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Hydraulic conductance and stomatal sensitivity to changes of leaf water status in six deciduous tree species

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Abstract

The relationship between shoot hydraulic conductance (L) and stomatal sensitivity to changes in leaf water status was studied in the saplings of six deciduous tree species. L increased significantly in sequence: *Acer platanoides* < *Tilia cordata* < *Padus avium* = *Quercus robur* < *Salix caprea* = *Populus tremula*. L was higher in the trees grown in soil with a higher nitrogen content and lower in the trees grown under mild water stress or kept in darkness for several days. L was higher in July than in September in all the species. L correlated positively with maximum photosynthesis, stomatal conductance and stomatal sensitivity to an increase in leaf water potential, but negatively with stomatal sensitivity to a decrease in leaf water potential. The correlations between L and any other parameter were approximated by three different curves: data for water-stressed plants fit to the first, data for plants kept in darkness fit to the second and all the other data fit to the third curve. The reasons of the differences of shoot hydraulic conductance in the different experimental sets and the mechanisms which may cause the correlation between L and the other characteristics are discussed.

Additional key words: *Acer platanoides, Padus avium, Populus tremula, Quercus robur, Salix caprea, Tilia cordata.*

Introduction

Shoot hydraulic conductance is an essential characteristic of the plant water regime because it influences the water supply. The hydraulic conductance of the xylem correlates with some of its anatomical parameters (Zimmermann 1983, Calkin *et al.* 1986, Ewers *et al.* 1990) and it changes also during short-term variations in water balance (Cochard 1992, Yang and Tyree 1993, Zotz *et al.* 1994, Kavanagh *et al.* 1999). Usually the hydraulic conductance of stems (without leaves) is directly measured (Sellin 1993, Tognetti *et al.* 1999a,b). The data of conductance in shoots with leaves are usually obtained by calculations using transpiration rates (Comstock and Mencuccini 1998, Bond and Kavanagh 1999). There is meagre data about hydraulic conductance of tree shoots obtained by direct measurements of the liquid water flow through the shoots with leaves (Sobrado 1997/1998, Wei *et al.* 1999a,b).

The path of water through the leaf to evaporation sites in intercellular spaces has been an object of discussions for a long time. The most widely accepted point of view is that water flows through the xylem and then through the parenchymal tissue before evaporation to the intercellular spaces (Boyer 1985, Steudle 1997). The diameters of the xylem conducting elements are relatively small in leaves (Esau 1965), therefore the xylem hydraulic conductance may also be low in the leaves. The hydraulic conductance in the mesophyll may not be much lower than in the xylem of the leaves. Studies which show that tree shoot hydraulic conductance can be limited by the hydraulic conductance in parenchymal cells in leaves are rare.

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Abbreviations: ABA - abscisic acid; E - transpiration rate; g_s - stomatal conductance; I - irradiance; L - hydraulic conductance; p - pressure; P_{max} - maximum photosynthetic rate; s_d - stomatal sensitivity to a decrease in leaf water potential; s_i - stomatal sensitivity to an increase in leaf water potential; v_d - maximum relative rate of stomatal closure; v_i - maximum relative rate of stomatal opening; w - leaf water content per area; x - leaf relative wet mass per area.

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The hydraulic conductance in the cell walls is several orders of magnitude higher than in the symplast (Fiscus 1986, Rüdinger *et al.* 1994, Steudle and Meshcheryakov 1996, Steudle and Heydt 1997). However, the volume of the cell walls in the leaf is lower than the volume of symplasts and vacuoles (Esau 1965). Therefore, the hydraulic conductance of these two compartments in the mesophyll may be comparable.

The rate of water loss from the leaf is dependent on stomatal conductance. A positive correlation exists between hydraulic conductance and stomatal conductance (Reich and Hinckley 1989, Jones and Sutherland 1991, Sõber 1997, Bond and Kavanagh 1999, Tognetti *et al.* 1999a,b). It is resonable to suppose, that the hydraulic conductance may be also correlated with the other essential stomatal parameter: stomatal sensitivity to changes of leaf water potential. Data about the correlation between hydraulic conductance and stomatal sensitivity are available only for the bean (*Phaseolus vulgaris* L.) (Sõber 1996, Sõber 1997). In these studies, a positive correlation between hydraulic conductance and stomatal sensitivity to an increase in the leaf water potential was found.

