



RESEARCH PAPER

Hydraulic efficiency and safety of leader shoots and twigs in Norway spruce growing at the alpine timberline

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Abstract

Xylem within trees varies in its hydraulic efficiency and safety. Trees at the alpine timberline were expected to exhibit a hydraulic architecture protecting the leader shoot from winter embolism. Hydraulic and related anatomical parameters were compared as well as seasonal courses of winter embolism in leader shoots and twigs of Norway spruce trees growing at 2000 m. Leader shoots had a 1.4-fold higher specific hydraulic conductivity (k_s) as well as a 4.9-fold higher leaf specific conductivity (k_l) than side twigs. Vulnerability to drought-induced embolism was lower in leader shoots with a 50% loss of conductivity occurring at a water potential (Ψ_{50}) 0.7 MPa lower than in twigs. Higher k_s and k_l were related to 1.2-fold wider tracheid diameters in leader shoots. Lower vulnerability corresponded to smaller pit dimensions but not to wood density. High k_s and k_l reflect the hydraulic dominance of the leader shoot, which is important for its water supply during summer. Low vulnerability protects the leader shoot from embolism during the winter season. In field measurements at the timberline during the winter of 2001/2002, conductivity losses of up to 56% were observed only in twigs while leader shoots showed little or no embolism. Results demonstrate that leader shoot xylem is both hydraulically efficient and safe.

Key words: Conductivity, conifer, hydraulic architecture, hydraulic efficiency, hydraulic safety, leader shoot, timberline, twig, vulnerability, winter embolism.

Introduction

Xylem within trees is non-uniform and optimized in its mechanical and hydraulic properties. Heterogeneity is

found at different scales from whole tree even to year ring (Gartner, 1995). The hydraulic architecture of trees (Zimmermann, 1978) is based on differences in the hydraulic properties of the xylem and is characterized by two important functional aspects, hydraulic efficiency and hydraulic safety.

The hydraulic efficiency increases with the specific hydraulic conductivity (k_s) of the xylem. k_s is high whenever conducting elements are wide (according to the Hagen–Poiseuille law) and resistance at conduit connections (pits) is small (Zimmermann, 1978; Tyree *et al.*, 1994). The water supply of leaves is optimal when k_s , as well as the ratio of conducting xylem area per supported leaf area (Huber value *HV*: Tyree and Ewers, 1991), are high, thus causing a high leaf specific conductivity (k_l).

The hydraulic safety describes the resistance of the xylem against embolism formation. In embolized xylem conduits, the transport of water is blocked by gas bubbles which interrupt the transmission of tension to the soil ('cohesion theory': Boehm, 1893; Dixon and Joly, 1894; Richter, 1972; Jackson and Grace, 1994). Embolism is caused by freeze–thaw events or drought. In freezing xylem, gas bubbles are formed because air is not soluble in ice. Depending on the bubble radius and the water potential (Ψ) of the xylem sap (Sperry and Sullivan, 1992; Tyree *et al.*, 1994; Davis *et al.*, 1999; Hacke and Sperry, 2001), enclosed gas bubbles can expand during thawing, which leads to embolism. Drought causes embolism when Ψ in conduits exceeds xylem-specific thresholds so that air can enter from adjacent, already air-filled spaces ('air seeding': Zimmermann, 1983). As air normally enters at the pits, vulnerability thresholds depend on the size of pit pores or, in the case of conifers, on the stability of the (sealed) pit apparatus (Tyree *et al.*, 1994). Embolism at conifer pits occurs when the torus is displaced from its sealing position at the pit porus. Note, that the pit

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Abbreviations: d_h , mean hydraulic diameter; *HV*, Huber value; k_l , leaf specific conductivity; k_s , specific hydraulic conductivity; Ψ , water potential; Ψ_{10} , potential at 10% loss of conductivity; Ψ_{50} , potential at 50% loss of conductivity.

porus of conifers (dealt with in this article) refers to the aperture of the pit and is not identical to the pores of an angiosperm pit membrane or conifer margo.

