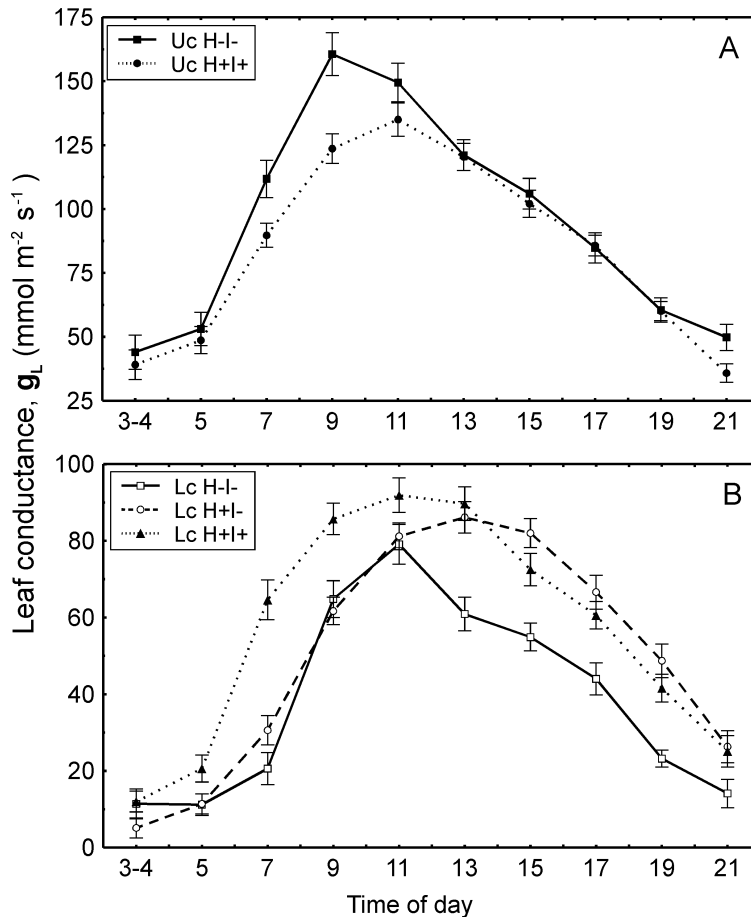


Figure 4. Daily dynamics of leaf conductance (g_L) in the upper (A) and lower-canopy foliage (B) in intact and experimentally manipulated shoots of silver birch. The bars indicate \pm SE of the means.

Higher irradiance level combined with improved leaf water supply (Lc H+I+) slightly increased maximum values of g_L in the shade foliage, but decreased

them in the sun foliage (Fig. 4A; see also Table 1 in III). Similarly, Hinckley et al. (1994) observed in their experiment with hybrid poplar trees that stomatal conductance of the excised branches under non-limiting light and water supply increased both in shade and sun-grown branches, however, the increase was bigger for the shade foliage. There is no unequivocal explanation for the statistically significant decrease in g_L in upper-canopy leaves with improved water supply in comparison with the control. One cannot exclude partial stomatal closure as a result of increased epidermal backpressure due to high turgor of the epidermal cells at improved water supply (Buckley et al., 2003).

At a glance, our results seem to contradict the traditional view, according to which the resistance to water movement in tree crowns rises with height above the ground, due to increasing effect of gravitational and frictional forces (Koch et al., 2004; Woodruff et al., 2004). However, the results accord with the data from several earlier studies performed in gymnosperms (Mecuccini and Grace, 1996; Protz et al., 2000) as well as in angiosperms (Clearwater and Meinzer, 2001; Lemoine et al., 2002b). The most recent papers confirm the same regularity. Aasamaa et al. (2004) indicated that maximum shoot hydraulic conductance increased acropetally in a temperate deciduous forest canopy. Branch hydraulic permeability in *Pinus taeda* L. decreased significantly with crown depth and it varied depending on crown size (Jerez et al., 2004). Even in the crowns of 60–67-m-tall trees of *Sequoia sempervirens* (D. Don) both sapwood-specific and leaf-specific hydraulic conductivity of branches increased with height (Burgess et al., 2005). All this evidence supports the idea that the leaves growing on lower long branches, characterised by small radial increments and containing smaller vessels/tracheids, are hydraulically more constrained, although this effect is not reflected in leaf water status. A less negative Ψ_L is necessary for preventing the formation of deleterious water potential gradients, which could damage the hydraulically less safe water-conducting system of the lower-crown foliage. Recent studies have demonstrated that extra-vascular resistance to water transfer in live leaf tissues may also be substantial, varying between crown positions with respect to light availability (Sack et al., 2003, 2005). Thus, the smaller G_T for the lower canopy layer compared to the upper canopy observed in this thesis could be related, at least partly, to the smaller hydraulic conductivity in the leaf extra-vascular pathway as well.

