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Sensitivity of stem and petiole hydraulic conductance of deciduous trees to xylem sap ion concentration

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Abstract

Hydraulic conductance of stem and petioles increased in response to an increase in xylem sap ion concentration, and decreased in response to a decrease in the ion concentration in six temperate deciduous tree species. The ion sensitivity of hydraulic conductance of stem and petioles was higher than the ion sensitivity of the stem alone. The ion sensitivity was lowest in the earliest developmental stages of the xylem, and had a seasonal maximum in the second half of summer. The ion sensitivity was highest in slow-growing species and lowest in fast-growing species. The ion sensitivity correlated negatively with mean radius of xylem conduits, hydraulic conductance of stem and petioles, hydraulic conductance of leaf laminae, and stomatal conductance, and positively with response of the hydraulic conductance of leaf laminae to $HgCl_2$, and stomatal response to a decrease in leaf water potential or abscisic acid. It was concluded that the high ion sensitivity of xylem hydraulic conductance is a relevant characteristic of slow growth and a conservative water use strategy.

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

Introduction

It was demonstrated recently that hydraulic conductance of xylem is sensitive to the xylem sap ion concentration – xylem hydraulic conductance increases in response to an increase and decreases in response to a decrease in the xylem sap ion concentration (Van Ieperen *et al.* 2000, Zwieniecki *et al.* 2001). Although this phenomenon had already been observed several decades ago (Huber and Merz 1958, Zimmermann 1978), until the above-mentioned studies it had not been subject to further attention and interpretation. The suggested mechanism is as follows: if the ion concentration of xylem sap increases, more ions bind to pectins in pit membranes that are located in the walls between both successive and adjacent conduits of the xylem and thus their porosity increases. If the ion concentration of xylem sap decreases, some ions are released from the pit membrane pectins, causing their swelling (Zwieniecki *et al.* 2001). It is known that ion concentration of xylem sap changes significantly in response to environmental changes (*e.g.* Loewenstein and Pallardy 1998, Bahrun *et al.* 2002, Siebrecht *et al.* 2003). The ion concentration of shoot xylem sap is mainly determined by ion influxes from roots (*e.g.* Miller 1985, Herdel *et al.* 2001, Peuke *et al.* 2002) and from living cells around the xylem conduits (Pate and Jeschke 1995, Zwieniecki *et al.* 2000, 2004, Salleo *et al.* 2006). Thus, the ion concentration effect on xylem hydraulic conductance can have great importance as a component of possible physiological adjustment of xylem hydraulic conductance to environmental changes.

It has also been found that the ion sensitivity of xylem hydraulic conductance differs between species (Boyce *et al.* 2004). Data about ion sensitivity of several woody

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Abbreviations: c_{ion} - xylem sap ion concentration; EC - electrical conductivity; K_s - hydraulic conductance of shoot stem; K_{sp} - hydraulic conductance of shoot stem and petioles; S_s - ion sensitivity of hydraulic conductance of shoot stem; S_{sp} - ion sensitivity of hydraulic conductance of shoot stem and petioles.

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plants can be gathered from several studies: *Laurus nobilis* (Zwieniecki *et al.* 2001, Gascó *et al.* 2006, 2007, 2008, Nardini *et al.* 2007), *Prunus laurocerasus* (Van Ieperen and Van Gelder 2006, Gascó *et al.* 2007, Nardini *et al.* 2007), *Acer rubrum* and *A. saccharum* (Zwieniecki *et al.* 2004), *Ceratonia siliqua* and *Phytolacca dioica* (Nardini *et al.* 2007, Trifilò *et al.* 2008), *Persea gratissima* (Nardini *et al.* 2007), *Phillyrea latifolia* (Gascó *et al.* 2007) and *Platanus orientalis* (Trifilò *et al.* 2008). Gascó *et al.* (2007) measured the ion sensitivity of *L. nobilis* monthly during one year and found significant seasonal changes in ion sensitivity. The present study concentrates on the ion sensitivity of the hydraulic conductance of the shoot stem and petioles of six temperate deciduous tree species with different early-age growth rates and water use strategies. We compare the ion sensitivity of the different species, and its seasonal courses, and clarify the ecological significance of the ion sensitivity by relating it to several other characteristics of water relations and growth of the species.

