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Xylem sap chemistry: seasonal changes in timberline conifers *Pinus cembra*, *Picea abies*, and *Larix decidua*

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Abstract

The seasonal course of xylem sap parameters (electrical conductivity EC, potassium concentration [K$^+$], and pH) of three conifers (*Pinus cembra*, *Picea abies*, and *Larix decidua*) growing at the alpine timberline was monitored. We also looked into possible effects of [K$^+$] and pH on the difference in hydraulic conductivity (Δk_s). In all studied species, EC, [K$^+$], and pH varied considerably over the year, with pH ranging between 7.3 (February) and 5.8 (June) and [K$^+$] changing between 0.4 (January) and 2.5 mM (June). The Δk_s was overall low with positive values during winter (up to +20 %) and negative values in summer (-15 % in August). Samples perfused with alkaline solutions showed higher Δk_s. Xylem sap parameters in all conifers under study were surprisingly variable over the year thus indicating either effects upon seasonal changes in environmental factors or active adjustments, or both. Although Δk_s values over the year were minor, observed induction of Δk_s by high pH might indicate a role for hydraulic adjustment in harsh winter periods.

Additional key words: European larch, ionic effect, Norway spruce, pH, potassium, stone pine.

Introduction

In alpine ecosystems, the progressive decrease in temperature with increasing elevation is the most relevant environmental factor influencing plant life (Körner 2003). Besides growth, low temperatures also affect plant hydraulics by increasing water viscosity (Tyree and Zimmermann 2002), thus reducing transport velocities (Sellin and Kupper 2007), which is of relevance under high transpiration conditions. When temperatures reach the freezing point, the water supply of plants breaks down (Sakai and Larcher 1987). At the timberline, ice formation in the soil and/or the stem base blocks the water uptake for months (Goldstein *et al.* 1985, Mayr 2007). Trees, with their upright habitus, are in close contact with the atmosphere, and only low-stature individuals are protected by the snow cover (Mayr 2007). As a consequence, particularly evergreen trees are likely to lose large amounts of water because of exposure to strong winds and overheating by high radiation. According to Tranquillini (1957), trees can lose more than the 50 % of their water content during winter months, reaching critically low water potentials (*e.g.*, -4 MPa for *Picea abies*, Mayr *et al.* 2002). Frost-drought and freeze-thaw events can also lead to xylem embolism (Sperry and Sullivan 1992, Mayr *et al.* 2003a,b, Mayr and Zublasing 2010). Conifers at the timberline can suffer up to 100 % loss of conductivity (Mayr and Charra-Vaskou 2007), but they also can repair embolism in late winter and spring (Sparks and Black 2000, Sparks *et al.* 2001, McCulloh *et al.* 2011, Mayr *et al.* 2014). The ability to repair embolised xylem has been documented in different plant species (*e.g.*, Christman *et al.* 2012, Secchi and Zwieniecki 2012, Mayr *et al.* 2014) and a number of mechanisms have been proposed to explain this phenomenon, including positive root pressure, osmotically driven flow, and phloem unloading (*e.g.*, Nardini *et al.* 2011a, Brodersen and McElrone 2013, Laur and Hacke 2014, Earles *et al.* 2016).

Plants can cope with embolism-induced loss of hydraulic conductance not only *via* short-term repair of embolised xylem (*e.g.*, Salleo *et al.* 1996) or long-term production of new xylem conduits, but also *via* ion-mediated changes in xylem hydraulic conductance ("ionic effect"; *e.g.*, Zimmermann 1978, Zwieniecki *et al.* 2001, Cochard *et al.* 2010, Nardini *et al.* 2011b, Trifilò *et al.*

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Abbreviations: EC - electrical conductivity; [K$^+$] - potassium concentration; WC - water content; Δk_s - difference in hydraulic conductivity; Ψ - water potential.