The main questions asked in the present work were: *1*) Does there exist a correlation between shoot hydraulic conductance, stomatal conductance and stomatal sensitivity to changes in the leaf water status in deciduous trees? *2*) Can changes which arise in the mesophyll during the water stress or in darkness influence the hydraulic conductance in deciduous tree shoots?

Materials and methods

Plants: The species studied in this work were: *Acer platanoides* L., *Tilia cordata* Mill., *Padus avium* Mill., *Quercus robur* L., *Salix caprea* L. and *Populus tremula* L. In the first series of experiments the trees were studied in the course of seasonal developement. The saplings were grown in Tartu, Estonia, (58°22′ N and 26°44′ E), in a small stand, in clay loam, in full sunlight. All the saplings were 8 - 10 years old. Their terminal branches (about 1 m tall) were cut under the water and were brought (the base of each branch remained submerged) to the laboratory in the late evening of the previous day before the experiment. The experiments were done in July and in September 1997.

In the second series of experiments, the influence of several growth conditions was studied. The pots with 3 year old saplings were brought to a greenhouse. The complex fertilizer was given to all the saplings. The relative content of the elements in the complex fertilizer was: N 10, P 7, K 16, Fe 0.6, Cu 0.4, Mn 0.08, Mo 0.08, Zn 0.07 and B 0.07 parts. Experiments were done in July 1998.

Data from eight experimental sets for each species (two sets from the first and six sets from the second series of experiments) were compared in this study. Some greenhouse-sets of *P. tremula*, *S. caprea* and *Q. robur* are absent because too many plants of these species (characterized by relatively insensitive stomata to a decrease in the leaf water content) did not survive transplanting to the pots.

Apparatus: The initial version of the apparatus is described by Sõber and Moldau (1977). The apparatus enables the simultaneous measurement of transpiration rate (by micropsychrometer), leaf temperature (by infrared termometer), photosynthesis rate (by gas analyzer *LI - 6262*, *Li-Cor*, Lincoln, USA) and the relative changes of leaf water content (by β-gauge technique) of the intact leaf in leaf chamber. The data are registered by computer. The temperature of the leaf chamber was held at 25 °C, the relative air humidity was 50 - 60 %, CO_2 pressure was near the normal ambient (345 μmol mol^{-1}) and the photosynthetic photon flux density was 1020 μmol m^{-2} s^{-1}. The pressure chamber was added to the system and leaf water content was incrased by means of the pressure chamber technique, for details see Rahi (1973).

Experiments: *a*) To observe an increase in the leaf water content a short (10 - 15 cm) shoot was cut under the water from the bigger branch and one leaf was put in the leaf chamber. The shoot was fixed in the water-filled pressure chamber so that the cut end of the shoot was in the water. After the stabilization of stomatal conductance, the CO_2 content of the air in the leaf chamber was quickly raised to 1760 μmol mol^{-1} for 4 min to detect values of maximum (independent of air CO_2 content) photosynthetic rate (P_{max}). When stomatal conductance was stabilized again at natural CO_2 content, the pressure in the pressure chamber was quickly raised from 0 to 0.2 MPa. The experiment was finished when water droplets appeared on the abaxial surface of the leaf. If there was no infiltration after 15 min of the pressure increase, the pressure in chamber was quickly raised to 0.4 MPa and then to 0.7 MPa (if needed), until a dense network of water droplets was seen on the abaxial surface of the leaf. For details see also Sõber (1996) and Sõber (1997).

b) To observe a decrease in the leaf water content the leaf was in the leaf chamber, the end of the shoot was in a water-vessel. After the stabilization of the stomatal conductance, the leaf petiole was cut. The experiment was finished when stomatal conductance reached values near zero.