Conifer axes were shown to be very resistant to drought-induced embolism (Sperry and Tyree, 1990; Cochard, 1992; Jackson *et al.*, 1995; Brodribb and Hill, 1999; Mayr *et al.*, 2002, 2003a). Their narrow tracheids also exhibit high resistance to freeze–thaw-induced embolism since small conducting elements contain small amounts of dissolved gas (Hammel, 1967; Sucoff, 1969; Sperry *et al.*, 1994; Davis *et al.*, 1999; Sperry and Sullivan, 1992; Feild and Brodribb, 2001; Sperry and Robson, 2001; Mayr *et al.*, 2003b). The overall high hydraulic safety of conifer xylem and its low efficiency indicate a trade-off between these hydraulic aspects (Tyree *et al.*, 1994).

Zimmermann (1978) showed that the hydraulic architecture of trees protects the main plant parts from embolism, while less important parts may be sacrificed ('segmentation hypothesis'). When trees transpire, the Ψ pattern within the plant depends on corresponding k_1 values and transpiration rates. Such a k_1 -based segmentation was also shown for conifers such as *Thuja occidentalis* (Tyree *et al.*, 1983), *Abies balsamea* and *Tsuga canadensis* (Ewers and Zimmermann, 1984a, b; Tyree and Alexander, 1993) or *Pseudotsuga menziesii* (Spicer and Gartner, 1998). Differences in hydraulic safety may also lead to a segmentation within tree crowns ('vulnerability segmentation', Tyree and Ewers, 1991). This has been demonstrated for angiosperms (Salleo and LoGullo, 1986; Lemoine *et al.*, 2002), but not yet for conifer species. Roots are more vulnerable to drought-induced embolism than stems (for conifers see Sperry and Ikeda, 1997; Kavanagh *et al.*, 1999; Hacke *et al.*, 2000), probably to protect the stem water transport system from embolism during periods of extreme drought.

In previous studies (Mayr *et al.*, 2002, 2003a), winter drought (Michaelis, 1934; Pisek and Larcher, 1954; Larcher, 1972; Tranquillini, 1980) and frequent freeze–thaw events (Mayr *et al.*, 2003a, b) were shown to induce excessive embolism in twigs of conifers at the alpine timberline. A survival of trees under these extreme conditions is probably only possible with an especially adapted hydraulic architecture. Therefore it was expected that important plant parts, such as the leader shoot, are protected from embolism by a higher hydraulic safety compared to twigs. This should be based on different anatomical properties also leading to differences in hydraulic efficiency.

In the present study, hydraulic (vulnerability thresholds, k_s , k_1 , HV) and related anatomical parameters (tracheid and pit dimensions) of leader shoots and sun-exposed twigs of Norway spruce trees (*Picea abies* L. Karst.) at the alpine timberline were analysed. Seasonal courses of embolism rates in exposed timberline trees should enable an

estimation of the eco-physiological relevance of hydraulic differences.

Materials and methods

Plant material

The study was done on Norway spruce specimens (*Picea abies* L. Karst.) at Mt Birgitzköpfl (2035 m), Central Alps, Tyrol. For conductivity measurements and anatomical analysis, leader shoots and twigs (sun-exposed twigs nearest to the tree top with a minimum length of 1 m) of up to 5 m high trees growing between 1800 m and 2000 m were harvested on 3 December 2001 (before embolism occurred). Prepared samples were between 3.5 mm and 8 mm in xylem diameter. Leader shoots and twigs for the seasonal course were taken at seven dates from 29 October 2001 to 31 May 2002 from trees growing at about 2000 m.

Anatomical investigations

Anatomical measurements were done on samples previously used for the analysis of hydraulic parameters (see below). In twig samples, only xylem areas opposite to compression wood were analysed. Mean tracheid lumen span (termed tracheid diameter here) was calculated assuming a rectangular shape from their areas in cross-section (Schlittenmikrotom OME, Reichert, Wien, Austria), which were determined microscopically (Olympus BX50, Olympus Austria Corporation, Vienna, Austria; 200-fold magnification) with an automated image analysis system (Optimas 6.0, Optimas Corporation, Washington, USA). Mean hydraulic diameter d_h was determined by weighting diameter distribution according to the Hagen–Poiseuille law (Zimmermann, 1983) as described in Kolb and Sperry (1999). From tracheids which averaged within $\pm 0.5 \mu\text{m}$ of d_h , span (b) and corresponding thickness of the double wall (t) were measured. According to Hacke *et al.* (2001), the ratio $(t/b)_h^2$ was calculated. From radial sections of leader shoots and twigs, pit and pit porus diameters within comparable earlywood tracheids (between 13 μm and 17 μm in diameter) were determined microscopically.