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2014). By adjusting the solute composition of the xylem sap, plants are able to modulate the hydraulic conductance on both diurnal and seasonal time scales (Siebrecht *et al.* 2003, Gascó *et al.* 2008, Trifilò *et al.* 2014). In a seasonal survey on *Laurus nobilis*, Gascó *et al.* (2007) demonstrated that the magnitude of the ionic effect is higher in winter months, concurrent with low temperatures and high embolism rates (percent loss of hydraulic conductivity > 65 %). Nardini *et al.* (2012) found that *Acer* species adapted to habitats with high irradiance and/or low water availability show a more pronounced ionic effect than congeneric species growing in shady or humid sites. A study investigating six different deciduous tree species showed a relation between changes in xylem sap ion concentrations and the magnitude of the ionic effect (Aasamaa and Sober 2010). In saline habitats, both trees (*i.e.*, mangroves, López-Portillo *et al.* 2014) and a grass (*i.e., Spartina patens*, Casolo *et al.* 2015) show the ability to optimize the hydraulic conductance by increasing the salt concentration in xylem sap, as a strategy for coping a restricted water supply. The underlying processes of the ionic effect are still contentious (Santiago *et al.* 2013). Most authors propose an ion-mediated swelling and shrinking of pectins (Lee *et al.* 2012, Zwieniecki *et al.* 2001) in pit membranes and/or an electroviscous effect in pit apertures (Santiago *et al.* 2013). Recent observations on the chemical identity of pit membranes apparently challenge the role of pectins in the ionic effect (Klepsch *et al.* 2016).

Besides the effects of different ions, also changes in pH of the xylem sap may play a role in the regulation of plant hydraulic conductance. In a study on *Zea mays*, Bahrun *et al.* (2002) reported that the xylem pH increases significantly while the xylem sap concentration of different ions (*e.g.* nitrate, ammonium, phosphate, potassium) decreases up to 50 % after a drought treatment. Many other studies documented changes in xylem pH in transpiring plants (Secchi and Zwieniecki 2012) as well as under drought conditions (Bahrun *et al.* 2002, Sobeih *et al.* 2004, Sharp and Davies 2009).

Most of the mentioned studies dealt with angiosperms, while information on xylem sap composition of gymnosperms and, in particular, of conifers growing at the alpine timberline is still lacking. Timberline conifers are of interest as they grow at the upper distributional border of respective species and show pronounced seasonal changes in terms of water content and xylem hydraulics. Information on possible variation in xylem sap composition and related physiological effects thus might be important to understand the hydraulic strategy of these trees. In this study, we analyzed the annual course of xylem sap electrical conductivity (EC), potassium concentration ([K^+]), and pH, and xylem water content (WC) and water potential (Ψ) of three dominant alpine conifers (*Pinus cembra*, *Picea abies* and *Larix decidua*) growing at the timberline. Further, the presence and magnitude of ionic effects in the xylem of studied conifers, as well as a possible influence of pH changes on the xylem hydraulic conductivity was investigated. We expected changes and effects to play a role during the "recovery" period in late-winter/spring (Mayr *et al.* 2014). During this period, changes in xylem sap might support refilling and xylem sap parameters were thus expected to mirror seasonal changes in hydraulic demands and limitations over the year.

Materials and methods

Plants: The study was performed on branches collected from three alpine conifers [*Pinus cembra* L., *Picea abies* (L.) H. Karst., and *Larix decidua* Mill.] growing at the timberline (1800 - 2100 m a.s.l.). The study site was located near Praxmar, Tyrol (1 750 m a.s.l., 47°14'N/11°13'E), on a south-east exposed slope in the Tyrolean Central Alps (Austria). Measurements were performed on 1 m long branches collected at breast height from the south-east exposed crown of 3 - 4 m tall trees.

Meteorological data (air temperature, soil temperature, air humidity, and precipitation) were recorded using a weather station (temperature and humidity sensor *EMS33*, precipitation sensor *MetOne 370/376*, and datalogger *ModuLog 3029* from *Environmental Measuring Systems*, Brno, Czech Republic) located near Praxmar. Measurements were taken at 1 min intervals and 15 min mean values were stored. Meteorological data are presented in Fig. 1 Suppl.