The leaf part, which had been in the leaf chamber was cut out and its fresh mass was determined in both experiments. The dry mass of the leaf segment was determined after drying it for two days at 80 °C.

Calculations: Stomatal conductance (for water vapour) (g_s) [mol m^{-2} s^{-1}] was calculated using measured values of transpiration rate and leaf temperature, according to Sõber and Moldau (1977).

Stomatal sensitivity to a decrease in leaf water potential (s_d) [% s^{-1}] was defined as a relative rate of stomatal closure:

$$s_d = v_d \times A \tag{1}$$

where v_d is the maximum relative rate of stomatal closure [% s^{-1}] and A is a scaling coefficient which transforms v_d to a common transpiration rate;

$$v_d = [\Delta g_s/(\Delta t \times g_{sa})] \times 100 \tag{2}$$

where Δg_s is the difference of stomatal conductances in the region of maximum rate of stomatal closure; Δt is the time interval [s], corresponding to Δg_s, and g_{sa} is an average stomatal conductance during Δt.

The relative rate of stomatal closure was determined, because stomatal conductance declined after the petiole was cut almost exponentially with time. Coefficient A was determined as:

$$A = E_{aa}/E_a \tag{3}$$

where E_a is the average transpiration rate [mol m^{-2} s^{-1}] during Δt and E_{aa} is the average of E_a for all the experiments (both the experiments of decreasing and increasing the leaf water potential). Coefficient A was defined by transpiration rates, because water potential probably dropped more rapidly after the leaf detachment in the cases of a higher transpiration rate. The maximum relative rate of stomatal closure was in a positive correlation with the transpiration rate (data not shown).

Stomatal sensitivity to an increase in leaf water potential (s_i) [% s^{-1}] was defined as a relative rate of stomatal opening:

$$s_i = v_i \times B \tag{4}$$

where v_i is the maximum relative rate of stomatal opening [% s^{-1}] and B is the coefficient which transforms v_i to a common transpiration rate and the pressure increase in the pressure chamber.

The value of v_i was obtained as:

$$v_i = \{\Delta g_s/[\Delta t \times (g_{smax} - g_{sa})]\} \times 100 \tag{5}$$

where g_{smax} is the maximum value of stomatal conductance after the pressure increase in the pressure chamber. The relative rate of stomatal opening was used because the opening of stomata after the pressure increase was also almost exponential with time.

B was obtained as:

$$B = (E_a \times \Delta p_{ra})/(E_{aa} \times \Delta p_r) \tag{6}$$

where Δp_r is the pressure increase in the pressure chamber [Pa], inducing an increase in leaf water potential; Δp_{ra} is the average of Δp_r for all the experiments. Coefficient B was defined by the transpiration rates and pressure increases, because the rate of water potential increase in the leaf is probably higher when the transpiration rate is lower and when the applied pressure is higher. Several aspects of the method of calculating the stomatal sensitivities were discussed by Sõber (1997) and Sõber and Sild (1999).

The shoot hydraulic conductance (L) [g m^{-2} s^{-1} Pa^{-1}] was calculated by the formula:

$$L = [(\Delta w/\Delta t) + E_a]/\Delta p \tag{7}$$

where Δp is the pressure difference at the path of the water from the pressure chamber to the intercellular spaces of the leaf. It was assumed that the water potential in the leaf intercellular spaces equals zero in the infiltrating leaves, and therefore Δp was equal to the pressure in the pressure chamber. $\Delta w/\Delta t$ is the maximum rate of increase in the leaf water content per leaf area [g m^{-2} s^{-1}] during leaf infiltration. Usually $\Delta w/\Delta t > E_a$ in our experiments. The relative values of leaf wet mass per area (x) were obtained as:

$$x = (\ln I - \ln I_b)/(\ln I_0 - \ln I_b) \tag{8}$$

where I_0 is irradiance in the absence of the leaf in the leaf chamber; I and I_b are current value of irradiance behind the leaf and the irradiance at the beginning of the experiment, respectively. The leaf absolute water content per area [g m^{-2}] was obtained as:

$$w = [(x \times w_{we})/x_e] - w_d \tag{9}$$

where x_e is the leaf relative wet mass per area at the end of the experiment, w_{we} is leaf absolute wet mass per area [g m^{-2}] at the end of the experiment, and w_d is leaf dry mass per area [g m^{-2}]. For other details see Mederski (1961), Sõber (1992), Moldau *et al.* (1993) and Sõber (1997).