Materials and methods

Plant material: Six temperate deciduous tree species with different early-age growth rates (Mathiesen 1934, Laas 1987) in the Estonian (temperate) climate were studied. The species were: fast-growers *Salix caprea* L. and *Populus tremula* L., slow-growers *Tilia cordata* Mill. and *Acer platanoides* L., and species with intermediate growth rates (classified both absolutely and relatively) *Quercus robur* L. and *Padus avium* Mill. Seeds were sown in spring in a stand in Tartu, Estonia (58°22´ N and 26°44´ E, elevation ~65 m above sea level), in a clay loam soil in full sunlight. The experiments began in the third spring at bud-break and were performed throughout the whole following growing season (~4 months), and thereafter also throughout the stages immediately preceding the abscission of leaves and about a month after the abscission. The top shoot with a 10-cm-long stem was used in the measurements of hydraulic conductance of all the species. At the time of bud-break (time: 0 months in Fig. 2), the previous years' stems (that had no leaves (and no petioles) were analysed. About one week after bud-break (time: 0.25 months), the previous years' stems with very short (some mm) young petioles (of the current year leaves) were analysed. About half a month after bud-break current year growth accounted for ¼ to ½ of the analysed top shoot's stem, and about three weeks after bud-break, ½ to ¾ of the stem. One month after bud-break, the whole of the analysed stem consisted of current year growth in fast-growing species. About 6 months after bud-break, leaves had been shed and therefore only stems were analysed again.

Determination of hydraulic conductance of shoot stem and petioles: The top shoot with 11 - 14 cm long stem was cut from the seedling while the stem was submerged in water. The shoot was brought to the laboratory, where the temperature was 25 °C. All the water used in this study was purified by *TKA MicroMed* (*TKA Water Purification Systems*, Niederelbert, Germany) reverse osmosis and ion exchange filters, and was degassed by boiling. The whole of the shoot was submerged in the deionised water, leaf laminae were cut from the shoot, and the length of the shoot stem was shortened to 10 cm. The shoot was fixed in the Scholander pressure chamber so that the cut base end of the shoot was outside the chamber and the remainder of the shoot was in the chamber filled with a 10 mM KCl solution. A pressure of 1 MPa was applied in the chamber (with nitrogen) and the solution flowed out from the chamber through the petioles and stem of the shoot for about 10 min. The high pressure in the chamber evidently eliminated xylem embolism in the shoot (Nardini and Pitt 1999, Tyree *et al.* 1999, Salleo *et al.* 2003), so that the maximum (*i.e.*, not decreased by the embolism) hydraulic conductance was determined in all the following experiments. In addition, most of the cations that had been bound to pectins of the xylem interconduit pit membranes were most likely exchanged by K^+ if a surplus of K^+ (KCl solution) was supplied to the xylem. Monovalent cations are less tightly associated with the negative charges of the walls than divalent cations (Grignon and Sentenac 1991), and they are possibly removed from the walls if the xylem is flushed with deionised water (Van Ieperen *et al.* 2000). The KCl solution in the chamber was changed to deionised water and a pressure of 0.2 MPa was applied in the chamber. The water that flowed out from the chamber through the cut base end of the stem during 1-min periods was collected and weighed. The maximum (leaf-specific) hydraulic conductance of the shoot stem and petioles (K_{sp}) was calculated as:

$K_{sp} = \Delta m/(\Delta t \times p \times \sigma A)$

where Δm is the mass of the water collected during the 1 min period (Δt), p is the pressure (0.2 MPa) in the pressure chamber, and σA is the summed area of all the leaves of the shoot. The hydraulic conductance stabilised (*i.e.*, stopped decreasing) about 5 - 10 min after the beginning of the treatment with deionised water. The stabilised conductance was taken as a base level (the lowest) hydraulic conductance of the shoot stem and petioles (K_{sp0}). Then the deionised water was changed to a solution of KCl, K_2SO_4 or $MgCl_2$ and K_{sp} was determined again. After 5 - 10 min of pressurising the shoot with the salt solution, the solution was changed to another, more concentrated solution and K_{sp} was determined again. The K_{sp} of one shoot was consecutively determined with up to 6 different solutions. Then the petioles were cut from the shoot and the same changes of solutions and measurements of conductance were performed with only the stem of the shoot. The maximum (leaf-specific) hydraulic conductances of the shoot stem (K_s) were calculated by above mentioned equation. All the solutions used in this study were filtered to 0.7 μm to remove debris.

Ion sensitivity of hydraulic conductance: The effect of salt solutions is most clearly visible if the hydraulic conductances in the salt solutions are compared with the lowest conductance - the conductance in deionised water. Therefore, the ion sensitivities (S_{sp} and S_s) of hydraulic conductance are shown here as relative hydraulic conductances of the shoot in the salt solution, as a percentage above K_{sp0} or above K_{s0}, respectively. For example, S_{sp30} indicates percentage increase in the hydraulic conductance in 30 mM salt solution in comparison with K_{sp0}. $S_{sp30} = (K_{sp30} \times 100)/ K_{sp0} - 100$.