From January 2015 to December 2015, the study site was visited monthly and on each sampling date three branches (from different, randomly selected individuals) per species were harvested. Before cutting, three end twigs (about 10 cm) per branch were cut off for water potential (Ψ) measurements. Then the branch was cut and all needles were removed (see Fig. 2 Suppl.). Defoliated branches were wrapped in black plastic bags and transported to the laboratory. Every branch was divided into three parts (Fig. 2 Suppl.) to be used for the following measurements: the apical part (30 - 40 cm) for testing ion-mediated changes in hydraulic conductivity (Δk_s), the middle part (about 3 cm) for water content (WC) measurements, and the remaining part (50 - 60 cm) for sap extraction and related analysis (potassium concentration [K^+], electrical conductivity (EC), and pH. All measurements were made on the day of sampling. Only Δk_s measurements were performed on the following morning. In addition, entire branches of *P. abies*, up to 1.5 m in length, were wrapped in plastic bags and transported to the laboratory for pH experiments.

Water potential and xylem water content: For Ψ determination, end twigs (Fig. 2 Suppl.) were measured with a *Scholander apparatus* (*model 1000*; *PMS Instrument Company*, Corvallis, OR, USA). Three end twigs per branch were measured, and Ψ was averaged per branch. Branch segments for WC measurements (Fig. 2 Suppl.) were debarked and weighed, both immediately and after 4 - 5 d of drying in an oven at 80 °C. Masses were measured with a *ME235P-OCE*, balance (*Sartorius AG*, Göttingen, Germany) and WC was calculated as [(FM - DM)/DM)] × 100, where FM and DM are fresh and dry masses, respectively.

Sap analysis: Stem segments (50 - 60 cm) cut off from the main branches (see Fig. 2 Suppl.) were completely debarked, washed with distilled water and dried with paper towels. Branches were debarked to avoid reverse osmosis from living cells during xylem sap extraction (López-Portillo *et al.* 2014). The apical stem section was sealed in a *Scholander apparatus* (*model 600-EXP Super Pressure Chamber*) and pressure was slowly raised up to 4 MPa. The sap dripping out of the basal cross section was collected in an Eppendorf vial, sealed to the protruding part of the branch (to avoid possible evaporation during the collection). For each sap sample, $[K^+]$, EC, and pH were measured by a $[K^+]$-selective electrode (*Cardy Compact Ion Meter, Model C-131,* a conductivity meter (*Twin Cond Conductivity Meter, Model B-173*) and a pH meter (*Twin pH Meter, Model B-212*); all from *Horiba*, Kyoto, Japan.

Ionic effect was tested with a 25 mM KCl-solution on branches stored overnight in a black plastic bag. KCl was used as a perfusion fluid because K^+ is the most abundant cation in the xylem sap and represents about 50 % of the total inorganic ion concentration (Siebrecht *et al.* 2003, Nardini *et al.* 2007). We used 25 mM KCl as a standard solution similarly as in other studies (Nardini *et al.* 2007, Trifilò *et al.* 2008, Oddo *et al.* 2014). The hydraulic conductivity (k_s) measured under KCl perfusion was compared with values recorded under perfusion with a reference solution [distilled and degassed water, filtered at 0.22 µm and containing 0.005 % (v/v) *Micropur* (*Katadyn Products*, Wallisellen, Switzerland) to prevent microbial growth].

Ion-mediated changes in k_s were quantified *via* a modified *Sperry apparatus* (Sperry *et al.* 1988, Chiu and Ewers 1993, Vogt 2001, Mayr *et al.* 2002). Briefly, the apparatus was based on silicon tubings and two and three-ways valves, which could be opened to remove air bubbles and change solutions. A source perfusion bag and a glass capillary were directly connected to a valve by silicon tubes and in turn connected to a *mini CORI-FLOW Mass Flow Meter* (*Bronkhorst Cori-Tech*, Ruurlo, The Netherlands). A hand pump allowed to pressurize a sealed bottle containing an infusion bag, connected to the apparatus and a gauge to check the pressure. This set-up allowed flushing samples at higher pressures to remove emboli.