Results

Shoot hydraulic conductance (L) increased significantly in sequence: *Acer platanoides* < *Tilia cordata* < *Padus avium* = *Quercus robur* < *Salix caprea* = *Populus tremula* (Fig. 1*A*). L was higher in July than in September for all the species. L was slightly higher in trees grown in soil with a higher nitrogen content for most of the species (*S. caprea* was an exception). L was lower in the trees grown under mild water stress for all the species. L was not very different between the trees which had been grown under a mild water stress since spring and the trees which suffered under the water stress for a only few days. L was the lowest in the trees kept in darkness and it was lower in the trees which were in darkness longer (6 d) compared to the trees which had been in darkness for 4 d (Fig. 1*A*). The relative decrease of L after a short-term mild water deficit or after keeping the trees in darkness was quite similar for the different species (Fig. 2).

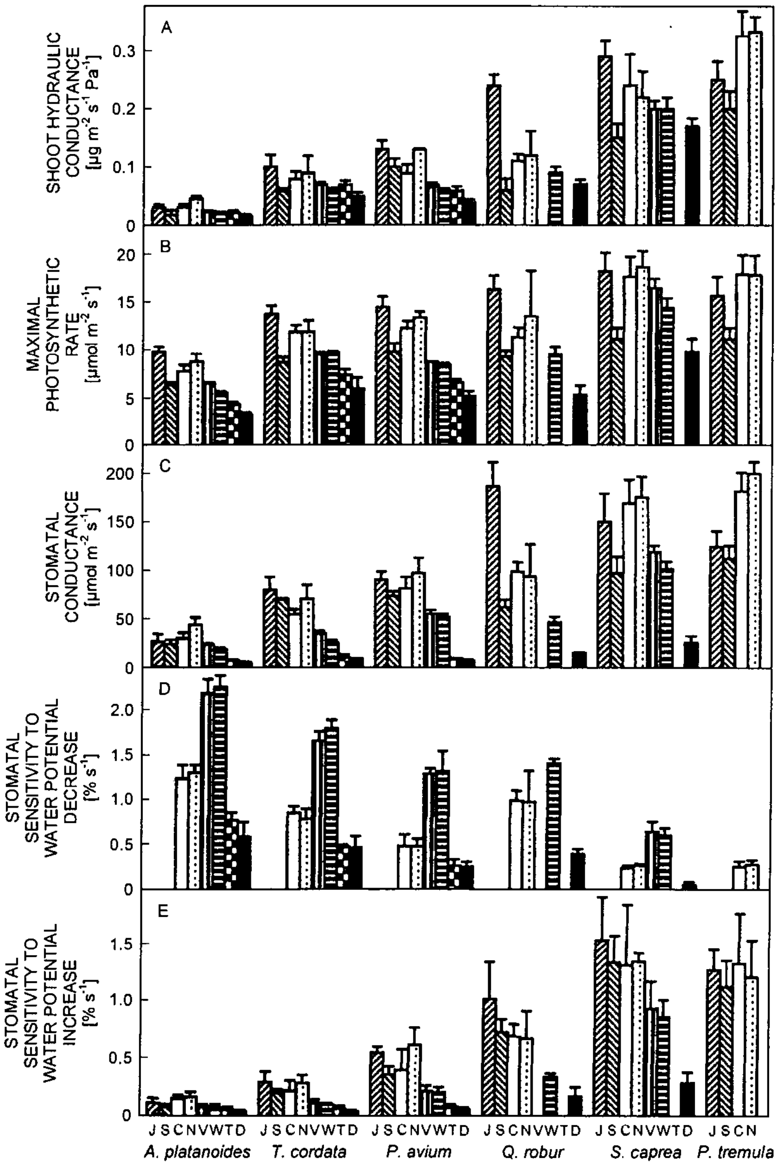


Fig. 1. Shoot hydraulic conductance (*A*), maximum photosynthetic rate (*B*), stomatal conductance (*C*), stomatal sensitivity to water potential decrease (*D*) and stomatal sensitivity to water potential increase (*E*). Means (n = 3 - 7) ± SE. Labelling: J - shoots from stand, July; S - shoots from stand, September; C - shoots from greenhouse, control; N - shoots from greenhouse, nitrogen-fertilized; V - shoots from greenhouse, water-stressed for 2 d; W - shoots from greenhouse, water-stressed since spring; T - shoots from greenhouse, kept in darkness for 4 d; D - shoots from greenhouse, kept in darkness for 6 d.

