

Winter-drought induced embolism in Norway spruce (*Picea abies*) at the Alpine timberline

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At the timberline in the Central Alps, climatic conditions during winter frequently cause excessive drought stress (frost drought, 'Frosttrocknis'), which we hypothesized to induce cavitation in trees. We investigated the extent of winter-embolism in Norway spruce (*Picea abies* (L.) Karst.) growing near the timberline and analysed adaptations in vulnerability and anatomy. We found conductivity losses of up to 100% at the highest elevation (2020 m) correlated with low water potentials down to -4.0 MPa. Vulnerability thresholds (50% loss in conductivity) decreased from -3.39 MPa at 800 m to

-3.88 MPa at 1600 m corresponding to a decrease in tracheid cross-sectional area as well as pit and pit pore diameters. These thresholds were lower than potentials measured in embolized twigs near the timberline at the sampling dates probably due to lower potentials and/or a role of freeze-thaw events earlier in winter. Data indicated refilling processes, which may be of particular relevance for trees at the timberline, since adaptations in drought-induced vulnerability failed to prevent winter-embolism.

Introduction

Water transport in vascular plants occurs — according to the cohesion theory (Boehm 1893, Dixon and Joly 1894) — under negative potential, which is transmitted to the soil via continuous water columns (e.g. Richter 1972, Jackson and Grace 1994). High tensions can lead to cavitation of these water columns by entry of air bubbles (airseeding) from adjacent air-filled conduits through the pores of the pit membrane (e.g. Zimmermann 1983, Tyree et al. 1994). Vulnerability analysis also revealed species-specific water potential (ψ) thresholds for the onset of cavitations for several conifers (e.g. Sperry and Tyree 1990, Cochard 1992, Jackson et al. 1995, Brodribb and Hill 1999). However, embolism caused by freeze-thaw events was reported to be of minor relevance in conifers (e.g. Sucoff 1969, Robson and Petty 1987, Robson et al. 1988, Sperry and Sullivan 1992).

Vulnerability to embolism is influenced by anatomical properties. Air seeding occurs more frequently in larger conduits (Sperry and Tyree 1988, Lo Gullo and Salleo 1991, Lo Gullo and Salleo 1993, Lo Gullo et al. 1995), and may be due to a greater number of pit pores (Harg-

rave et al. 1994). In conifers the peculiar anatomy of pit membranes prevents air movement by sealing of the torus against the overarching border of the pit (Sperry and Tyree 1990). Also, larger conduits tend to be more vulnerable to freeze-thaw events (e.g. Sperry and Sullivan 1992, Lo Gullo and Salleo 1993, Sperry et al. 1994) due to formation of larger bubbles in the centre of freezing conduits.

In the European Alps, winter conditions can cause multiple freeze-thaw events as well as excessive drought stress, especially in woody plants growing at the timberline. This frost-drought ('Frosttrocknis', e.g. Michaelis 1934, Pisek and Larcher 1954, Larcher 1972, Tranquillini 1980) occurs as a result of water losses caused by intensive radiation and high wind speeds, and a permanently blocked water transport caused by frozen soil and xylem. Considering these extreme conditions we hypothesized winter-drought to induce embolism in trees growing at the timberline. We analysed the extent of embolism in twigs of Norway spruce (*Picea abies* (L.) Karst.) growing between 1820 m and 2020 m. Based on vulnerability and anatomical investigations we inter-

preted the field situation and analysed possible adaptations that may lessen susceptibility to cavitation.

Materials and methods

Plant material and study sites

Measurements were made on twigs of Norway spruce (*Picea abies* (L.) Karst.) trees growing at the North exposed slope of Birgitz Köpfl (2035 m), Tyrol, Central Alps in winter 1999–2000. Representative climatic data of two nearby situated meteorological stations are given in Table 1.

Vulnerability curves were determined along an altitudinal transect on about 35 twigs at 800, 1300 and 1600 m, respectively. At each altitude south-exposed twigs, up to 1.5 m long, were harvested at breast height (1.3 m) from 4 to 6 different trees (height about 15 m). These twigs were detached between January 15 and February 25, early in the morning, when xylem was frozen, transported to the laboratory in a plastic bag, re-cut under water while still frozen and hydrated for 24 h. During different periods of dehydration (up to 4 days) water potential and corresponding loss of conductivity were determined.