The disparity between our findings and the studies revealing no differences in branch hydraulic capacity between the upper and lower crown (Cochard et al., 1997; Hubbard et al., 2002) can be explained by different exposition of the sample trees. Our studies in spruce and birch were carried out on closed-canopy forest trees, while those referred to have been performed on trees experiencing relatively uniform irradiance and VPD within their canopies. Even environmental conditions throughout the whole crown probably did not promote the development of differences in hydraulic properties of branches between different crown layers (Cochard et al., 1997; Hubbard et al., 2002). This

supposition is also confirmed by data obtained on open-grown trees of *Pinus contorta* Dougl. ex Loud. (Protz et al., 2000) and sparsely growing orchard trees of *Prunus armeniaca* L. (Alarcon et al., 2003). As for European larch (IV), the light conditions within the crowns of larch saplings growing in a sparse mountainous community were also relatively uniform. Nevertheless, the competition for sunlight probably led to differences in xylem hydraulic properties between the upper and lower branches. Beside immediate effects of irradiance on plant water relations, we also have to consider possible changes in the light regime that have occurred during the plant's life history, the effects of which may cumulate from year to year (Protz et al., 2000).

The soil-to-leaf hydraulic conductance in Norway spruce and silver birch varied also between the study years. In the cool and rainy summer of 2000, the water supply for Norway spruce foliage turned out to be less critical and the co-ordination between the liquid and gaseous phase conductance less tight than in summer 1997 (Fig. 8 in I). In 2000, the average G_T for the upper canopy of the same trees was 1.3–1.4 times higher than in 1997 (Fig. 4 in I), when the second half of the study period was characterised by very warm and dry weather in Estonia. In silver birch the mean G_T for both canopy layers was on average ten per cent higher in 2001 than in 2002 (Fig. 3), which most likely also resulted from differences in weather conditions. High VPD probably induced embolism in the water transport pathway, leading to dynamic water stress in both species, despite sufficient water reserves in the soil. Although, several studies have suggested that the whole-tree hydraulic conductance declines with decreasing soil water content under drought conditions (Irvine et al., 1998; Addington et al., 2004), the interyear variation in G_T of our sample trees could not be attributed to soil water availability. In both cases the soil water content was rather high, and in Järvselja Experimental Forest the soil was characterized by large water storage capacity. The variation among the study years gave evidence of the impact of meteorological conditions on the hydraulic capacity of the trees' water-conducting system, thus involving factors other than soil water content.

3.4. Effects of branch structural characteristics

Patterns of the branch structural traits with respect to crown position accord with the spatial variation in physiological characteristics described above. The differential in G_T revealed between the lower and upper canopy could most likely be attributed to variation in xylem anatomical structure and/or the number of branch junctions on the path that water must take to get from the soil to a certain leaf (Rust and Hüttl, 1999; Tyree and Zimmermann, 2002). The observed variability in tracheid diameter (D_T) indicated that sapwood permeability was probably responsible for the decrease in hydraulic capacity in

the lower-crown branches of European larch trees (Table 4 in IV). The difference in the mean values of D_T between the crown positions was not large (ca. 2 μm), but given that water transfer in xylem conduits obeys Hagen-Poiseuille's equation (Nobel, 1999), small changes in capillary radius bring about substantial changes in capillary hydraulic conductivity. Other studies in the wood anatomy of sun versus shade branches performed in multiple species show the same regularity (Protz et al., 2000; Lemoine et al., 2002a; Mayr et al., 2003).

Several studies have indicated that a decrease in leaf area to sapwood area ratio (A_l/A_s) could offset the effect of increased hydraulic resistance due to longer flow path for water transfer in trees (Schäfer et al., 2000; McDowell et al., 2002; Barnard and Ryan, 2003). A very recent work carried out on tall *Sequoia sempervirens* trees revealed that the upper-crown branches had significantly higher Huber values (reciprocal of A_l/A_s) than the branches located in the lower crown (Burgess et al., 2005). In contrast, our results in European larch and silver birch demonstrated that lower-crown branches were characterised by smaller A_l/A_s (i.e. larger Huber values) than the upper-crown branches (Fig. 5A; see also Table 4 in IV). In silver birch, there was on average 28.7% and 68.3% more sapwood per unit leaf area for the lower-crown branches compared to the middle and upper-crown branches, respectively (V). Smaller leaf to sapwood area ratio in lower branches relative to upper branches have also been observed in both closed and open-canopy trees of *Pinus contorta* (Protz et al., 2000). Within crowns of *Pinus sylvestris*, however, the A_l/A_s did not exhibit a unidirectional trend: it was lower in the middle region and increased both in basal and apical directions (Berninger and Nikinmaa, 1994).