The values of S_{sp30} 3 months after bud-break were chosen for presentation here as sample values of the ion sensitivity because: *1*) 30 mM is close to the maximum ionic strengths found in xylem of transpiring plants (Schurr and Schulze 1995, Herdel *et al.* 2001, Siebrecht *et al.* 2003), and EC of the 30 mM solutions was also close to the maximum EC of natural xylem sap analysed in this study (~2 mS cm^{-1}); *2*) S_{sp30} is near S_{sp} maximums in all the species; *3*) the seasonal maximums in S_{sp} were attained about 3 months after bud-break (in August) in all the species. It was demonstrated recently that the ion sensitivity of maximum hydraulic conductance (*i.e.*, the conductance of non-embolised xylem) of some species is greatly decreased if Ca^{2+} solution (and not deionised water) is used as the reference solution (Van Ieperen and Van Gelder 2006). Therefore, the species in the present study were also tested for existence of the Ca^{2+}-effect on their ion sensitivity. If 1 mM $CaCl_2$ solution was used as the reference solution (instead of deionised water), the ion sensitivity of *S. caprea* and *Populus tremula* did not change, the ion sensitivity of *A. platanoides* and *T. cordata* decreased somewhat (but not significantly), and the ion sensitivity of *Q. robur* and *Padus avium* was decreased by about 50 %, as compared to the ion sensitivity measured with calciumless xylem sap (data not shown). We decided that the use of deionised water as the reference solution is rational in this study for the following reasons: *A*) The ion sensitivities of the species with antagonistic growth strategies that we compared in this study (fast-growers *S. caprea* and *Populus tremula*, and slow-growers *A. platanoides* and *T. cordata*) were not significantly affected by Ca^{2+}; *B*) Ca^{2+}-effect is not significant in partially embolised xylem (Nardini *et al.* 2007). Because xylem is almost always partially embolised in field conditions, it is likely that the Ca^{2+}-effect does not have significant role in nature.

Determination of radius of xylem conduits: Other shoots, beside the shoots used in the measurements of hydraulic conductances of the shoot stem and petioles, were taken for measurements of all other characteristics. The radius of the xylem conducting elements was measured from permanent slices of the petiole cross-sections that were stained with safranin O (*Sigma*, St. Louis, MO, USA). The standard method of making the permanent slices is described in: Aasamaa *et al.* 2001. The measurements were performed with a light microscope (*PZO*, Warsaw, Poland) and ocular micrometer *MOB-1* (*LOMO*, Moscow, Russia).

Determination of xylem sap electrical conductivity: The shoots for the xylem sap analysis were taken in the morning, during 4 h following sunrise. Shoot was fixed in the Scholander pressure chamber so that only the cut base end of the shoot protruded from the chamber. The pressure was raised in the chamber until a pressure balance with the shoot water potential was attained and water started to flow out from the shoot through the cut base end of the shoot. The chamber pressure was then raised up to 0.5 MPa above the balancing pressure and the exuded sap was collected. The first 0.005 cm^3 of the sap was discarded to avoid contamination of the xylem sap by phloem fluids. The electrical conductivity (EC) of both the natural xylem sap and artificial xylem sap (*i.e.*, the salt solutions used in determination of the ion sensitivity) were measured (at 25 °C) with an analyser *Consort C833* (*Consort nv*, Turnhout, Belgium).

Determination of characteristics of water relations: Hydraulic conductance of leaf laminae was determined using a high-pressure method as described in detail by Aasamaa *et al.* (2005), and by Aasamaa and Sõber (2005). It is the maximum (*i.e.*, not decreased by xylem embolism) hydraulic conductance of the laminae. Treatment of the shoots with $HgCl_2$ is described by Aasamaa and Sõber (2005). Stomatal conductance (g_s) was measured with gas analysers *CIRAS-1* (*PP Systems*, Hitchin, United Kingdom) and *LI-1600* (*LI-COR*, Lincoln, NE, USA). Stomatal sensitivity to leaf water potential decrease (s_d) or to exogenous abscisic acid (ABA) (s_a) was calculated as the relative rate of the decrease in the stomatal conductance following the leaf excision from the shoot, or following the supply of the shoot with 5 μM solution of ABA (*Sigma*) (for detail see Aasamaa *et al.* 2001).

Results

Sensitivity of hydraulic conductance to xylem sap ion concentration: The hydraulic conductance of the shoot stem and petioles (K_{sp}) was sensitive to the xylem sap ion concentration (c_{ion}) in all the species: K_{sp} increased in response to an increase, and decreased in response to a decrease in c_{ion}. Hydraulic conductances with salt solutions in xylem were significantly higher than the hydraulic conductance of the shoot measured with deionised water in all the species (average $P = 0.001$; *ANOVA*). The effect of changes in c_{ion} was most pronounced at the lowest values of c_{ion}, and the effect decreased nearly exponentially with increasing c_{ion}.

Changes in ion concentrations above a threshold concentration ($c_{ion(thresh)}$) no longer had a significant effect on K_{sp}. Therefore, the ion sensitivity of hydraulic conductance of the shoot stem and petioles (S_{sp}) (defined here as the relative to K_{sp0}) was characterised by a near exponential dependence on c_{ion} (Fig. 1*A*). The effect of solutions of different salts did not differ significantly.