For the investigation of the field situation we measured xylem conductivity and water potential for trees at different elevations near the alpine timberline. South-exposed twigs of trees growing between 1820 m (light forest stand, tree height about 10 m) and 2020 m (solitary trees with a height of about 1 m) were harvested on March 3 and March 13. It is important to note that the first collections were made within a period of cold weather (air temperatures below -10°C), whereas one week later, when the second set of samples was collected, air temperatures were up to $+10^{\circ}\text{C}$ and intensive rainfall occurred even at the timberline. End segments of twigs were harvested early in the morning, immediately put in a plastic bag, kept frozen in a cold box and transported to the laboratory. Potentials were measured after twigs were allowed to thaw in the sealed bags. For conductivity measurements, segments (length 10 cm, diameter <1.0 cm) of twigs used for water potential determination were cut under water early in the morning (xylem was frozen) and transported in a water-filled bottle to the laboratory.

Water potential

Water potentials were determined with a pressure chamber (SKPM1400, Skye Instruments Ltd, Llandrindod Wells, UK). For measurements we used twig end segments (length <10 cm). The bark and needles were removed at the base (1 cm) to enable better sealing in the pressure chamber. Because of the inadequate sealing mechanism, pressure values below -4.5 MPa could not be measured. Exceeding this threshold led to a sudden deformation of the sealing rubber and an outflow of air from the pressure chamber. However, measurements above this threshold and used for calculations, are absolutely correct.

Measurements of conductivity

Conductivity measurements were carried out with a modified Sperry apparatus (Sperry et al. 1988, Chiu and Ewers 1993, Vogt 2001). We constructed an apparatus from acrylic glass, permitting gentle handling of the hydraulic system. Conductivity measurements were made on up to 10 twig segments before and after repeated and simultaneous flushing. The hydraulic system was controlled with a set of Teflon two-way valves, which could be opened to remove air bubbles from the hydraulic system. We prepared twig segments of about 2.5 cm length with diameters between 5 and 8 mm immersed in distilled water, less the bark and periderm, before sealing in the silicone tubes for measurement of their hydraulic conductivity. Measurement pressure was set to 0.004 MPa (controlled via a 0.4 m glass capillary). Flow rate was measured with a PC-connected balance (Sartorius BP61S, 0.0001 g precision, Sartorius AG, Göttingen, Germany) by weight registration every 10 s; flow rate was calculated by linear regression over 200 s. Flushing was carried out with a pressure-resistant bottle containing distilled, filtered ($0.22\ \mu\text{m}$) and degassed water and a rubber balloon expanded to 0.13 MPa. For all twig segments flushing (30 min) was repeated until measurements showed no further increase in conductivity. Loss of conductivity in percent was calculated from the ratio of initial to maximal conductivity. To prevent microbial growth, the apparatus was flushed at intervals with 70% ethanol.

Table 1. Air temperatures ($^{\circ}\text{C}$) and precipitation (mm) during winter 1999/2000 in Rinn (918 m) and at Mt. Patscherkofl (2246 m) near the investigated elevational transect. Data from ZAMG — Zentralanstalt für Meteorologie und Geodynamik, Innsbruck, Austria.

	Oct 99	Nov 99	Dec 99	Jan 00	Feb 00	Mar 00
Mt. Patscherkofl						
Mean temperature	2.2	-4.8	-6.6	-7.1	-5.9	-4.7
Minimum temperature	-6.5	-15.7	-16.5	-19.5	-15.8	-15.0
Precipitation	28.0	123.0	26.0	37.0	57.0	253.0
Rinn						
Mean temperature	8.6	-0.3	-1.8	-4.4	0.7	3.5
Minimum temperature	-2.5	-12.0	-13.6	-17.9	-8.2	-5.9
Precipitation	4.0	8.2	3.3	27.1	41.2	159.9

Vulnerability curves

Vulnerability curves were obtained by plotting per cent loss of hydraulic conductivity vs. water potential. Curves were fitted with the exponential sigmoidal equation (Equation 1) given in Pammenter and Vander Willigen (1998):

$$PLC = 100 / (1 + \exp(a(\Psi - b))) \quad (1)$$

where PLC is the per cent loss of conductivity, Ψ is the corresponding water potential and a and b are constants.