One may conclude that smaller A_l/A_s observed in the lower-crown branches of both larch and birch trees mitigated differences in xylem hydraulic capacity between the lower and upper canopy positions caused by the smaller sapwood permeability of the lower-crown branches. In the tall *Sequoia sempervirens* trees, the opposite trend in leaf area to sapwood area ratio was revealed (Burgess et al., 2005). However, the distance between the upper and lower sample branches in the *Sequoia* trees was very large (30 m), and the higher Huber values in upper-crown branches probably improved the water supply for photosynthetically more effective foliage. In smaller trees, in which the size-related biophysical constraints resulting from frictional forces and gravitation are not so substantial, effects of light availability on branch hydraulic properties seem to be primarily responsible for changes in A_l/A_s . In accordance with our results, some recent studies have indicated that xylem hydraulic conductivity indeed promotes the changes in A_l/A_s , and therefore, increasing crown height *per se* is not necessarily responsible for a decrease in this characteristic (Mokany et al., 2003; Phillips et al., 2003a).

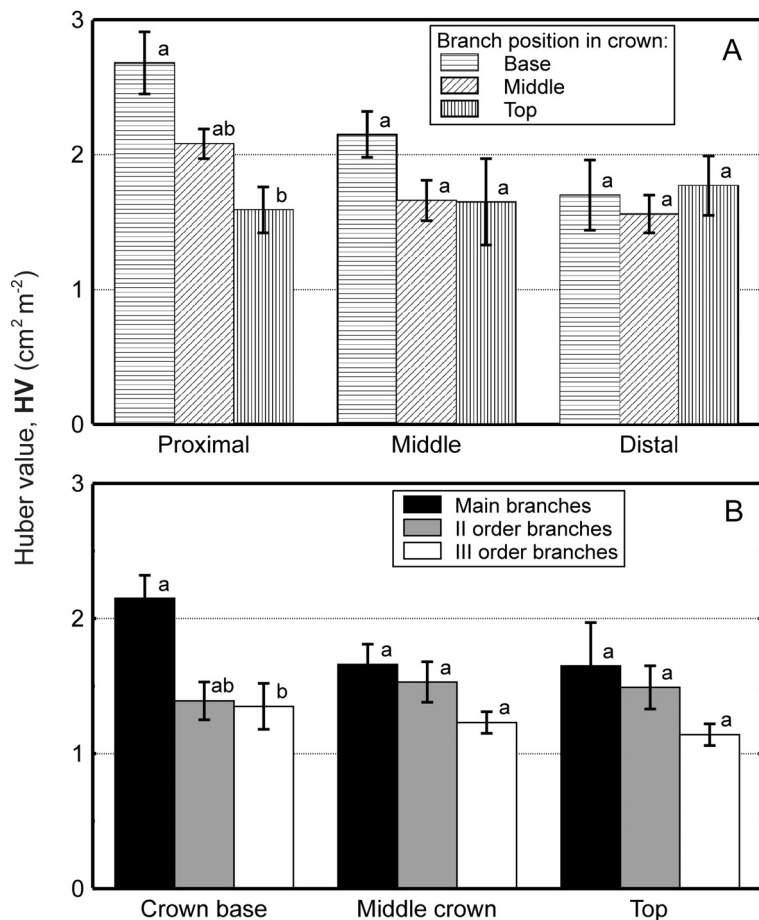


Figure 5. Spatial variation of Huber value within the crown of silver birch. A, variation with branch vertical position in a crown, indicated separately for branch proximal, middle and distal parts; B, variation with branch orders. The bars indicate \pm SE of means; different letters at the columns denote statistically significant ($P < 0.05$) differences.

In silver birch, the leaf area to sapwood area ratio increased also with increasing branch order, although a statistically significant trend appeared only at the crown base (Fig. 5B). This pattern favours the hydraulic dominance of primary branches over the branches of higher orders; the result is in accordance with the hydraulic segmentation hypothesis (Tyree and Zimmermann, 2002). 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.

3.5. Responses to elevated CO₂ concentration

The saplings of Norway spruce grown both at ambient and elevated CO₂ concentrations showed significantly higher values of xylem sap flux in the upper crown position compared to the whole tree (Fig. 1 in VI), reflecting better water supply of the upper-canopy foliage. The trees grown at ambient CO₂ demonstrated higher values of G_T in the upper crown position, whereas no remarkable differences in G_T were found between the upper crown and the whole tree in the elevated CO₂ treatment (Table 2 in VI). Recent studies have suggested that atmospheric CO₂ enrichment enables mitigation of the light limitation of photosynthesis in shaded foliage of Norway spruce (Marek et al., 2001, 2002). The enhanced photosynthesis, in its turn, may increase the branch growth rate, especially in the lower crown position, and therefore, the sapwood permeability and/or relative sapwood area is expected to increase too. Thus, we suppose that a causal linkage could exist between atmospheric CO₂ enrichment and branch hydraulic capacity to supply water to leaves. Studies in *Larix sibirica* Ledeb. and *Larix kaempferi* (Lamb.) Carr. seem to support this idea, indicating that elevated CO₂ concentration may increase the lumen diameter of tracheids, although the effect was statistically insignificant (Yazaki et al., 2001, 2004). However, the experiments with saplings of *Pinus sylvestris* proved that plants grown at elevated CO₂ had both larger earlywood share and tracheid diameter (Ceulemans et al., 2002).