Branches were immersed in water, the bark was removed and samples were recut several times with a sharp wood carving knife to gradually release tension (Wheeler *et al.* 2013) and obtain segments 4 - 5 cm in length and 3 - 6 mm in diameter. Samples were connected to a 5-fold valve (*Luer-lock system, neoLab Migge Laborbedarf-Vertriebs*, Heidelberg, Germany) connected to the hydraulic apparatus. Measurement pressure was set to 0.004 MPa. All samples were first flushed with the reference solution (see above) for 10 min at 0.06 MPa, and flushing was repeated until it yielded no further change in conductivity. Samples were then perfused with the KCl-solution for 30 min at 0.004 MPa before measuring again k_s. All hydraulic measurements were conducted at room temperature. Conductivity values were corrected for water viscosity at 20 °C. Δk_s was calculated as: $(1 - k_{flush}/k_{KCl}) \times 100$, where k_{flush} and k_{KCl} are the hydraulic conductivity measured after the flush with the reference solution and after the perfusion with the KCl-solution, respectively.

Changes in hydraulic conductivity mediated by pH: The pH-mediated increase in branch hydraulic conductivity (Δk_s) was tested in October 2015 on fully hydrated samples by perfusing them with eight different citrate-phosphate buffer solutions (at pH of 5, 6, 7, and 8). At each pH, 25 mM K^+ solutions or 25 mM Na^+ solutions were used to test the role of different cations in any possible pH-related hydraulic effect. Four branches per solution were measured. Samples preparation and Δk_s calculation were made following the procedure described above.

Statistical analysis: All values are given as means ± standard errors (SEs). Differences were tested using a one-way analysis of variance followed by a Fischer's LSD test post hoc comparison (pH experiment, seasonal courses) or by the Student's *t*-test, after testing for normal distribution and homoscedasticity. Correlation analysis was carried out using the Pearson product-moment correlation and is reported in Table 1 Suppl. All tests were conducted using *SPSS* software *v. 21.0* (*SPSS Inc.*, Chicago, IL) at a probability level of 5 %.

Results

In all species, the water potential reached lowest values in February (-1.5 ± 0.1, -2.2 ± 0.4, and -2.3 ± 0.2 MPa in *P. cembra*, *P. abies* and *L. decidua*, respectively; Fig. 1*A*). During the vegetation period, Ψ fluctuated due to changes in transpiration rates. The water content showed no significant changes over the year (P = 0.740, 0.795, and 0.222; Fig. 1*B*). The Ψ was significantly correlated with $[K^+]$ in *P. cembra* (P = 0.011), while no significant correlations were found between Ψ and WC.

Xylem sap ionic composition and pH changed considerably over the year. In all species, pH was significantly lower ($P < 0.001$) in summer than in winter months (*i.e.*, decreasing from 6.70 ± 0.15 to 5.93 ± 0.14, from 7.27 ± 0.14 to 6.23 ± 0.32, and from 6.67 ± 0.24 to 5.50 ± 0.00 from February to June in *P. cembra*, *P. abies* and *L. decidua*, respectively; Fig. 2*C*). The [K$^+$] trend corresponded to the EC trend (Fig. 2*A*,*B*) resulting in a significant correlation between these two parameters ($P < 0.001$). [K$^+$] and EC significantly increased ($P < 0.001$) from January to June. In *P. abies* and *L. decidua*, both EC and [K$^+$] values dropped significantly ($P < 0.001$) in July, and returned to higher values in September-October. Subsequently, values decreased and in December, similar values to the ones obtained in the preceding January were recorded. In contrast, *P. cembra* showed a nearly linear and significant ($P < 0.001$) decrease of [K$^+$] and EC from May to July, and then, for the rest of the year, values remained around 0.50 mM and 200 µs cm^{-1} for [K$^+$] and EC, respectively. Although all investigated species showed similar trends, significant correlations between pH and [K$^+$] were found only for *L. decidua* ($P = 0.009$) and between pH and EC for *P. cembra* and *L. decidua* ($P = 0.015$ and $P < 0.001$), respectively.