Anatomical investigations

Anatomical properties were measured on twigs used for vulnerability analysis. Tracheid cross-sectional areas (radial diameter multiplied by tangential diameter) were determined microscopically (800-fold magnification) on twig cross-sections.

Pit as well as pit pore diameters were determined by scanning electron microscopic photos (XL20, Philips, Germany; 1400-fold magnification) of radial sections. To compare pit properties of specimens harvested at different elevations we analysed pits of earlywood tracheids with radial diameters between 13 and 19 μm , calculating the ratio of pit diameter to tracheid diameter as well as of pit pore diameter to pit diameter, respectively. Earlywood properties are expected to determine the upper vulnerability threshold (Cochard 1992).

Number of samples, statistics

Vulnerability curves are based on water potential and conductivity data acquired from 27 (1600 m), 69 (1300 m) and 67 (800 m) twig segments. The frequency distribution of tracheid cross-sectional area was determined along three random radii within the youngest tree ring of 5 representative twig cross-sections from each altitude. Additionally 104 (1900 m), 79 (1600 m), 55 (1300 m) and 83 (800 m) pits were analysed.

Conductivity and water potentials were measured at each of the two sampling dates on twigs collected from 18 trees homogeneously distributed over the range from 1825 to 2020 m.

All values are given as mean \pm standard error. Differences were tested with Student's t -test at $P \leq 0.05$ after checking for normal distribution and variance of the data. Differences of tracheid cross-sectional area distribution were tested with the Kruskal–Wallis-Test at $P \leq 0.01$ followed by multiple Mann–Whitney-Tests at a Bonferroni-corrected probability level ($P \leq 0.0083$).

Results

Vulnerability analysis

Vulnerability measurements during winter showed a shift of the cavitation threshold to more negative water poten-

Table 2. Vulnerability curve parameters according to Pammenter and Vander Willigen (1998) of Norway spruce twigs harvested at 800, 1300 and 1600 m. Parameter a is related to the slope of the conductivity loss, parameter b is equivalent to water potential at 50% loss of conductivity. Values of each column not followed by the same letter differ significantly at $P \leq 0.05$ (Student's t -test).

Altitude (m)	Parameter a (curve slope)	Parameter b (50% conductivity)
1600	3.15 ± 0.58^a	-3.88 ± 0.06^a
1300	3.32 ± 0.37^a	-3.56 ± 0.04^b
800	8.25 ± 1.28^b	-3.39 ± 0.02^c

tials with increasing altitude (Table 2, Fig. 1). 50% loss of conductivity was reached at a water potential of -3.39 ± 0.02 MPa at 800 m and of -3.88 ± 0.06 MPa at 1600 m. According to Pammenter and Vander Willigen (1998), parameter ' a ' of the exponential sigmoidal equation (Equation 1) represents the maximum rate that conductivity decreases with falling water potentials; parameter ' b ' corresponds to the water potential at a 50% loss in conductivity.