The spruce trees grown at elevated CO₂ concentration exhibited significantly higher xylem sap flux compared to the trees at ambient CO₂ concentration (Fig. 6). We suppose that the difference between the two CO₂ treatments was related to higher soil water content in deeper soil layers in the dome with an elevated CO₂ atmosphere, which had already formed before we started our measurements. This could have resulted from the lower transpiration rate of the trees growing at elevated CO₂, a very common phenomenon under conditions without water limitation (Kellomäki and Wang, 1998; Wullschlegler et al., 2002; Bunce, 2004). Although coniferous species generally demonstrate rather weak response to elevated atmospheric CO₂, the results in Norway spruce have indicated that stomatal conductance will substantially decline at elevated CO₂ concentration (Medlyn et al., 2001). Therefore, one may suppose that the spruce trees grown at elevated CO₂ level probably did not deplete soil water storage as fast as the trees grown at ambient CO₂. Also, the sap flow studies carried out on Scots pines have indicated that elevated CO₂ concentration could have an important influence on trees' seasonal water use (Kellomäki and Wang, 1998). Thus, the trees grown at elevated CO₂ partial pressure could have an advantage over the trees at the ambient CO₂ because of their more economical use of soil water reserves. However, a concurrent increase in leaf area index, common in environments with elevated CO₂, could diminish such advantage (Schäfer et al., 2002).

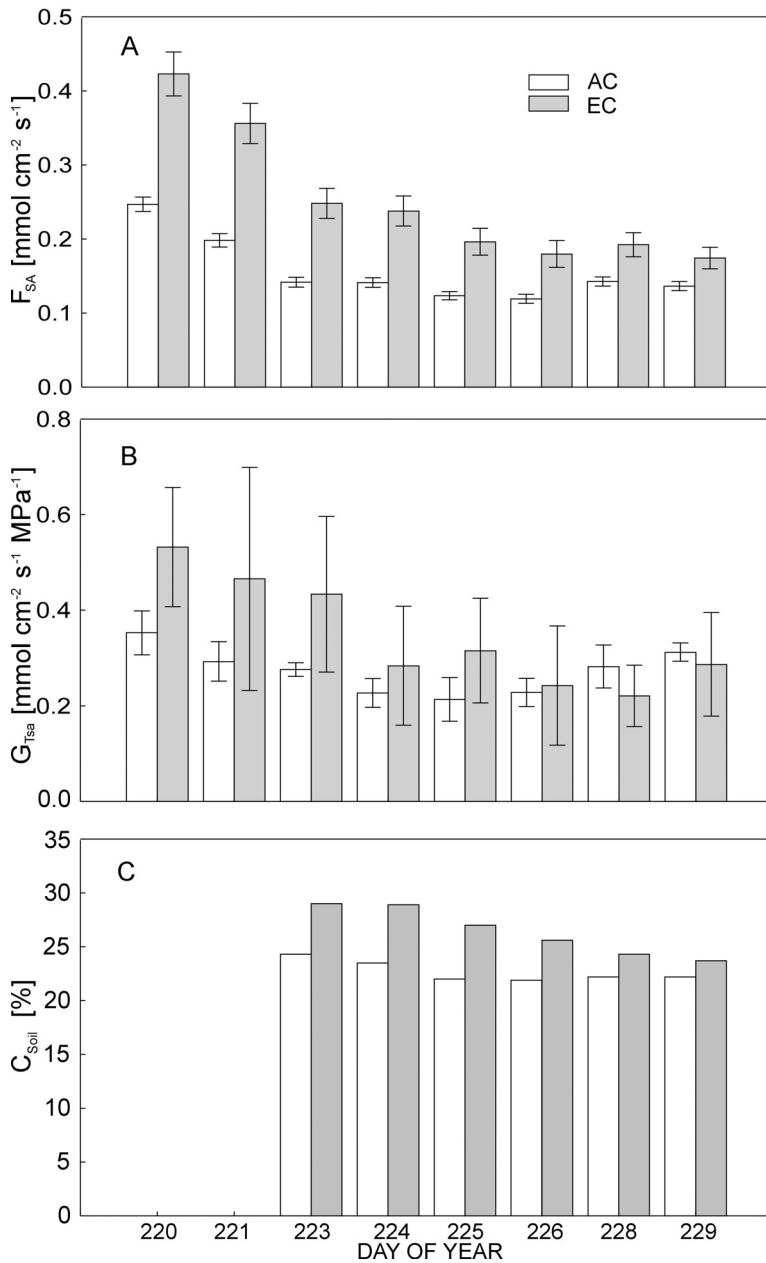


Figure 6. Water relations of Norway spruce trees grown at ambient (AC) and elevated CO₂ concentrations (EC): A, mean daily sap flux density expressed per sapwood area (F_{SA}); B, mean soil-to-leaf hydraulic conductance expressed per sapwood area (G_{Tsa}); C, soil volumetric water content (C_{Soil}) of the wettest soil layer in early morning. The bars indicate \pm SE of means.