Measurements of embolism rates and specific hydraulic conductivity (k_s)

Conductivity of xylem samples was measured with a modified Sperry apparatus (Sperry *et al.*, 1988; Chiu and Ewers, 1993; Vogt, 2001) described in Mayr *et al.* (2002). Embolism rates were quantified by the determination of the increase in hydraulic conductivity after the removal of enclosed air by repeated high pressure flushing. Samples were prepared as described in Mayr *et al.* (2002, 2003a). Measurement pressure was set to 4 kPa. The flow rate was determined with a PC-connected balance (Sartorius BP61S, 0.0001 g precision, Sartorius AG, Göttingen, Germany) by weight registration every 10 s and linear regression over 200 s. Flushing (0.13 MPa, 20 min) and conductivity measurements were done with distilled, filtered (0.22 μm) and degassed water containing 0.005% (v/v) 'Micropur' (Katadyn Products Inc., Wallisellen, Switzerland) to prevent microbial growth (Sperry *et al.*, 1988). Flushing was repeated until measurements showed no further increase in conductivity. Loss of conductivity in per cent was calculated from the ratio of initial to maximal conductivity.

Specific hydraulic conductivity k_s was calculated from fully hydrated leader shoots and twigs as in equation 1

$$k_s = Q / (A_c \Delta P) \quad (1)$$

where k_s is in $\text{m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$, Q is the volume flow rate ($\text{m}^3 \text{s}^{-1}$), l is the length of the segment (m), A_c is the xylem cross-sectional area (m^2 , calculated from the sample diameter), and ΔP is the pressure

difference between the segment ends (MPa). Calculations were corrected to 20 °C to account for changes in fluid viscosity with temperature.

Huber value and leaf specific conductivity

The Huber value (*HV*; Tyree and Ewers, 1991) is the ratio of xylem cross-sectional area (A_c) to supported (distal) leaf area (projected needle area A_l , equation 2).

$$HV = A_c / A_l \quad (2)$$

For the determination of A_l , the dry weight and projected needle area of a representative amount of needles were determined for each leader shoot and twig with a digital video camera (Leaf Area and Analysis System SI 721, Skye Instruments Ltd., Llandrindod Wells, UK). Based on this ratio of area to dry weight, A_l was calculated from the dry weight of all needles of leader shoots and twigs, respectively.

The leaf specific conductivity k_1 is the volume flow rate (per sample length and applied pressure) per distal leaf area and can be calculated using k_s and *HV* (equation 3):

$$k_1 = k_s HV \quad (3)$$

Vulnerability curves

Vulnerability curves were obtained from twigs dehydrated to various extents by plotting the percentage loss of hydraulic conductivity versus water potential (Ψ). Ψ was measured with a pressure chamber (Model 1000 Pressure Chamber, PMS Instrument Company, Corvallis, OR, USA). Measurements were done on end segments (length <5 cm) of twigs and leader shoots before samples for conductivity measurements were prepared. Curves were fitted with an exponential sigmoidal equation (equation in Pammenter and Vander Willigen, 1998):

$$PLC = 100 / (1 + \exp(a(\Psi - \Psi_{50}))) \quad (4)$$

where *PLC* is the percentage loss of conductivity, Ψ is the corresponding water potential and *a* is a constant related to the curve slope. Ψ_{50} corresponds to the water potential at 50% loss of conductivity.

Number of samples, statistics

Anatomical measurements were done on 10 leader shoot and twig samples, respectively. Vulnerability was analysed on 57 leader shoot and 36 twig samples, whereby Ψ determination was done on at least three parallel end segments. Other hydraulic parameters (k_s , *HV*, k_1) were calculated from 12 leader shoot and 12 twig samples. For the seasonal course, embolism rates of at least three parallel samples were determined at each sampling date.

Values are given as mean \pm standard error. Differences were tested with Student's *t*-test (5% probability level) after checking for normal distribution and variance of the data or with the Mann-Whitney test (tracheid diameter distributions, 1% probability level).