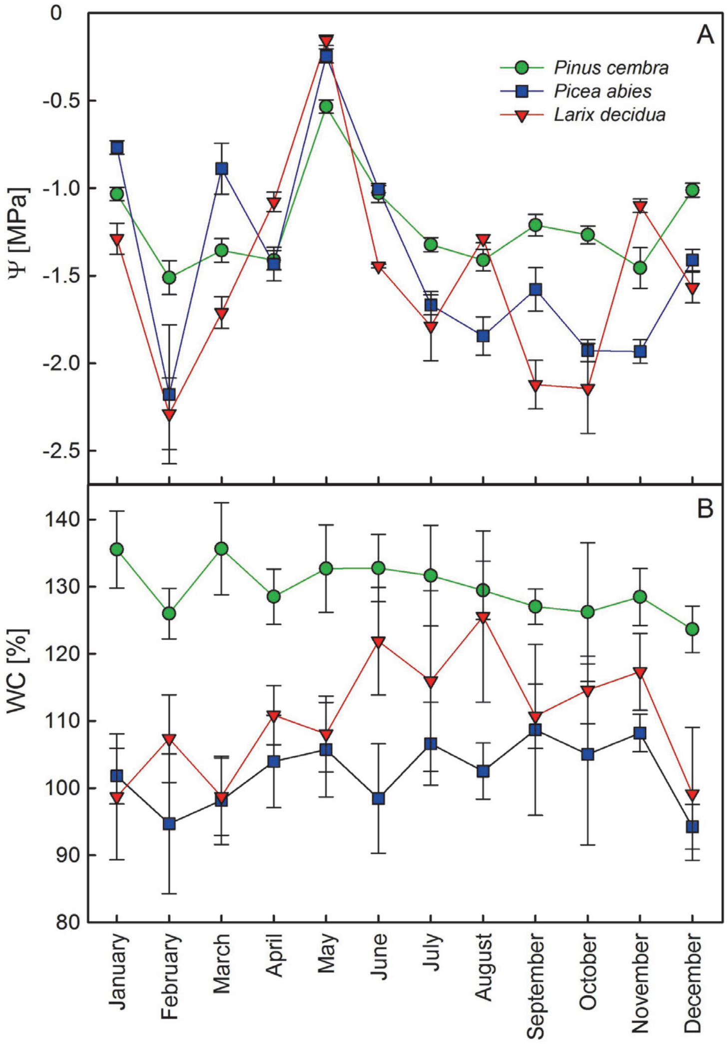

Fig. 1. Seasonal variations of water potential, Ψ (*A*) and xylem water content, WC (*B*) of *Pinus cembra* (*dots*), *Picea abies* (*squares*), and *Larix decidua* (*triangles*) branches collected every month during year 2015. Means ± SEs, $n = 3$.

In all species, Δk_s showed an overall similar trend over the year (Fig. 3). During the first three months, Δk_s values were about +5 - 10 %, and they were around 0 % from April to July. In August, the negative values (*ca* -15 ± 5 %) were observed. For the rest of the year, Δk_s values were only slightly above 0 %, except in November, when *P. cembra* and *L. decidua* showed Δk_s +15 - 20 %. The Δk_s values showed no significant correlation with other xylem sap parameters.

Meteorological data are presented on Fig. 1 Suppl. Significant negative correlations between both Δk_s (Fig. 3) and pH (Fig. 2*C*) and the monthly mean temperature (Fig. 1*A* Suppl.) were found for *P. abies* ($P = 0.042$ and $P = 0.005$, respectively). In both *P. cembra* and *P. abies*, pH values were negatively correlated to monthly mean precipitation ($P = 0.001$ and

$P < 0.001$, respectively) (Fig. 1*B* Suppl.). In *L. decidua*, WC was significantly correlated with both temperature ($P = 0.005$) and precipitation ($P < 0.001$).

Fully hydrated samples of *P. abies* showed the highest Δk_S values when perfused with buffer solutions at pH 8 (10.7 ± 8.0 and 8.9 ± 5.9 % when perfused with Na^+- and K^+-solutions, respectively), but low or even negative values when perfused with solutions at lower pH (Na^+-solutions at pH 7, -9.2 ± 1.6 %; K^+-solution at pH 6, -9.2 ± 4.9 %; Fig. 4). Latter values significantly differed to the ones obtained at pH 8.