4. CONCLUSIONS

1. Responses of leaf conductance to irradiance and atmospheric evaporative demand vary widely within a canopy of woody plants, depending significantly on both leaf position and water status. Trees are able to adjust their water relations to the prevailing environment by coordinating the transport capacity of the water-conducting system with changes in stomatal conductance to prevent leaf water potential from reaching critical values. The liquid-phase transport capacity largely determines the maximum levels of g_L , while stomatal sensitivity to hydraulic and environmental signals varies between crown positions and years.
2. The results, based on both porometric and sap flow measurements, supported the hypothesis that stomatal conductance at the base of the live crown is limited not only by low light availability but also by a plant's inner hydraulic constraints. In the forenoon, g_L in the shade foliage is primarily limited by low light availability, in the afternoon, by limited water supply.
3. The water flow from bulk soil to the shade foliage located at the crown base has to overcome a bigger resistance than to the sun foliage located at the treetop. Therefore, the length of the water transport pathway from soil to leaf cannot be the primary term responsible for the variation in soil-to-leaf conductance within tree crowns. Environmental gradients occurring in forest canopies promote differentiation in wood hydraulic properties with respect to crown positions. The differences in G_T between the lower and upper canopy could be attributed to variation in size of xylem conduits. Smaller G_T revealed for the lower-canopy foliage is associated with more conservative water economy if compared to the upper canopy.
4. The differences in G_T revealed between different crown positions did not result from variation in leaf area to sapwood area ratio of the branches. On the contrary, the smaller A_l/A_s observed in the lower-crown branches may be considered as a means to mitigate differences in xylem water transport capacity between the lower and upper canopy. The variability in A_l/A_s with respect to branch orders contributes to preferential water flow along the main axis, potentially providing better water supply for the branch apical bud and foliage located in the better-insolated outer part of the crown.
5. Changes in atmospheric CO_2 concentration modify foliage water relations, while a tree's responses to elevated CO_2 depend on soil water availability. Elevated CO_2 can improve water supply for foliage located in lower canopy under shade conditions, smoothing differences in G_T between the crown layers.

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SUMMARY IN ESTONIAN

Hüdrauliliste ja keskkonna piirangute mõju puulehtede veevahetusele sõltuvalt asukohast võras

Puude suurtest mõõdetest tuleneb keskkonnatingimuste oluline varieeruvus puuvõrade sees. Tihedas puistus varieeruvad keskkonna parameetrid eelkõige vertikaalselt – ülemised oksad ja lehed on atmosfäärifaktoritele paremini eksponeeritud kui võra alusel kasvavad lehed (Rijkers et al., 2000). Võra alumises osas paiknevad varjulehed saavad vähem valguskiirgust, nende temperatuur on harilikult madalam ülemiste lehtede omast, lisaks on ka õhu niiskusesisaldus võra alusel tavaliselt suurem kui puistu kohal tsirkuleerivas õhus. Taoline keskkonnatingimuste ruumiline varieeruvus tingib paratamatult lehestiku kohanemise konkreetsetele mikrokeskkonna tingimustele (Niinemets et al., 1998; Sellin, 2001), millest olulisim on valguse kättesaadavus. Ehkki varjulehed kasutavad valgust efektiivsemalt, on nii nende fotosünteesi tase kui ka õhulõhede juhtivus ning transpiratsiooni intensiivsus (**E**) märgatavalt väiksemad valguslehtede omast. Lehes paiknevate õhulõhede veeauru juhtivus ongi üks olulisemaid füsioloogilisi karakteristikuid, mis kontrollib taime veevahetust ja selle regulatsiooni. Kuna läbi õhulõhede toimub lisaks veeaurule ka fotosünteesil seotava süsihappegaasi difusioon lehe sisemusse, siis on õhulõhede juhtivus ja fotosüntees omavahel tihedalt seotud (Nobel, 1999).