Results

Anatomy

Twigs had significantly smaller tracheid diameters than leader shoots (Fig. 1; Table 1). Mean tracheid diameter as well as mean hydraulic diameter of leader shoots were about 1.2-fold those of twigs. In consequence, leader shoots exhibited a significantly smaller $(t/b)_h^2$ ratio (0.78-fold) than twigs, although *t* did not differ (Table 1). Within

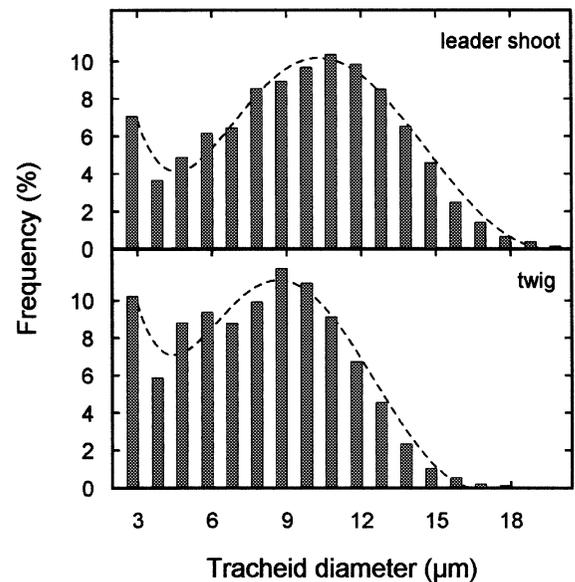


Fig. 1. Frequency distribution of tracheid cross-sectional diameters (lumen) in leader shoots and twigs. Frequency distributions differ significantly at $P < 0.01$.

comparable earlywood tracheids (13–17 μm), pit diameters were larger (+6%), but pit porus diameters were smaller (–5%) in leader shoots than in twigs. Compression wood of twigs was not included in the measurements, otherwise the differences would be even greater.

Hydraulic parameters

Leader shoots showed a 1.4-fold higher k_s , a 3.5-fold higher Huber value and, in consequence, a 4.9-fold higher k_1 compared to twigs (Table 2). The observed difference in k_s was not significant because k_s measurements showed high variation, probably due to differences in (less conductive) compression wood portions and in sample age. Vulnerability analysis revealed that the potential at 10% loss of conductivity (Ψ_{10}) was 0.5 and Ψ_{50} was 0.7 MPa lower in leader shoots than in twigs (Fig. 2; Table 2). No significant difference in vulnerability curve slope was detected.

Seasonal course

Relevant conductivity losses were found in twigs but not in leader shoots (Fig. 3). Conductivity losses of twigs were at a maximum on 4 January ($55.8 \pm 4.3\%$), decreased to 17.8% on 26 February and reached about 33% in March and April. Embolism rates were near zero in May.

Discussion

Leader shoots of Norway spruce were found to be both hydraulically efficient and safe. Hydraulic efficiency was higher in leader shoots which exhibited a 1.4-fold higher k_s

Table 1. Anatomical parameters of leader shoots and twigs (opposite wood) of Norway spruce

Pit dimensions were analysed within comparable earlywood tracheids (tracheid diameter between 13 and 17 μm). Mean hydraulic diameter d_h was calculated according to Kolb and Sperry (1999), the parameter $(t/b)_h^2$ was calculated from the wall thickness t and the conduit wall span b according to Hacke *et al.* (2001). Values of twigs marked by an asterisk differ significantly from that of leader shoots at $P < 0.05$ (Student's t -test). Mean \pm SE.

	Leader shoot	Twig
Mean tracheid diameter (μm)	9.19 \pm 0.06	7.55 \pm 0.05*
Maximum tracheid diameter (μm)	19.51	19.30
Earlywood pit diameter (μm)	12.72 \pm 0.14	12.06 \pm 0.13*
Pit porus diameter (μm)	4.21 \pm 0.14	4.45 \pm 0.09*
d_h (μm)	13.19 \pm 0.001	11.39 \pm 0.001*
t (μm)	4.93 \pm 0.16	4.84 \pm 0.15
$(t/b)_h^2$	0.149 \pm 0.01	0.192 \pm 0.01*