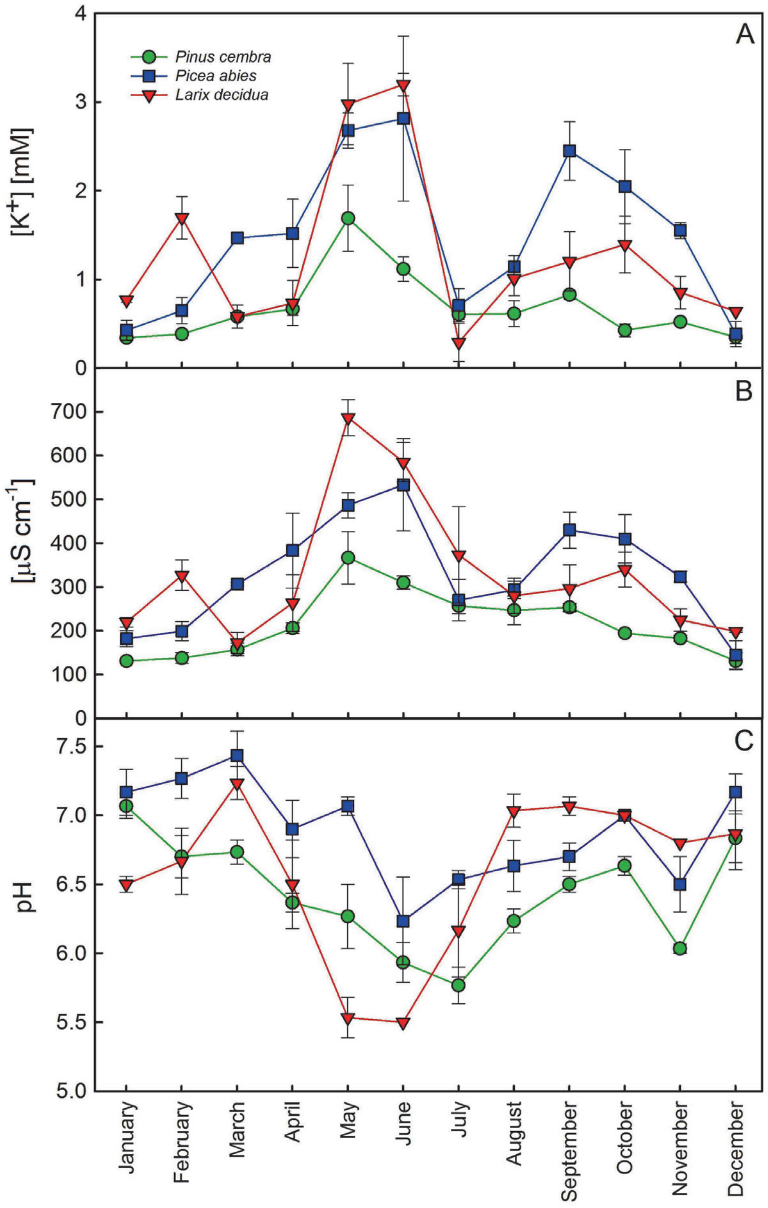

Fig. 2. Seasonal variations of xylem sap potassium concentration, $[K^+]$ (*A*), electrical conductivity, EC (*B*), and xylem sap pH (*C*) of *Pinus cembra* (*dots*), *Picea abies* (*squares*), and *Larix decidua* (*triangles*) branches collected every month during year 2015. Means ± SEs, $n = 3$.

Discussion

Seasonal courses of analyzed parameters demonstrated pronounced changes in xylem sap composition and properties, which were similar in all species. In contrast, the "ionic effect" was overall small and not related to the refilling period (*e.g.*, late winter and beginning of spring). However, induction of the ionic effect by alkaline solutions might indicate a role in extreme weather during winter period.