Hästi teada on asjaolu, et valgustingimused mõjutavad lisaks fotosünteesi fotofüüsikalistele protsessidele ka õhulõhede juhtivust, veelgi enam — vähest valgust peetakse peamiseks faktoriks, mis piirab õhulõhede juhtivust võra sisemuses või selle alusel (Morecroft and Roberts, 1999; Lemoine et al., 2002b). Viimase kümnendi jooksul läbi viidud uurimused aga näitavad, et ka vedela faasi (s.o. hüdrauliline) juhtivus taimede juhtkudedes avaldab mõju õhulõhede avatusele, olles seotud õhulõhede hüdroaktiivsete reaktsioonide (Buckley, 2005) ja lehe veevarustusega (Meinzer, 2002). Nii on mõnedel puuliikidel leitud, et võra alusel kasvavate varjuokste hüdrauliline juhtivus on sageli väiksem kui valgusele hästi eksponeeritud ülemistel okstel (Cochard et al., 1999; Lemoine et al., 2002a; Mayr et al., 2003). Madalama hüdraulilise juhtivuse põhjused võivad olla erinevad: trahheede ja trahheiidide väiksemad mõõtmed (Tyree and Zimmermann, 2002; Sperry et al., 2005), lühivõsude ja eraldusvõtmete moodustumine (Rust et al., 2004), suurem sõlme- või harunemiskohtade arv (Rust and Hüttl, 1999).

Tänaseks päevaks pole veel kaugeltki selge, mis määrab konkreetse lehe veevahetuse parameetrid puuvõras ja kuidas on need seotud taime hüdraulilise arhitektuuriga tervikuna (Cruiziat et al., 2002; Tyree and Zimmermann, 2002; Burgess et al., 2005). Käesoleva töö eesmärgiks oli hinnata hüdrauliliste ja keskkonnast tulenevate piirangute mõju lehestiku veevahetusele sõltuvalt lehtede asukohast võras. Selleks viidi läbi eksperimendid kolmel puuliigil —

harilikul kuusel (*Picea abies* [L.] Karst.), arukasel (*Betula pendula* Roth) ja euroopa lehisel (*Larix decidua* Mill.). Katsete tulemused on avaldatud/ avaldamisel kuues artiklis. Vaatluse all oli lehejuhtivuse (g_L) ja lehestiku veevahetuse sõltuvus nii võra sees valitsevatest keskkonnatingimustest (valguse kättesaadavus; veeaururõhkude erinevus lehe ja atmosfääri vahel, **VPD**) kui ka taime sisestest hüdraulilistest parameetritest (lehe/võrse veepotentsiaal; vedela faasi juhtivus mullast leheni, G_T). Töö peamiseks hüpoteesiks oli, et võra varjuosas kasvavate lehtede juhtivust veeaurule ei määra ainuüksi valgustingimused, vaid olulisel määral ka taimesisesed hüdraulilised piirangud, mis eeldatavalt johtuvad taimede ehituslikest iseärasustest. Seepärast vaadeldakse töös füsioloogiliste näitajate (g_L , **E**, ksüleemivoolu intensiivsus, G_T) kõrval ka veevahetuse seisukohalt oluliste struktuursete parameetritele (trahheiidide valendiku läbimõõt; lehtede pindala ja maltspuidu ristlõikepindala suhe, A_L/A_S) varieeruvust võra erinevates osades kasvavatel okstel. Lisaks on tähelepanu all ka kõrgenenud süsihapegaasi kontsentratsiooni mõju lehestiku veevahetusele. Teadmised sellest, kuidas ja mis põhjustel lehtede vee- ja gaasivahetus võras varieerub, võimaldavad senisest paremini iseloomustada ning ennustada metsapuude talitlust ja kasvu muutuvates keskkonnatingimustes.

Töö tulemused näitasid, et lehejuhtivuse reaktsioonid valgusele ja veeaururõhu defitsiidile varieerusid ulatuslikult puude võras, sõltudes oluliselt nii lehe asukohast kui ka veestaatusest. Puud on võimelised seadistama oma veevahetust vastavalt keskkonna-tingimuste muutustele, koordineerides veejuhtesüsteemi transpordivõimet õhulõhede juhtivusega veeaurule, vältides samal ajal lehe veepotentsiaali langemist allapoole liigimast kriitilist piiri. Lehejuhtivuse maksimumväärtused on suures osas määratud juhtkudede vedela faasi juhtivusega, kusjuures õhulõhede tundlikkus nii hüdraulilistele kui ka keskkonnast tulevatele signaalidele varieerub olulisel määral sõltuvalt asukohast võras ja vaatlusaluse aasta ilmastikust. Nii poromeetrilisel kui ksüleemivoolu meetodil saadud tulemused toetasid hüpoteesi, et madal g_L , mis on iseloomulik võra varjuosas kasvavatele lehtedele, ei ole tingitud üksnes vähesest valguse kättesaadavusest, vaid ka taime sisemistest hüdraulilistest piirangutest vee liikumisele. Hüdrauliliste ja keskkonnast tulenevate piirangute osatähtsus võrastiku piires varieerus, sõltudes samas ka kellaajast. Kui ennelõunal oli g_L võra varjuosas limiteeritud peamiselt valguse poolt, siis peale lõunat osutus limiteerivaks eelkõige lehtede veevarustus.