The rate that hydraulic conductivity was reduced for

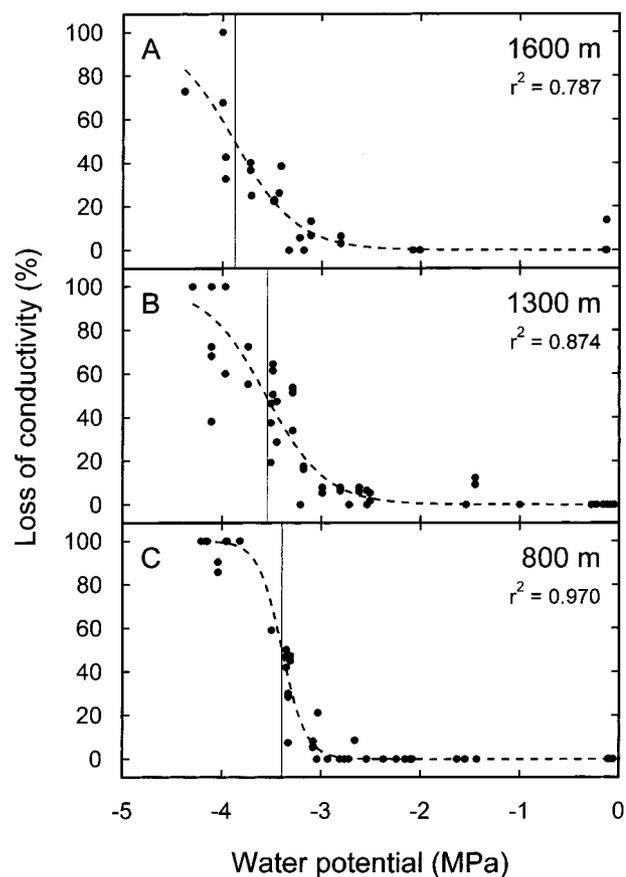


Fig. 1. Vulnerability curves (loss of conductivity vs. water potential) of Norway spruce twigs harvested at 800, 1300 and 1600 m. Curves were fitted by the equation described in Pammenter and Vander Willigen (1998). 50% loss of conductivity is indicated by vertical lines.

a comparable drop in water potential was significantly higher on twigs collected from trees growing at 800 m than those growing nearer the timberline (Table 2).

It has to be mentioned that complete refilling of tracheids in twigs embolized to a high extent or fully was not possible, as repeated flushing did not result in conductivity values comparable to unembolized twigs. Possibly this is due to an irreversible sealing of tori in conifer wood during long-term dehydration (Sperry and Tyree 1990). This effect may slightly alter the shape of the vulnerability curve, nevertheless the resulting underestimation of the lower potential thresholds is negligible, as zero-values of conductivity are not affected.

We were not able to measure vulnerability on twigs collected at the timberline (1900 m) because of high natural embolism rates (see measurements at the alpine timberline), which persisted during rehydration.

Anatomical investigations

Analysis of the frequency distribution of tracheid cross-sectional areas showed a similar two-peaked pattern (corresponding to early and late wood) at all elevations along the investigated altitudinal transect (Fig. 2). We found significant differences ($P < 0.001$) between the

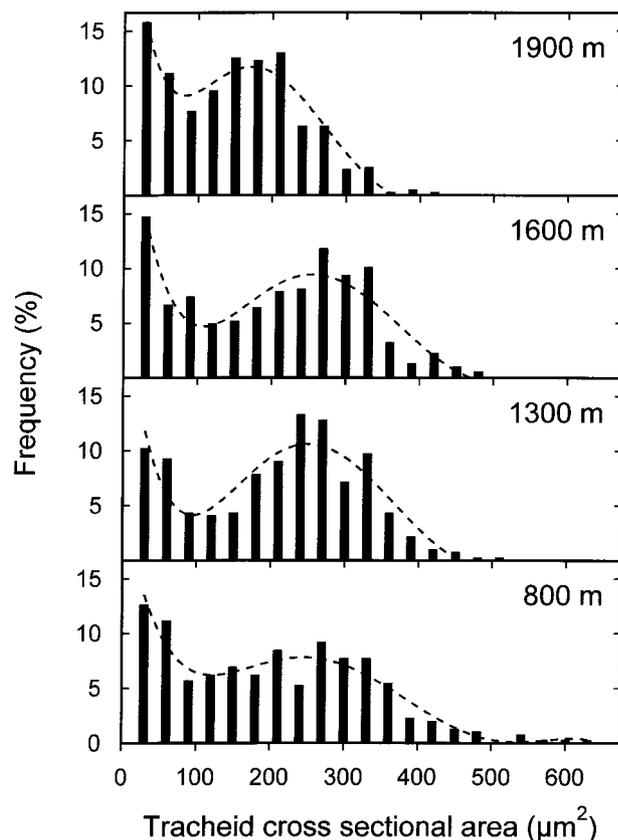


Fig. 2. Frequency distribution of tracheid cross-sectional areas within the youngest tree ring in twigs of Norway spruce harvested at 800, 1300, 1600 and 1900 m. Curves are fitted by quintic regressions. Kruskal–Wallis Test revealed significant differences at $P \leq 0.01$.