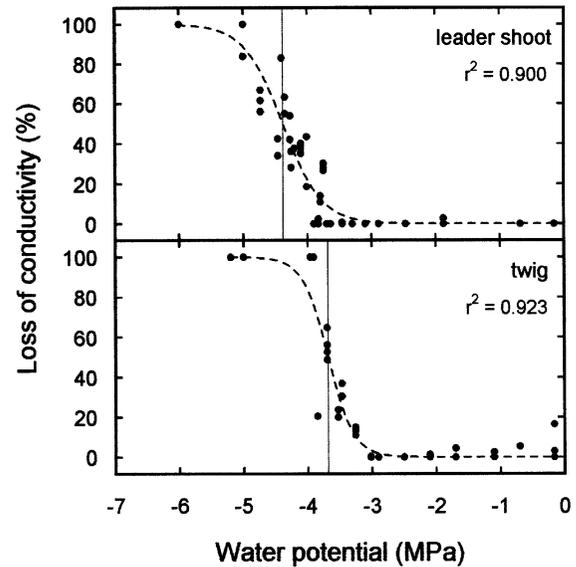
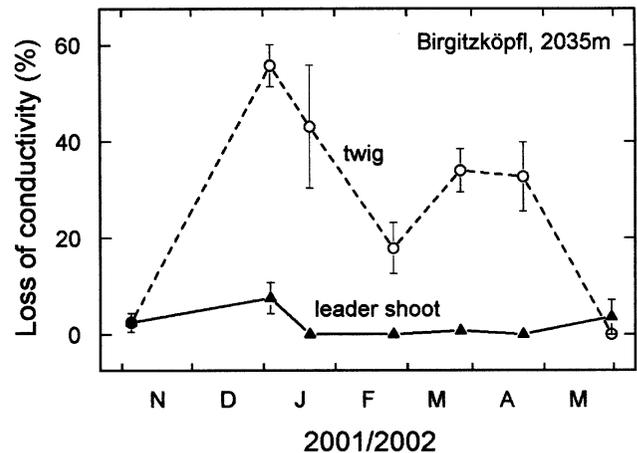
Table 2. Hydraulic parameters of leader shoots and twigs of Norway spruce k_s is the specific hydraulic conductivity, HV the Huber value and k_l the leaf specific conductivity.

Vulnerability curve parameter a , Ψ_{50} and Ψ_{10} were calculated according to Pammenter and Vander Willigen (1998). Values of twigs marked by an asterisk differ significantly from that of leader shoots at $P < 0.05$ (Student's t -test). Mean \pm SE.

	Leader shoot	Twig
k_s ($\text{m}^{-2} \text{s}^{-1} \text{MPa}^{-1} \times 10^{-4}$)	3.32 \pm 0.55	2.36 \pm 0.35
HV ($\times 10^{-4}$)	11.5 \pm 0.98	3.25 \pm 0.19*
k_l ($\text{m}^{-2} \text{s}^{-1} \text{MPa}^{-1} \times 10^{-7}$)	3.58 \pm 0.58	0.73 \pm 0.11*
Parameter a	3.34 \pm 0.35	5.10 \pm 0.88
Ψ_{50} (MPa)	-4.38 \pm 0.03	-3.68 \pm 0.03*
Ψ_{10} (MPa)	-3.72 \pm 0.10	-3.25 \pm 0.11*

and a 4.9-fold higher k_l than twigs (Table 2). k_s values corresponded to tracheid and hydraulic diameters and may also be influenced by tracheid length or pit architecture (Table 1). It has to be considered that compression wood was not included in anatomical analysis, but influenced conductivity measurements by its low k_s (Spicer and Gartner, 1998; Mayr and Cochard, 2003). An increased hydraulic efficiency of the main axes was also shown for *Thuja occidentalis* (Tyree *et al.*, 1983), *Abies balsamea* and *Tsuga canadensis* (Ewers and Zimmermann, 1984a, b, Tyree and Alexander, 1993). In *Pseudotsuga menziesii*, Spicer and Gartner (1998) observed about 2.2-fold higher k_s and about 5-fold higher k_l in 3-year-old leader shoots compared to twigs.