The maximum photosynthetic rate (at saturating concentration of carbon dioxide) (P_{max}), stomatal conductance at the beginning of the experiment (before changing of the water potential of the leaf) (g_{s0}), stomatal sensitivity to a decrease in leaf water potential (s_d) and stomatal sensitivity to an increase in leaf water potential (s_i) also varied between the species and between the experimental sets within the species (Figs. 1*B*-*E*). In general, P_{max}, g_{s0} and s_i varied in parallel with L: they were the lowest in *A. platanoides* and the highest in *P. tremula* and *S. caprea*. They were higher in July than in September and usually somewhat higher in trees grown in soil with a higher nitrogen content. P_{max}, g_{s0} and s_i were lower in the trees grown under mild water stress and still more significantly lower in the trees kept in darkness (Figs. 1*A*,*B*,*C*,*E*).

In most cases, s_d decreased (Fig. 1*D*) when L and the other parameters increased (Figs. 1*A*,*B*,*C*,*E*): s_d was the lowest in *P. tremula* and *S. caprea* and the highest in *A. platanoides* and higher in the trees grown under mild water stress. But s_d was also lower in all the trees kept in darkness (compared with the trees of the control set) (Fig. 1). The absolute differences in s_d between the experimental sets inside the species were more pronounced in the species characterized with a relatively high s_d in the control set (Fig. 1*D*).

The both sensitivities, s_i and s_d, were almost equal in the well-watered trees of *P. avium* and *Q. robur*. s_d was many times higher than s_i in the species characterized with a low L (*A. platanoides* and *T. cordata*) and s_i was several times higher than s_d in the species characterized with a high L (*S. caprea* and *P. tremula*). The differences between s_d and s_i were the greatest in *A. platanoides*, the species with the lowest L (Figs. 1*A*,*D*,*E*).

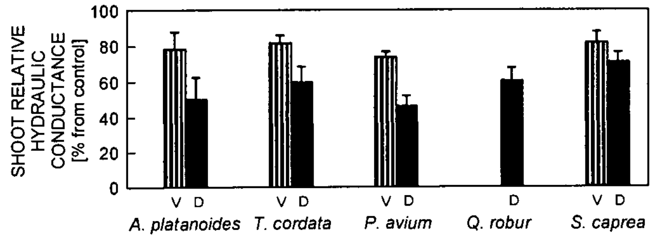
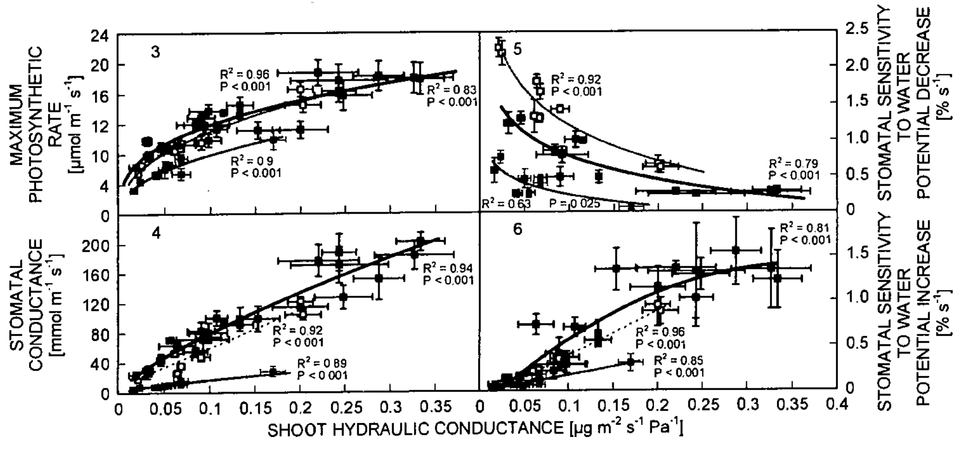