Table 3. Ratios of pit diameter to tracheid diameter and of pit pore diameter to pit diameter determined in early wood tracheids (exhibiting radial diameters between 13 and 19 μm) of Norway spruce twigs harvested at 800, 1300, 1600 and 1900 m. Values of each column not followed by the same letter differ significantly at $P \leq 0.05$ (Student's *t*-test).

Altitude (m)	Pit per tracheid diameter (%)	Pore per pit diameter (%)
1900	77.9 \pm 0.9 ^a	25.7 \pm 0.3 ^a
1600	77.7 \pm 1.1 ^a	27.8 \pm 0.3 ^b
1300	78.9 \pm 1.1 ^a	27.8 \pm 0.3 ^b
800	82.9 \pm 0.9 ^b	32.4 \pm 2.6 ^c

four stands, mainly caused by a shift to smaller tracheid cross-sectional sizes at the highest altitudes ($P < 0.001$): maximum tracheid cross-sectional area decreased from 611 μm^2 at 800 m to 398 μm^2 at 1900 m.

Pit diameter to tracheid diameter ratio (within earlywood) was similar at 1300, 1600 and 1900 m, leading to smaller absolute pit sizes due to the observed smaller tracheid diameters. Only at 800 m did the tracheids exhibit significantly larger pits as well as an increased pit pore diameter (Table 3).

Conductivity and water potentials at the timberline

Near the timberline, an abrupt decrease in conductivity with increasing elevation was observed (Fig. 3A) at the two sampling dates in March 2000. Above 1950 m twigs did not conduct water (100% loss of conductivity), whereas at 1820 m, hydraulic conductivity was at its maximum. Conductivities significantly increased from the first sampling date with cold, dry weather to the second sampling date after about 1 week of warm weather and rainfall.

Water potentials also significantly decreased with increasing altitude (Fig. 3B). The lowest potential (-4.0 MPa) was found at the first sampling date in a twig of a tree growing at 2010 m. About 1 week later water potentials were higher overall (lowest potential: -2.16 MPa) but still correlated significantly with altitude.

Discussion

In our investigations we found an altitude-related decrease of water potentials down to extreme values at the mountaintop as well as an increase of embolism rates up to 100% in twigs from near the timberline (Fig. 3). The significant correlation between water potentials and conductivity losses within only 200 m indicates winter drought to be an important pre-condition or even the main reason for the observed embolism. We suppose that low potentials are the cause and not the consequence of embolism — occurring embolism cannot further impair water status of twigs as water supply is already blocked to 100% (permanently frozen stem and soil). In contrast, the observed deficits in water status of twigs must be due to water losses caused by frost drought. Winter embolism has been shown in several