In the different species, both the values of S_{sp} and $c_{ion(thresh)}$ were different. The species ranked in order of increasing S_{sp} as follows: *S. caprea* < *Populus tremula* < *Padus avium* < *Q. robur* = *T. cordata* < *A. platanoides*. S_{sp} was only about 5 % in the fast-growers *S. caprea* and *Populus tremula*, but up to 20 % in the slow-grower *A. platanoides*. $c_{ion(thresh)}$ was also the lowest in the fast-growing species and the highest in the slow-growing species. In *S. caprea* and *Populus tremula*, $c_{ion(thresh)}$ was only about 20 mM. In *A. platanoides* and *T. cordata*, $c_{ion(thresh)}$ was more than two times higher: 40 - 50 mM. In the species with intermediate growth rates (*Padus avium* and *Q. robur*), S_{sp} and $c_{ion(thresh)}$ also had intermediate values (Fig. 1*A*).

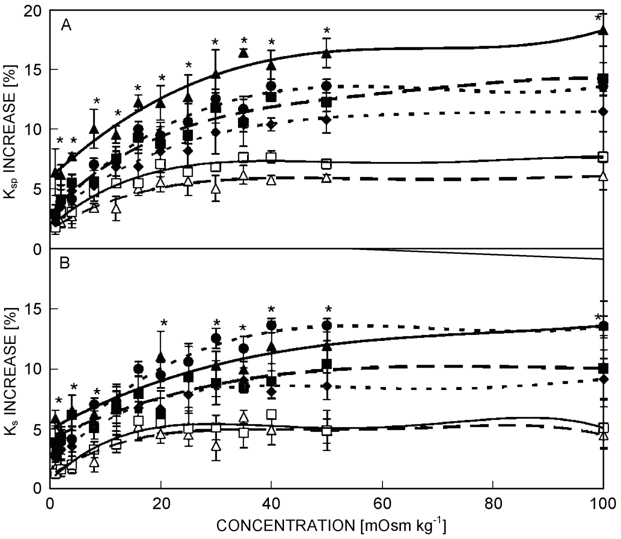

Fig. 1. Relative differences between xylem hydraulic conductance in deionised water and the xylem hydraulic conductance in the ion solutions. Deionised water or the ion solutions were flushed through stem with petioles (*A*), or through stem (without petioles) (*B*) of six deciduous tree species, three months after bud-break. Means ± SE, *n* = 3 - 4, * - mean values of the different species significantly different ($P < 0.1$) according to one-way *ANOVA*. Symbols: *Acer platanoides* (*closed triagles*), *Tilia cordata* (*closed squares*), *Quercus robur* (*closed circles*), *Padus avium* (*closed rhombs*), *Salix caprea* (*open triagles*), *Populus tremula* (*open squares*).

Hydraulic conductance of the shoot stem (K_s) was also sensitive to c_{ion} in all the species. The ion sensitivity of the hydraulic conductance of the shoot stem (S_s) was related to c_{ion} similarly as S_{sp}. Yet, the values of S_s were somewhat lower than the values of S_{sp} in all the species (except in *Q. robur* – the species characterised by exceptionally short petioles). $c_{ion(thresh)}$ also tended to decrease in response to cutting off the petioles of the shoots in all the species (except *Q. robur*) (Fig. 1*A*,*B*). The *P*-values concerning the difference between S_{sp} and S_s (Fig. 1) were as follows: $P < 0.001$ in *Populus tremula*, *T. cordata* and *A. platanoides*; $P = 0.116$ in *S. caprea*; $P = 0.16$ in *Padus avium*; $P = 0.99$ in *Q. robur*.

The interspecies variability in S_s was very similar to that in S_{sp}. The most remarkable trait of the interspecific variability of S_s was that the S_s of *A. platanoides* (the species characterised by exceptionally long petioles) was not higher than the S_s of all the other species, but was almost equal to the S_s of *Padus avium* and *Q. robur* (Fig. 1). Thus, the exceptionally high S_{sp} of *A. platanoides* is most likely related to the exceptionally long length of petioles of this species.