Kuna transporditeede hüdrauliline juhtivus mullast kuni alumiste lehtedeni oli oluliselt väiksem kui mullast ülemiste lehtedeni, siis on alust arvata, et veetranspordi teekonna pikkus uuritud puuliikidel ei olnud määravaks faktoriks G_T võrasisese varieeruvuse kujunemisel. Tulemused viitavad, et valgustingimuste heterogeensus puude võras võib oluliselt mõjutada maltspuidu hüdraulilisi omadusi sõltuvalt asendist võras. G_T erinevused võra alumiste ja ülemiste lehtede vahel on tõenäoliselt tingitud ksüleemi juhtelementide mõõtmete erinevusest võra sees. Väiksem G_T võra alaosas, võrreldes ülaosaga, on seotud varjulehtede konservatiivsema veekasutusega, võimaldades ühtlasi ülemise,

fotosünteesiliselt efektiivsema lehestiku paremat veevarustust. Hüdraulilise juhtivuse erinevused võra erinevates kihtides ei olnud tingitud lehtede pindala ja maltspuidu ristlõikepindala suhte varieerumisest võras. Võime väita hoopis vastupidist, alumiste okste väiksem A_l/A_s , pigem leevendas ksüleemi erijuhtivusest tulenevaid erinevusi alumiste ja ülemiste okste vahel. A_l/A_s trend sõltuvalt okste järgust näitas, et võra arhitektuur soodustab veevoolu oksa peateljes, võimaldades oksa apikaalsete pungade ja võra välimise, valgusele paremini eksponeeritud lehestiku efektiivsemat veevarustust.

Süsihappegaasi kontsentratsioonide muutused atmosfääris modifitseerisid lehestiku veevahetust, kusjuures puude reaktsioon kõrgenenud süsihappegaasile sõltus mullavee kättesaadavusest. Kõrgenenud CO_2 kontsentratsioonil kasvanud puudes olid ksüleemivoolu intensiivsus ja hüdrauliline juhtivus suuremad kui puudes, mis kasvasid tavapärase CO_2 taseme juures. Saadud tulemused näitasid ka seda, et suurenenud süsihappegaasi kontsentratsiooniga keskkonnas võib lehestiku veega varustatus võra alumises osas paraneda.

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PUBLICATIONS

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II. Research history

- 1. Research interests:** water relations and gas exchange in woody species

2. Publications:

- Kupper, P. and Sellin, A. 2003. Canopy gas exchange and stomatal conductance of European larch in half-open alpine community. — In: Frey T. (ed.), Kaas-aegse ökoloogia probleemid. Eesti ökoloogia globaliseeruvus maailmas. Tartu, Teadusühing IM SAARE, pp. 94–101. /in Estonian/
Kupper, P., Tulva, I. and Mänd, P. 2003. From dusk to dawn: do plants sleep deeply? — In: Tammaru T., Puura I. (eds.), Puhkuse Teooria. Schola Biotheoretica XXIX. Tartu, OÜ Sulemees, pp. 21–25. /in Estonian/
Kupper, P. 2004. Water relations of trees — thoughts about stability. — In: Tulva I., Öpik M., Puura I. (eds.), Tasakaalu Teooria. Schola Biotheoretica XXX. Tartu, OÜ Sulemees, pp. 21–25. /in Estonian/

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- Sellin, A. and Kupper, P. 2005. Variation in leaf conductance of silver birch: effects of irradiance, vapour pressure deficit, leaf water status and position within a crown. *Forest Ecology and Management* **206**: 153–166.
- Sellin, A. and Kupper, P. 2005. Effects of light availability versus hydraulic constraints on stomatal responses within a crown of silver birch. *Oecologia* **142**: 388–397.
- Kupper, P., Sellin, A., Klimankova, Z., Pokorný, R. and Puértolas, J. 2006. Water relations in Norway spruce trees growing at ambient and elevated CO₂ concentrations. *Biologia Plantarum*. /in press/
- Kupper, P., Sellin, A., Tenhunen, J., Schmidt, M. and Rahi, M. 2006. Effects of branch position on water relations and gas exchange of European larch trees in an alpine community. *Trees — Structure and Function*. /in press/
- Sellin, A. and Kupper, P. 2006. Spatial variation in sapwood area to leaf area ratio and specific leaf area within a crown of silver birch. *Trees — Structure and Function*. /in press/

3. Grants and scholarships:

- Scholarship for doctoral students from the Ministry of Education and Research of Estonia (DBGBO 2349)
- DAAD scholarship: 2002
- Scholarship in frame of MERCI project (EC Fifth Framework Programme “Human Potential Research Improving — Transnational Access to Research Infrastructure”): 2003
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- Travel scholarship for participation in NorFA course: 2004