Fig. 2. Shoot relative hydraulic conductance after mild water stress for two days or darkness for six days (compared with shoot hydraulic conductance of control-set of the species) (means (n = 4 - 7) ± SE). Labelling as in Fig. 1.



Figs. 3 - 6. Relationships between shoot hydraulic conductance and maximum photosynthetic rate (Fig. 3), stomatal conductance (Fig. 4), stomatal sensitivity to water potential decrease (Fig. 5) and stomatal sensitivity to water potential increase (Fig. 6). Means ± SE; n = 3 - 7). Figs. 3, 4, 6: upper curve - well-watered trees, not kept in darkness (C-, N-, J- and S-set); middle curve - water-stressed trees (V- and W-set); lower curve - trees, kept in darkness (T- and D-set). Fig. 5: middle curve - well-watered trees; upper curve - water-stressed trees; lower curve - trees kept in darkness.

L was positively correlated with P_{max} (Fig. 3), g_{s0} (Fig. 4) and s_i (Fig. 6), and negatively with s_d (Fig. 5). Keeping in darkness for several days and the mild water deficit changed the correlation curves. Keeping in darkness lowered P_{max}, g_{s0}, s_i, and s_d significantly more than L (Figs. 3 - 6)). Mild water stress affected s_d and s_i differently: s_d (compared at some equal L values) was significantly increased (Fig. 5), but s_i was slightly decreased (Fig. 6).

Discussion

As shoot hydraulic conductance was variable between different tree species grown in the same conditions, the role of genetical factors in its determination may be strong. One important reason for the differences in L may be the different structure of the xylem in the trees. It is found that the largest conducting elements in the xylem are considerably smaller in maple, than in aspen (Holdheide 1951, Carlquist 1988). Also, the xylem conducting elements are smaller in the plants grown under water stress (Doley and Leyton 1968, Bissing 1982, Arnold and Mauseth 1999) and wider in plants grown in nutrient-rich soil (Shan and Mehta 1978). Hydraulic conductance in the xylem vessels is in a positive correlation with the diameter of the vessels (Calkin *et al.* 1986). Thus, it is probable that the differences of L between the species and experimental sets were caused partially by the different hydraulic conductance of their xylem.

We found that L in the tree shoots changed significantly during only a few days of mild water stress or starvation in darkness. Cavitation in the xylem vessels (Sperry *et al.* 1994, Zwienieckin and Holbrook 1998, Magnani *et al.* 2000) can be one important reason for the decrease of L in water-stressed plants and at the end of the growing season. But cavitation is unprobable in the well-watered trees in darkness and there are no data about other such rapid changes in the xylem vessels during such a short time. It is known that several detrimental changes take place in the other tissues of leaves during starvation (Neumann *et al.* 1989, Pell and Dann 1991). Thus, it is possible that the decrease of L was caused by the changes of the parenchymal tissues in leaves. Consequently, it was probable that hydraulic conductance in leaf parenchymal tissues affected the values of shoot hydraulic conductance in trees in some cases.