Seasonal courses of the ion sensitivity: In spring, at the time of bud-break, S_{sp} was relatively high in the previous years' stems. During the first month, S_{sp} mostly decreased along with the increase in the relative proportion of current year growth in the analysed (10 cm long) shoot stem tip. S_{sp} reached a minimum level about one month after bud-break. The whole or almost the whole of the analysed tip section consisted of current year growth at this time. Thus, S_{sp} was the lowest in shoots with the youngest tissues (Fig. 2*A*). Thereafter, S_{sp} increased along with the increase in the age of the shoot tip. S_{sp} attained maximums about 3 - 4 months after bud-break (in August). Then, S_{sp} slightly decreased, but remained higher than it had been at the time of bud-break. The shape of the seasonal courses of S_{sp} was similar in all the species, yet, the seasonal changes were greatest in the slow-growing species (characterised also by the highest

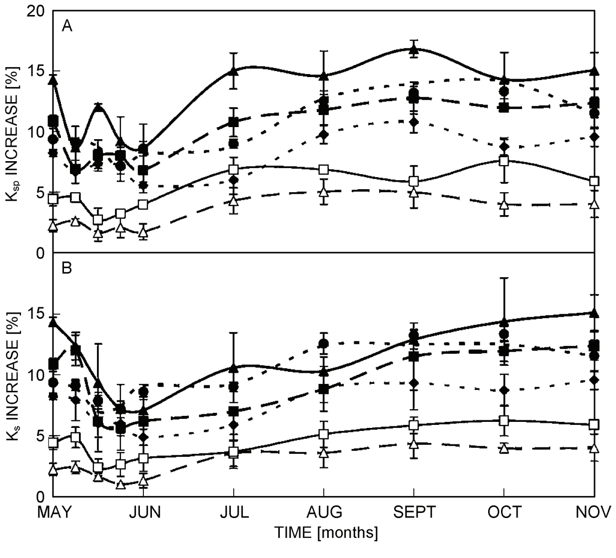

Fig. 2. Seasonal courses of relative difference between xylem hydraulic conductance in deionised water and the xylem hydraulic conductance in 30 mM ion solution. Deionised water or the ion solution was flushed through stem with petioles (*A*), or through stem (without petioles) (*B*) of six deciduous tree species. Means ± SE, *n* = 3 - 4. The same symbols as in Fig. 1.

values of S_{sp}). The seasonal relative changes in S_{sp} were similar in all the species (Fig. 2*A*). The interspecies differences in S_{sp} were significant ($P < 0.1$) throughout the whole season.

The seasonal courses of S_s were similar to the courses of S_{sp} (Fig. 2*B*). However, the increase in S_s along with the increase in the age of the stem (since the second month) was more gradual than the contemporaneous increase in S_{sp}. Therefore, the maximum values in S_s were attained about a month later than the maximum values in S_{sp}. The seasonal relative changes in S_s were similar in the different species. The interspecies differences in S_s were significant ($P < 0.1$) throughout the whole season.

Xylem dimensions and ion sensitivity: S_{sp} correlated negatively with the average radius of the widest conduits in the xylem of petioles of the shoot (Table 1). S_s was lower than the S_{sp} – the ion sensitivity of the shoot xylem hydraulic conductance decreased as a result of excising petioles from the shoot stem. The relative decrease (ΔS) in the ion sensitivity as a consequence of the excising of petioles correlated strongly and positively with the relative part of the average length of the petioles in the length of the whole shoot (Table 1).

Natural xylem sap electrical conductivity and ion sensitivity: EC was the lowest and about equal in *S. caprea*, *Padus avium* and *Q. robur*. The other species ranked in order of increasing EC as follows: *T. cordata* < *Populus tremula* < *A. platanoides* (Fig. 3). Yet EC did not correlate significantly with S_{sp} or S_s of the species (data not shown). During these 6 months, EC of the natural xylem sap changed slightly (remarkably less than the ion sensitivities) in all the species: decreased during the first month, and thereafter increased until the end of the studied period (Fig. 3). Interspecies differences in EC were significant ($P < 0.1$) throughout the whole season. The seasonal courses of EC correlated strongly and positively with the seasonal courses of both S_{sp} and S_s ($r_{\text{Pearson}} = 0.96 - 0.66$, $P < 0.04$).

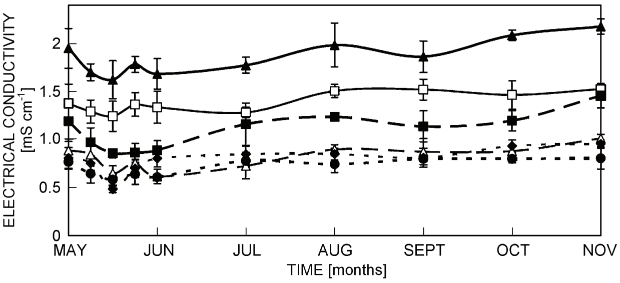

Fig. 3. Seasonal courses of electrical conductivity of natural xylem sap of shoots of the six deciduous tree species. Means ± SE, *n* = 3 - 4. The same symbols as in Fig. 1.

The ion sensitivity and the characteristics of water relations and the shoot growth rate: The seasonal maximums of S_{sp30} (three months after bud-break) correlated with the simultaneous values of other characteristics of water relations in these species as follows: strongly negatively with K_{sp0}, with hydraulic conductance of leaf laminae and with stomatal conductance, and strongly positively with the stomatal sensitivity to a decrease in the leaf water potential and with the stomatal sensitivity to (exogenous) abscisic acid. The seasonal maximums of S_{sp30} also correlated positively with the sensitivity of the hydraulic conductance of leaf laminae to $HgCl_2$ (Table 1).