All investigated parameters ([K$^+$], EC, and pH) changed significantly during the year. In general, [K$^+$] started to increase at the beginning of the growing period (*ca*. April - May) and decreased in the hardening phase (autumn months) (Fig. 2*A*). Significantly higher [K$^+$] in xylem sap during the growing season has been reported in *Pyrus communis* by Wang *et al.* 2015), and a significant increase in [K$^+$] from spring to summer in *Ceratonia siliqua*, *Phytolacca dioica*, and *Platanus orientalis* by Trifilò *et al*. (2008). Low values of [K$^+$] during winter months might be due to reduced access to soil sources because of freezing temperatures (Goldstein *et al.* 1985, Mayr 2007), while under mild spring temperatures, plants are able to satisfy the demand of mineral nutrition. Higher [K$^+$] values during the vegetation period might help trees to increase whole plant hydraulic conductance and transpiration, as reported Oddo *et al.* (2011) in a short-term potassium fertilization experiment with *Laurus. nobilis.* The [K$^+$] is also important for regulation of stomatal aperture optimizing the water-use efficiency (Egilla *et al.* 2005). In the present study, the seasonal increase in [K$^+$] was not related to low WC and thus not due to passive changes of concentrations, as WC values were rather constant over the year (Fig. 1*B*). In *P. cembra*, [K$^+$] and Ψ values were even positively related and showed the highest [K$^+$] and most moderate Ψ in May (Figs. 1*A* and 4*A*). Around July, both [K$^+$] and EC values decreased significantly in all three species under study. At this time of the year, conifers at the timberline have their maximum rates of evapotranspiration, and potassium represents the major osmotically active cation taken up by guard cells to open stomata (Andrés *et al.* 2014, Anschütz *et al.* 2014). Overall, [K$^+$] and EC values recorded in the three conifer species under study were much lower than those reported for angiosperms (*e.g.*, Bahrun *et al*. 2002, Goodger *et al*. 2005, Trifilò *et al*. 2008, 2014, Aasamaa and Sober 2010).

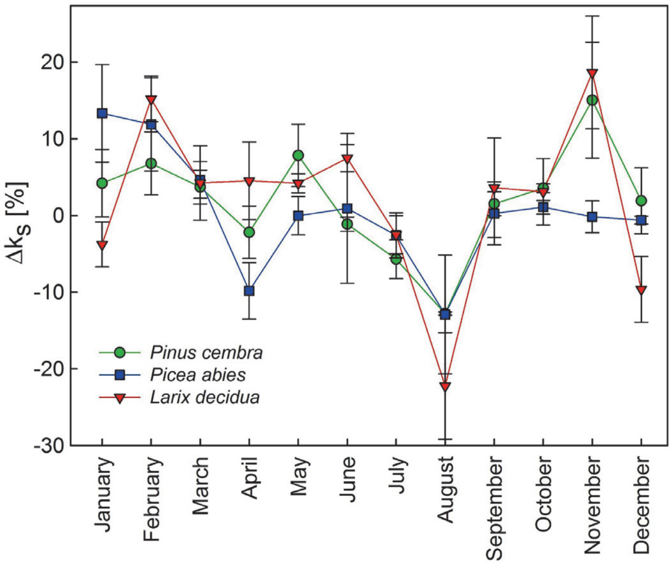

Fig. 3 Seasonal variation of ion-mediated changes in hydraulic conductivity, Δk_s of *Pinus cembra* (*dots*), *Picea abies* (*squares*), and *Larix decidua* (triangles) branches collected every month during year 2015. Means ± SEs, *n* = 3.

Xylem sap pH values were within the range reported in other studies (4.5 - 7.4, Teskey *et al*. 2008). Summer pH values were similar to those obtained by Sharp and Davies (2009) in *Abies koreana* (pH 5.85 in well-watered plants) and by Carter and Larsen (1965) in *Pinus taeda* (pH 5.6). All studied species showed similar changes in sap pH over the year (Fig. 2*C*). Xylem sap tended to become more acidic during spring (from February to June - July) and reached almost neutral values at the end of the second half of the year. A similar trend has been reported by Sauter (1988) and Fromard *et al*. (1995). An increase in xylem sap pH, in combination with increased abscisic acid concentrations, plays a role as a signal for limiting water loss *via* stomatal closure (Lambers *et al.* 2008). Therefore, higher pH from the end of autumn until the end of winter might help trees to maintain reduced stomatal conductance. In contrast, the acidification of the xylem sap in spring might be based on a combination of increased soil activities, leading to enhanced soil CO$_2$ production, and an increase in [K$^+$]. Indeed, pH changes might be a footprint of increasing [K$^+$], as H$^+$ ions linked to the tori's pectic matrix of pit connections may be released into the xylem sap by a substitution for K$^+$, as hypothesized by Gascó *et al.* (2008). Accordingly, *L. decidua* showed a significant negative correlation between pH and [K$^+$], and *L. decidua* and *P. cembra* showed similar correlations between pH and EC. In a recent study, Secchi and Zwieniecki (2016) reported progressive acidification of xylem sap in poplar plants subjected to drought stress and suffering xylem embolism. Xylem sap acidification was coupled to transport of soluble sugars into xylem conduits, possibly contributing to the generation of the osmotic forces that have been postulated to be involved in the mechanisms of embolism repair by ‘novel refilling’ (Nardini *et al.* 2011a). Secchi and Zwieniecki (2016) thus suggested that xylem sap acidification under drought might ‘prime’ the xylem for refilling, favouring the process of embolism repair once plants rehydrate and xylem tension is released. Conifers at the timberline have been reported to reverse xylem embolism at the end of winter and spring (Mayr *et al.* 2014). It is thus likely that the drop in xylem sap pH during this period, as recorded in the present study, plays a role in xylem refilling.