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- Scientific research in Bayreuth University, Bayreuth, Germany: Jul. — Nov. 2002
- Scientific research in Mendel Agricultural University, Brno, Czech Republic: Aug. 2003
- Participation in the NorFA course “Effects of management practices on carbon sequestration in forest ecosystems”, Joensuu, Finland: Sept. 2004

CURRICULUM VITAE

I. Üldandmed

- 1. Ees- ja perekonnanimi:** Priit Kupper
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6. Praegune töökoht, amet: Tartu Ülikool, botaanika ja ökoloogia instituut, erakorraline teadur
7. Haridus: Põltsamaa Keskkool: 1993
Tartu Ülikool, *baccalaureus scientiarum* zooloogia erialal: 1998
Tartu Ülikool, *magister scientiarum* ihtüoloogia ja kalanduse erialal: 2001
8. Keelteoskus: eesti, inglise, saksa
9. Teenistuskäik: Eesti Maaülikool, loomakasvatus instituut, ihtüopatoloog (1998–2001)
Tartu Ülikool, botaanika ja ökoloogia instituut, doktorant (2001–2006)
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II. Teaduslik ja arendustegevus

- 1. Peamised uurimisvaldkonnad:** puittaimede vee ja gaasivahetus
- 2. Publikatsioonide loetelu:**
Kupper, P. and Sellin, A. 2003. Võrastiku gaasivahetus ja õhulõhede juhtivus euroopa lehisel poolavatud alpikoosluses. — In: Frey T. (toim.), Kaasaegse ökoloogia probleemid. Eesti ökoloogia globaliseeruvus maailmas. Tartu, Teadusühing IM SAARE, lk. 94–101.
Kupper, P., Tulva, I. and Mänd, P. 2003. Ehast koiduni: kas taim magab sügavalt? — In: Tammaru T., Puura I. (toim.), Puhkuse Teooria. Schola Biotheoretica XXIX. Tartu, OÜ Sulemees, lk. 21–25.
Kupper, P. 2004. Mõnda puude veevahetusest — mõeldes tasakaalule. — In: Tulva I., Öpik M., Puura I. (toim.), Tasakaalu Teooria. Schola Biotheoretica XXX. Tartu, OÜ Sulemees, lk. 21–25.

- Sellin, A. and 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. *Annals of Forest Science* **61**: 419–429.
- Sellin, A. and Kupper, P. 2005. Variation in leaf conductance of silver birch: effects of irradiance, vapour pressure deficit, leaf water status and position within a crown. *Forest Ecology and Management* **206**: 153–166.
- Sellin, A. and Kupper, P. 2005. Effects of light availability versus hydraulic constraints on stomatal responses within a crown of silver birch. *Oecologia* **142**: 388–397.
- Kupper, P., Sellin, A., Klimankova, Z., Pokorný, R. and Puértolas J. 2006. Water relations in Norway spruce trees growing at ambient and elevated CO₂ concentrations. *Biologia Plantarum*. (in press)
- Kupper, P., Sellin, A., Tenhunen, J., Schmidt, M. and Rahi, M. 2006. Effects of branch position on water relations and gas exchange of European larch trees in an alpine community. *Trees — Structure and Function*. (in press)
- Sellin, A. and Kupper, P. 2006. Spatial variation in sapwood area to leaf area ratio and specific leaf area within a crown of silver birch. *Trees — Structure and Function*. (in press)

3. Saadud uurimistoetused ja stipendiumid:

- Eesti Vabariigi Haridus- ja Teadusministeeriumi doktorandi stipendium (DBGBO 2349)
- DAAD (Deutscher Akademischer Austauschdienst) stipendium: 2002
- Stipendium MERCI projekti (EC viies raamprogramm “Human Potential Research Improving — Transnational Access to Research Infrastructure”) raames: 2003
- Stipendium, osalemiseks 14-ndal rahvusvahelisel FESPB kongressil: 2004
- Reisistipendium, osalemiseks NorFA doktorikoolis: 2004

4. Konverentside ettekanded:

“Variability of gas exchange, hydraulic conductance and leaf-to-sapwood area ratio within crowns of European larch trees” (stendi ettekanne), 14-s FESPB kongress, Krakow, Poola, 23–27 august, 2004.

III. Erialane enesetäiendus

- Teadustöö Bayreuth’i Ülikoolis, Bayreuth, Saksamaa: juuni — november, 2002
- Teadustöö Mendeli-nimelises Põllumajandus Ülikoolis, Brno, Tšehhi Vabariik: august, 2003
- Osamine NorFA kursusel “Effects of management practices on carbon sequestration in forest ecosystems”, Joensuu, Soome: september, 2004