In all the species, the seasonal course of S_{sp} correlated strongly positively with the seasonal course of K_{sp0}

Table 1. Species-specific values of relative increase in hydraulic conductance of shoot stem and petioles in response to increasing ion concentration of the xylem sap from 0 to 30 mM (S_{sp30}) [%], hydraulic conductance of shoot stem and petioles in deionised water (K_{sp0}) [mmol m^{-2} s^{-1} MPa^{-1}], hydraulic conductance of leaf laminae of the shoot (K_{lamina}) [mmol m^{-2} s^{-1} MPa^{-1}], relative decrease in hydraulic conductance of laminae in response to $HgCl_2$ ($\Delta K_{l(Hg)}$) [%], stomatal conductance (g_s) [mmol m^{-2} s^{-1}], stomatal sensitivity to a decrease in leaf water potential (s_w)[% s^{-1}], stomatal sensitivity to (exogenous) abscisic acid (s_{ABA}) [% s^{-1}], average radius of the widest conduits in the xylem of petioles of the shoot (r) [µm], relative decrease in the ion-mediated enhancement of xylem hydraulic conductance in response to excising petioles from the shoot (ΔS) [%], relative part of mean length of petioles in the length of the shoot (Δl_p) [%] three months after bud-break and annual increment of tree top shoot height at the year of experiments (l_{shoot}) [cm]. Means ± SE, *n* = 3 - 12. Lower section: Pearson correlation coefficients (and *P*-values) between mean values of S_{sp30} and the following eight characteristics (from third to tenth column) and between ΔS and Δl_p (the last column).

Species	S_{sp30}	K_{sp0}	K_{lamina}	$\Delta K_{l(Hg)}$	g_s	s_w	s_{ABA}	l_{shoot}	r	ΔS	Δl_p
Acer platanoides	14.7±2.0	14.0±2.7	5.5±0.6	57.3±10	30.1±6.1	1.24±0.15	0.082±0.010	8.5±1.3	5.6±0.1	29.7±5.3	33.7±1.3
Tilia cordata	11.8±1.3	22.2±2.0	7.0±0.1	55.9±13	55.2±5.3	0.86±0.08	0.057±0.001	7.0±0.7	5.3±0.1	25.3±4.1	25.8±2.2
Quercus robur	12.7±1.6	43.0±6.7	9.9±1.1	31.7±3.9	99.9±10	1.01±0.11	0.043±0.006	29.5±1.3	7.4±0.1	0	2.7±0.2
Padus avium	9.8±0.7	42.1±2.1	10.4±1.1	45.5±6.3	82.5±12	0.49±0.13	0.031±0.005	18.4±1.5	7.0±0.1	9.2±2.0	14.0±0.6
Salix caprea	5.0±1.1	84.7±14	13.6±0.5	29.6±3.0	170.3±24	0.25±0.03	0.022±0.004	66.9±8.0	8.5±0.1	28.2±11	14.8±0.3
Populus tremula	6.9±0.2	62.3±5.2	12.8±1.5	37.9±5.8	183.1±19	0.27±0.06	0.019±0.005	54.8±7.2	8.7±0.1	25.4±5.2	19.4±1.3
	r_{Pearson}	-0.93	-0.92	0.65	-0.90	0.97	0.89	-0.88	-0.82	r_{Pearson}	0.81
	P-value	0.007	0.009	0.166	0.014	0.001	0.018	0.02	0.048	*P*-value	0.05

($r_{\text{Pearson}} = 0.98 - 0.81$, $P < 0.014$), and the seasonal course of S_s correlated positively with the course of K_{s0} ($r_{\text{Pearson}} = 0.92 - 0.56$, $P < 0.09$). The seasonal maximums of S_{sp30} correlated strongly negatively with the annual increments in shoot height of the species in the year of the measurements (Table 1).

Discussion

The ion sensitivity in the different shoots: The shapes of the dependency curves between ion concentrations and hydraulic conductances are similar to the shape of a typical saturation curve of a chemical reaction. This result indicates that the ion sensitivity is most likely based on a chemical reaction between the ions and some component(s) of the shoots. At low c_{ion} concentrations of xylem sap, changes in c_{ion} are most effective in changing the hydraulic conductance, because the reaction is limited mainly by the ion concentration. At high (above $c_{\text{ion(thresh)}}$) ion concentrations of xylem sap, the changes in c_{ion} do not have an effect, because the chemical reaction most likely is limited by the concentration of another reactant – the component of the shoot. Since a significant proportion of xylem resistance resides in interconduit pit membranes (Sperry *et al.* 2005, Choat *et al.* 2006), and pectin is a typical component of the pit membranes (Brett and Waldron 1996), which swells and shrinks as a consequence of releasing or binding ions (Thakur *et al.* 1997, Ryden *et al.* 2000, Ridley *et al.* 2001), it is supposed (*e.g.* Zwieniecki *et al.* 2001, Holbrook *et al.* 2002, Zwieniecki *et al.* 2004, López-Portillo *et al.* 2005, Gascó *et al.* 2006) that the pectin of xylem interconduit pit membranes is probably the 'shoot reactant'. If the pectin is the 'shoot reactant', the ion sensitivity should be positively correlated with the amount of interconduit pit membranes in shoots.