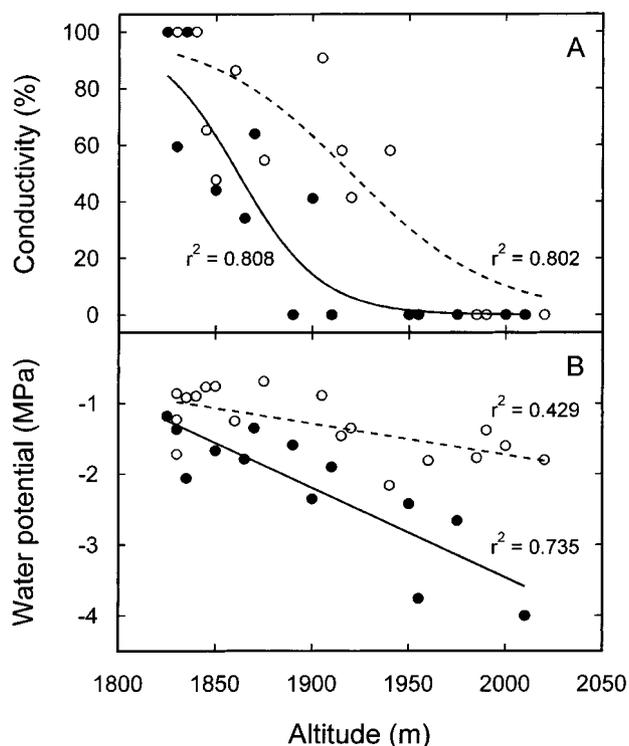


Fig. 3. Conductivity and water potential in twigs of Norway spruce trees growing at different elevations between 1820 and 2020 m. Correlations (Conductivity: logistic sigmoid function, water potential: linear) at March 6 (solid symbols, solid line) and March 13 (open symbols, dashed line) differ significantly at $P \leq 0.05$.

species, for example in *Quercus ilex* (Lo Gullo and Salleo 1993), *Fagus sylvatica* (Magnani and Borghetti 1995), *Rhododendron maximum* (Lipp and Nilsen 1997) or *Pinus contorta* (Sparks et al. 2001). Kullman (1996) hypothesized embolism caused by winter desiccation in Norway spruce in the Swedish Scandes. In contrast, Sperry et al. (1994) reported that in conifers (*Abies lasiocarpa*, *Larix laricina*, *Picea glauca*) growing in Utah and Alaska cavitations occurring during winter, were not associated with increased water stress.

Our vulnerability analysis showed a decrease of the vulnerability threshold to lower water potentials in drought-induced vulnerability (Fig. 1) in twigs of Norway spruce growing at higher altitudes, which indicates an adaptation to the observed altitudinally-increasing drought-stress. Vulnerability thresholds found at low altitudes are similar to those of Norway spruce described by Cochard (1992), who reported a 50% conductivity loss at about -3.3 MPa in trees growing at 250 m in France.

Parameters of the sigmoidal equation used to fit vulnerability curves (Table 2) were expected to reflect embolism-related anatomical properties as described in Pammenter and Vander Willigen (1998). The positions of vulnerability curves (50% loss of conductivity = parameter b) clearly correspond to tracheid sizes as well as pit sizes and/or pit pore sizes (Fig. 2, Table 3). Sperry

and Tyree (1990) suggested that pit membrane flexibility determines the vulnerability threshold of sealed pits whereby membrane flexibility probably depends on pit diameter: air bubbles pass between tracheids only when the pressure difference becomes large enough to rip the torus out of its sealed position. Parameter a (the range over which conductivity is lost) is thought to reflect the variability of tracheid vulnerability thresholds. Our data show a significant decrease of parameter a (increased curve slope, Fig. 1) at 800 m corresponding to an increase of relative pit sizes as well as pit pore sizes within the early wood (Table 3). We suggest a non-linear change of vulnerability-related pit properties. Possibly pit membrane flexibility is similar above a distinct pit size leading to similar vulnerability thresholds in large tracheids.

Although vulnerability analysis of twigs harvested at the alpine timberline (1900 m) was not possible (see Materials and methods) we expect similar or even lower vulnerability thresholds than at 1600 m because of smaller tracheid sizes which correspond to the observed trend of altitude-dependent anatomical changes. According to this assumption a plot of conductivity losses vs. water potential from field measurements at the timberline should result in a curve like the experimentally analysed vulnerability curve at 1600 m. As shown in Fig. 4 curve shapes were similar, which supports our hypothesis of a causal link between drought and embolism formation. However, potentials measured in embolized twigs at the timberline were less negative compared to experimentally determined vulnerability thresholds, which resulted in a curve-shift of about 2.4 MPa. This discrepancy may be due to the following reasons: (1) The experimentally determined vulnerability curves presented reflect only drought- but not freeze-thaw induced embolism. Is it possible that during winter at the alpine timberline not only drought stress (causing the observed correlation