What may be the mechanism of change of hydraulic conductance in the mesophyll in darkness? There are no data about such rapid changes of anatomy in the parenchymal tissues of full-grown leaves, but several changes can take place in physiology. Changes in hydraulic conductance in leaves accompany variations in apoplastic pH (Sõber and Aasamaa 1998). The polysacharide cell wall is known to be a sparse structure, with large holes between chains of the polymers (Brett and Waldron 1996). In light of the present knowledge of cell wall physiology, it is unprobable that rapid changes in water permeability of such a sparse, well water-permeable structure take place. Variations in apoplastic pH have a rapid influence on the structures of the plasmalemma (Michelet and Boutry 1996). The revolutionary discoveries of the last decade have shown that rapid changes in hydraulic conductance in the symplast can be induced by changing the conductance of aquaporines - proteins, that form channels for water in plasmalemma and tonoplast (Fray *et al.* 1994, Maggio and Joly 1995, Steudle and Henzler 1995, Steudle and Frensch 1996, Maurel 1997, Schütz and Tyerman 1997, Steudle 1997, Eckert *et al.* 1999). The functioning of the water channels needs energy (Johansson *et al.* 1998, Tyerman *et al.* 1999). Therefore, the reason for a decrease in L may be the lack of energy to keep aquaporins in working order in the starving plants.

Thus, it is probable that the rapid changes in shoot hydraulic conductance were caused by changes in the symplasts of the leaf mesophyll during light deprivation. Therefore, the cell-to-cell pathway may be important in the leaves of deciduous trees.

We found that the relative decrease of L during darkness was similar in the different species. If the hydraulic conductance of symplast was close to zero after six days in darkness (about 50 % of control) reflects the hydraulic conductance in the leaf apoplast. It can be concluded that the proportion of symplastic and apoplastic components of transpirational flow is about 1:1 in the non-stressed leaves and this proportion is not very different in the tree species.

The positive correlation between L and the stomatal characteristics g_{s0} and s_i and the negative correlation between L and s_d occurred in most cases. One reason for the correlation between L and s_i may be that the water flows more rapidly in the shoots which have a higher L and the leaf water potential rises also more rapidly, and therefore the stomatal opening is more rapid. One of the reasons for the negative correlation between L and s_d may be similar: in the shoots which have higher L, the water flows to the stomatal region more rapidly and the water potential of the epidermis is lowering at a lower rate. For this reason, the stomatal closure proceed at a lower rate.

In addition, the correlation between L and the stomatal characteristics may be caused by some other physiological mechanisms. The abscisic acid (ABA) content increases in leaves when a water deficit arises in the soil and/or the leaf water potential decreases (Simpson 1981, Mansfield and Atkinson 1990, Jarvis and Davies 1997, Wilkinson and Davies 1997, Niinemets *et al.* 1999). The ABA content also increases in leaves in the course of senescence during the growing season (Laurière 1983, Nooden 1988, Pell and Dann 1991, Smart 1994, Wingler *et al.* 1998). The decrease in stomatal conductance is induced by the addition of ABA, even for a well-watered leaf (Cousson 1999, Leymarie *et al.* 1999). ABA is responsible for changing the activity of membrane channels (Owen 1988, Hahn 1996, Du *et al.* 1997, Roberts 1998, Barkla *et al.* 1999, Blatt 1999, Cousson 1999, Frank *et al.* 2000, Li *et al.* 2000). The addition of ABA induces increase of water permeability of roots (Cram and Pitman 1972, Tardieu and Davies 1993), it is possible, that ABA rises the water permeability of membranes in roots (Pitman and Wellfare 1978). But many effects of ABA are contrary in leaves and roots (Hsiao and Jing 1987, Saab *et al.* 1990, Hetherington and Quatrano 1991, Jackson 1991, Spollen *et al.* 1993). Therefore, we hypothesize that probably L, g_{s0}, and s_i are low and s_d is high in the shoots characterized with a high content of ABA.

The trees kept in darkness for several days had very low values of all the measured parameters. The reactions for changing and maintaining stomatal conductance in leaves are energy-consuming (MacRobbie 1981, Hedrich and Schroeder 1989, Armstrong and Blatt 1995). Probably s_d and s_i fell in the leaves because there was not enough energy and also the shortage of sugars as osmoticum. The starvation stress exerts a notably stronger influence on the stomata and photosynthesis than to L. We suppose, that the reason for this difference may be that one part of the L - the apoplastic component of water flow did not decrease in darkness; apoplastic conductivity is probably rather insensitive to physiological conditions in the leaf.

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