We found, that: *1*) the ion sensitivity of a species correlated negatively with the average radius of the xylem conduits of the species. It has also been found that width of xylem conduits correlates positively with the length of the conduits (Zimmermann and Jeje 1981, Ewers and Fisher 1989, Sperry *et al.* 1994, 2006). In long conduits, the frequency of end walls between subsequent conducting elements is low (Brett and Waldron 1996, Dickison 2000), and thus the amount of end wall pits is also low. The width of a conduit has been found to be negatively correlated with the fraction of conduit side area that is in contact with adjacent conduits and also with the fraction of inter-conduit area occupied by pit membranes (Wheeler *et al.* 2005, Ellmore *et al.* 2006, Hacke *et al.* 2006). Thus, we found that the ion sensitivity was highest in the species that most likely contain the largest amount of interconduit pit membranes, and lowest in the species with the lowest content of the pit membranes. *2*) The ion sensitivity of a shoot always decreased as a consequence of excising petioles, and the decrease was proportional to the length of the petioles. As the interconduit pit membranes of petioles were also excised from the shoots by the excision of the petioles, the amount of interconduit pit membranes was lower in the 'naked' stems than in the stems with petioles. Thus, our results concerning relations between ion sensitivity and anatomical characteristics of xylem corroborate the view (*e.g.* Zwieniecki *et al.* 2001, 2004, Gascó *et al.* 2006) that ion sensitivity is based on the reactions between ions and xylem interconduit pit membranes.

Of course, the ion sensitivity is most likely determined not only by the quantity but also by qualitative characteristics of the interconduit pit membranes: *1*) The porosity of the pit membranes. *Salix* species have been shown to have very porous pit membranes while *Acer* species tend to have thicker, less porous membranes (Sano 2005). Swelling and shrinking of pectin in the membrane with large pores probably has a weaker effect on the hydraulic conductance of the membrane. *2*) The lignification of the pit membranes (Boyce *et al.* 2004). A smaller amount of pectins is available (for swelling and shrinking) in more lignified membranes. *3*) The amount and density of pectins in a pit membrane. *4*) Composition of the pectins: amount of galacturonic acid residues and their degree of methyl esterification. The question: "Which of the characteristics is the prevalent determinant of ion sensitivity?" would be object of future studies.

Seasonal changes in the ion sensitivity: Temperate tree shoots grow most rapidly in the first months after bud-break; thereafter the growth gradually diminishes (Kozlowski and Pallardy 1997). The seasonal dynamics of ion sensitivity was very similar to the growth dynamics of the shoots. This great similarity indicates that growth and development of hydraulic architecture can be a relevant determinant of the seasonal changes in ion sensitivity.

During the first month, the relative part of early wood increased gradually in the analysed top section of the shoots. Early wood conduits are long and wide (Brett and Waldron 1996, Dickison 2000). As mentioned above, the amount of both end-wall pits and side-wall pits is probably low in xylem with long and wide conduits. We suggest that the paucity of pit membranes (pectin) in early wood is an important reason why the ion sensitivity was the lowest in the early wood shoots. A widening of stem xylem takes place throughout the whole growing season, but the later conduits become shorter and narrower (Kozlowski and Pallardy 1997), and thus, probably contain more and more end-wall and side-wall pits. Therefore, the increase in the ion sensitivity during the season was most likely caused by the seasonal increase in the pit membrane pectin content of the shoot. During winter, part of the xylem conduits, especially the narrowest conduits, clog with tyloses and thereby lose their functionality as conducting elements (Cochard and

Tyree 1990, Gorsuch and Oberbauer 2002, Gajardo-Caviedes *et al.* 2005). The decrease in the number of functional narrow (frequently pitted) conduits is a plausible cause of the decrease in the ion sensitivity of the shoots during winter.

The length of the growth period of petioles differs from that of the stem: the growth of petioles is almost completed during the first months following bud-break (Maillette 1992, Kozlowski and Pallardy 1997). The difference between the lengths of the growth periods of petioles and the stem is most likely an important cause for the difference between the shapes of the seasonal courses of S_{sp} and S_s. The seasonal increase in S_s is steady and long lasting, as is also the growth of the stem. However, the seasonal increase in S_{sp} takes place earlier and is more rapid, probably because the growth of petioles is concentrated in an earlier and shorter period.