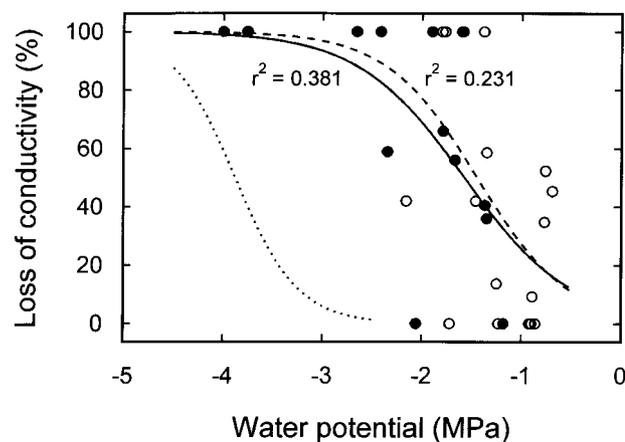


Fig. 4. Comparison of experimentally analysed drought-induced vulnerability curves (curve of 1600 m, dotted line) and conductivity vs. water potential plots of measurements carried out at different elevations at the alpine timberline (March 6 — solid symbols, solid line; March 13 — open symbols, dashed line). All curves are fitted by the equation described in Pammenter and Vander Willigen (1998).

with conductivity losses) but also freeze-thaw events (causing the curve shift) are relevant for the formation of embolism? Sperry et al. (1994) did not find freeze-thaw related cavitations (freezing at -10°C , thawing at 20°C , one cycle) in *Picea glauca* and even 11 temperature cycles (freezing at -20°C , thawing at 20°C) induced only minor conductivity losses in *Juniperus scopulorum* and no loss at all in *Abies lasiocarpa* (Sperry and Sullivan 1992). Sperry and Robson (2001) conclude from inter- and intra-specific comparisons that freeze-thaw induced cavitation does not occur in tracheids smaller than $30\ \mu\text{m}$ in diameter, which is the case for the investigated xylem cross-sections. Nevertheless, the number of freeze-thaw cycles in twigs exposed to alpine winter conditions may be much higher than in experimental studies. Groß et al. (1991) describe up to about 50 days with one or more frost alterations during winter in needles of Norway spruce growing at the timberline. In a recently published study Sparks et al. (2001) found water potential as well as the number of freeze-thaw events to be correlated to rates of winter-embolism in *Pinus contorta*. The authors suggest that development of winter-embolism depends on the shoot water potential during thawing of the tissue and the number of freeze-thaw events during winter. In contrast to our data, potentials of *P. contorta* did not reach the vulnerability threshold of drought induced embolism. (2) Water potentials measured at the sampling dates probably do not reflect the potentials occurring at the time of cavitation. Our first measurements were carried out during a very cold week, nevertheless potentials might have been lower in a previous period. It has to be noticed that the second measurements done only 1 week later gave already higher potentials (Fig. 3B). Possible reasons for the changes in water potential are water shift between stem and twigs or water uptake of branches during warm or rainy periods as reported by Katz et al. (1989) and Sparks et al. (2001). In any case our data prove that water potentials may fluctuate in winter so that conductivity-potential relations of field measurements may not directly correspond to experimental vulnerability analysis.

We also observed increasing hydraulic conductivities (Fig. 3A) between the two sampling dates, which can only be explained by refilling of embolized tracheids. The warm and rainy weather situation before the second sampling probably provided optimal conditions for such a process. Refilling of embolized conduits — even under negative potentials — was published, e.g. for *Pinus sylvestris* (Borghetti et al. 1991, Sobrado et al. 1992, Edwards et al. 1994), for *Abies lasiocarpa*, *Larix laricina*, and *Picea glauca* (Sperry et al. 1994) and *Picea rubens* (Zwieniecki and Holbrook 1998).

Embolism of the observed extent is certainly costly, as trees have to reactivate water transport after the winter season to maintain vitality and growth. Since anatomical adaptations are not sufficient to prevent cavitation at the alpine timberline, refilling of embolized tracheids may be of particular importance — reactivation of water

transport only by formation of new wood in spring would lead to a critical shortening of the already brief vegetation period. Future investigations will focus on these aspects, which may influence survival of Norway spruce at its altitudinal limit.

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