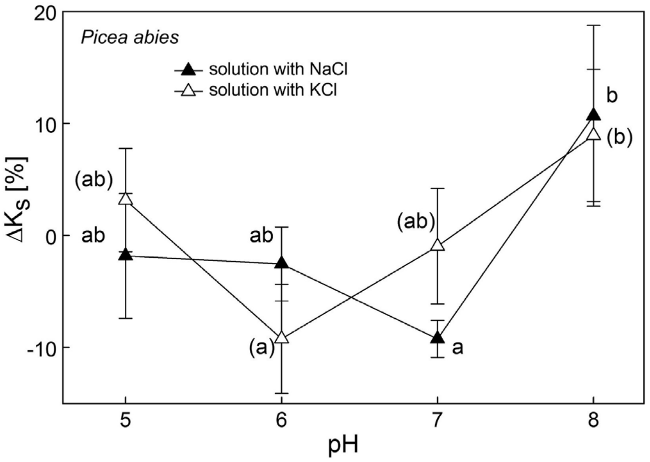

Fig. 4. Effect of pH on hydraulic conductivity (Δk_s) of *Picea abies* branches obtained by perfusion with different pH citrate-phosphate buffer solutions containing either 25 mM of NaCl (*white triangles*) or 25 mM of KCl (*black triangles*). Means ± SEs, *n* = 4; different letters indicate significant differences ($P < 0.05$) between means. Letters in brackets refer to KCl perfusions.

Despite significant changes in xylem sap composition and in contrast to our hypothesis, ionic effects were overall minor and no significant seasonal trends were observed (Fig. 3). We found small positive as well as small negative Δk_s values similarly as reported by Cochard *et al.* (2010) on five angiosperms and two conifers. We can offer two explanations for this lack of clear ionic effects. First, the potential influence of ions on the xylem hydraulic conductivity might differ between angiosperms and conifers due to the special conifer pit architecture (with margo and torus fulfilling the demands of hydraulic safety and efficiency). Pectin swelling might affect pores in angiosperm pit membranes but not the large margo pores in conifers. In this case, the relevance of the ionic effect would be generally low in conifers. Second, the present study was performed in a rather mild winter and possible frost-related ionic effects were thus not fully visible.

In *P. abies*, Δk_s values increased when samples were perfused with both K^+- and Na^+-buffer solutions at pH 8 (Fig. 4). This effect was obviously independent of the solution used to adjust pH and in contrast to results reported by Zwieniecki *et al.* (2001), who found no effect using solutions with pH between 5.8 - 8. The winter during the present study was rather mild and Ψ moderate so that changes in pH and consecutive effects on Δk_s were not pronounced. Though the observed response to more alkaline solutions might be hydraulically relevant in the pre-growth period after winters with intense frost drought and freezing stress at the alpine timberline, when trees reach critically low Ψ (Mayr *et al.* 2002). *P. abies* thereby was found to reach lower Ψ than other species (Mayr *et al.* 2003b, Mayr 2007) and accordingly, xylem sap pH of these species was more alkaline and peaked in March (7.4 ± 0.18; Fig. 2*C*).

Our data show marked changes in xylem sap chemistry ([K^+], EC and pH) over the course of the year, and significant effects of pH on xylem hydraulics. However, further studies extending over several years and with a particular focus on the critical times highlighted by this study are required to elucidate the possible functional roles of changes in xylem sap chemistry and the importance of these phenomena for conifers.

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