Role of the ion sensitivity: The result that hydraulic conductance was significantly sensitive to the xylem sap ion concentration in all the species, indicates that ion sensitivity is a significant determinant of the values of xylem hydraulic conductance and it could be inserted into mechanistic models of xylem hydraulic conductance (K_{xylem}):

$$K_{xylem} = k \times K_{xylem0} \times S_{xylem} \times c$$

where K_{xylem0} is the xylem hydraulic conductance in deionised water, S_{xylem} is the ion sensitivity of the xylem hydraulic conductance, c is ion concentration in xylem sap, and k is the correlation coefficient. A negative correlation between K_{sp0} and S_{sp} of the species points that it would be very incorrect to estimate the *in situ* values of xylem hydraulic conductance on the basis of measurements with deionised water. Due to the ion sensitivity, the values of the xylem hydraulic conductance in intact trees can be significantly higher than K_{sp0}, especially in the species with low K_{sp0}.

We found that ion sensitivity was highest in the slow-growing species and lowest in the fast-growers. Therefore, we suggest that high ion sensitivity can be included in the characteristics of slow-growers, and low ion sensitivity in the characteristics of fast-growers. Changes in porosity of the pit membranes change the hydraulic conductance of the xylem, but also change the overall sectoriality of the shoot (Orians *et al.* 2005, Ellmore *et al.* 2006, Zanne *et al.* 2006) and can change the vulnerability of the xylem to embolism (Jarbeau *et al.* 1995, Choat *et al.* 2004). Thereby, the ion sensitivity of pit membrane permeability is probably versatile and efficient in adjusting the shoot physiology to environmental conditions. It has been found that growth rate of slow-growing tree species is more tolerant to shortages of water, nutrients or light (Chapin *et al.* 1993, Weih 2001, Marron *et al.* 2003, Galmés *et al.* 2005, Castro-Díez *et al.* 2006) than of fast-growers. The high tolerance of slow-growers to shortages of environmental resources may be enabled by the high ion sensitivity of these species.

We also found that the species-specific values of ion sensitivity were high in the species that were characterised by low hydraulic conductances of the stem, petioles and leaf laminae, low stomatal conductance, highly sensitive stomatal responses to the factors of water deficit (leaf water potential decrease and abscisic acid concentration increase), and also by a high role of protoplasts in water flow through leaf parenchymal tissues (see details of the latter characteristic from Aasamaa and Sõber 2005). Low stomatal conductance and high stomatal sensitivity are classical characteristics of conservative water use strategy of woody plants (*e.g.* Passioura 1982, Johansson and Tuomela 1996, Li 1999, Donovan *et al.* 2000, Querejeta *et al.* 2003). It has been found that the tree species with conservative water use strategy are also characterised by low hydraulic conductances and a high relative importance of protoplasts as a water flow path in foliar parenchymal tissues (Aasamaa and Sõber 2001, 2005, Aasamaa *et al.* 2004). Because of the strong correlation between ion sensitivity and the other traits, we suggest that ion sensitivity is also significant as a characteristic of water use strategy. High ion sensitivity can be included in the set of characteristics of conservative water use strategy, and low ion sensitivity is a characteristic of more prodigal water use strategy.

The correlations of the seasonal course of ion sensitivity with the seasonal courses of the other characteristics: positive correlations with the courses of K_{sp0} and EC, and a negative relationship with the dynamics of the shoot growth rate, were quite surprising results. During the periods of the lowest K_{sp0} and xylem sap ion concentration, the highest ion sensitivity would compensate for the lowness of the formers. High ion sensitivity during the periods of the highest growth rate would be needed to provide the growing organs with the optimal amount of water. But on the other hand, soil water resources are usually most abundant in spring, decrease gradually during the growing season, and reach their minimums in the second half of summer in a temperate climate. Therefore, it could also be supposed that at the beginning of the growing season, the water supply of the trees is so sufficient that an increase in their hydraulic conductance through high ion sensitivity is unnecessary. As the soil water deficit progresses in the course of the growing season, both high K_{sp0} and high ion sensitivity and also high ion concentration of xylem sap are needed in order to survive the late summer droughts. Thus, ion sensitivity can also be an important tool in adapting the deciduous trees water relations to seasonal changes in growth environment. A similar conclusion was also drawn in studies of mostly evergreens (Gascó *et al.* 2007, Trifilò *et al.* 2008).

To sum up, we conclude that high ion sensitivity of xylem hydraulic conductance is very important in assuring the survival of slow-growing temperate deciduous trees. Also, high ion sensitivity is a relevant characteristic of conservative water use strategy. Ion sensitivity can also be important for the adaption of trees to seasonal changes in growth environment.

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