The hydraulic safety of leader shoots was higher than in twigs (Fig. 2; Table 2), differences in drought-induced vulnerability could be related to anatomical parameters: in earlywood, diameters of whole pits were wider, but pit porus diameters were smaller in leader shoots compared to twigs (Table 1). It is suggested that the sealing position of a torus after aspiration is more stable when it occurs at a

**Fig. 2.** Vulnerability curves (loss of conductivity versus Ψ) of leader shoots and twigs. Curves were fitted by the equation described in Pammenter and Vander Willigen (1998). Ψ_{50} is indicated by vertical lines.**Fig. 3.** Seasonal course of embolism. Embolism rates (loss of conductivity) in leader shoots (triangles) and twigs (circles) at Mt Birgitzköpf (2035 m) in winter 2001/2002 (November–May). Mean \pm SE.

small porus. This may contribute to the lower drought-related vulnerability of leader shoot xylem. Along an altitudinal transect, a similar correlation between pit porus dimensions and vulnerability to drought-induced embolism was observed (Mayr *et al.*, 2002). Another study demonstrated that susceptibility to freeze–thaw-induced embolism in conifers is highest at the upper drought-related vulnerability threshold (Mayr *et al.*, 2003b). The low drought-related vulnerability of leader shoots, therefore, should also lower their risk of freeze–thaw-induced embolism.

For an ecological interpretation of observed safety and vulnerability properties in trees at the alpine timberline, the different situations in summer and winter have to be considered: in summer, trees at the alpine timberline are not usually exposed to drought stress (Tranquillini, 1976) so that the observed differences in vulnerability seem not to be of relevance. On the other hand, high k_s and k_1 values reflect the hydraulic dominance of the leader shoot as shown for other conifer species (Ewers and Zimmermann, 1984a, b). When the plant transpires, hydraulic resistances influence the water supply of the leader shoot and the twigs (Zimmermann, 1978).

In winter, the uptake of water is blocked by the frozen soil and stem (Mayr *et al.*, 2003a). Conductivity properties, therefore, cannot lead to hydraulic segmentation: only at sufficient transpiration rates could different hydraulic resistances cause different Ψ and, consequently, protect xylem sections with higher k_1 from embolism (Zimmermann, 1978; Tyree and Ewers, 1991). At the alpine timberline, low transpiration rates (Mayr *et al.*, 2003a) prevent the development of steep Ψ gradients. Nevertheless, trees lose water by cuticular transpiration, so that Ψ slowly decreases during the winter months even to critical values (Mayr *et al.*, 2002, 2003a).

The question may arise whether leader shoots and twigs were exposed to similar stress intensities: Xylem temperatures were measured in leader shoots and in sun-exposed twigs of a Norway spruce tree growing at the alpine timberline (Mayr *et al.*, 2003b). The number of freeze–thaw events was nearly identical and the longest period with permanently frozen xylem was 8 d (data not shown). It was concluded that water potentials must have equilibrated every few days within the upper tree sections (and, therefore, in leader shoots and twigs compared in this study) and that freeze–thaw stress was also identical. Therefore, the observed lack of conductivity losses in leader shoots during the winter 2001/2002 (Fig. 3) was based on their high hydraulic safety leading to a vulnerability segmentation (Tyree and Ewers, 1991). Twigs exhibited embolism similar (in extent and course) to other stands (Mayr *et al.*, 2003a) and refilling processes already during winter.

But why is twig xylem not as safe as leader shoot xylem? There are probably several other costs limiting the hydraulic properties of twig xylem. Twigs, for example, have higher gravity loads (e.g. excessive snow loads during winter) and therefore are optimized mechanically. The necessary compression wood is more vulnerable than normal wood (Mayr and Cochard, 2003). This may also explain why the observed vulnerability properties of leader shoots and twigs did not correspond to $(t/b)_h^2$. This parameter (related to wood density) was correlated with hydraulic safety (Hacke *et al.*, 2001; Hacke and Sperry, 2001). In leader shoots $(t/b)_h^2$ was even smaller (due to wide tracheid diameter: Table 1) although hydraulic safety

was higher than in twigs. Hydraulic aspects of $(t/b)_h^2$ were probably masked because the mechanical requirements predominantly influenced the xylem structure.

The observed hydraulic design of Norway spruce which protects the water transport system of the leader shoot is only one of several adaptations to winter embolism found in conifers at the alpine timberline (Mayr *et al.*, 2002, 2003a, b). As conifers dominate the timberline ecotone, the results may indicate that embolism influences the altitudinal limit of trees.

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