

The hydraulic architecture of *Juniperus communis* L. ssp. *communis*: shrubs and trees compared

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ABSTRACT

Juniperus communis ssp. *communis* can grow like a shrub or it can develop a tree-like habit. In this study, the hydraulic architecture of these contrasting growth forms was compared. We analysed the hydraulic efficiency (leaf-specific conductivity, k_l ; specific conductivity, k_s ; Huber value, HV) and the vulnerability to cavitation (the water potential corresponding to a 50% loss of conductivity, Ψ_{50}), as well as anatomical parameters [mean tracheid diameter, d ; mean hydraulic diameter, d_h ; cell wall reinforcement $(t/b)_h^2$] of shrub shoots, tree stems and tree branches. Shrub shoots were similar to tree branches (especially to lower branches) in growth form and conductivity ($k_l = 1.93 \pm 0.11 \text{ m}^2 \text{ s}^{-1} \text{ MPa}^{-1} 10^{-7}$, $k_s = 5.71 \pm 0.19 \text{ m}^2 \text{ s}^{-1} \text{ MPa}^{-1} 10^{-4}$), but were similar to tree stems in their vulnerability to cavitation ($\Psi_{50} = -5.81 \pm 0.08 \text{ MPa}$). Tree stems showed extraordinarily high k_l and k_s values, and HV increased from the base up. Stem xylem was more vulnerable to cavitation than branch xylem, where Ψ_{50} increased from lower ($\Psi_{50} = -6.44 \pm 0.19 \text{ MPa}$) to upper branches ($\Psi_{50} = -5.98 \pm 0.13 \text{ MPa}$). Conduit diameters were correlated with k_l and k_s . Data indicate that differences in hydraulic architecture correspond to changes in growth form. In some aspects, the xylem hydraulics of tree-like *Juniperus communis* differs from that of other coniferous tree species.

Key-words: embolism; hydraulic conductivity; hydraulic efficiency; vulnerability; xylem anatomy.

INTRODUCTION

The growth habit of *Juniperus communis* L. ssp. *communis* (in the following referred to as *J. communis*) is highly variable in natural populations. It can grow either as a shrub or as a tree several metres tall (Zoller 1981; Van Der Merwe *et al.* 2000; Adams & Pandey 2003; Thomas, El-Barghathi & Polwart 2007). There are a number of indications that environmental factors drive its development and growth habit, and that these are not simply derived from different geno- or ecotypes. Although *J. communis* is a highly variable species in respect to its morphology, habit and genetics (Van Der Merwe *et al.* 2000; Adams & Pandey 2003), no correlations between growth forms and DNA markers have

yet been found (Van Der Merwe *et al.* 2000; Adams & Pandey 2003). Furthermore, both of the growth forms can occur side by side and within a single population (Van Der Merwe *et al.* 2000; Adams & Pandey 2003). During the transition from shrub to tree, *J. communis* undergoes a reorganization of its architecture. First, a shoot emerges that looks similar to the others but it develops in a more upright (vertical) direction. Subsequently, this shoot shows increased radial and longitudinal growth, while the other non-upright shoots typically senesce. After several years, a typical tree form is developed with a main stem bearing a hierarchically composed branch architecture. The driver for these changes may be environmental factors such as shade, grazing and exposure (see Ewald 2003; Ewald & Müller 2003; Thomas *et al.* 2007). Accordingly, young dendriform individuals were absent from our study site and Ewald and Müller (2003) reported a decrease in dendriform individuals under changing environmental conditions.

These contrasting growth forms are interesting from a hydraulic point of view as transport distances, hydraulic resistances, morphological (e.g. branching pattern, leaves) and anatomical features (e.g. conduit diameter, cell wall reinforcement) differ (Ewers & Fisher 1991; Gartner 1991; Tyree & Ewers 1991; Patiño, Tyree & Herre 1995) and result in a changed hydraulic architecture. A plant's hydraulic architecture is determined by specific patterns in several hydraulic parameters, for example, hydraulic efficiency and vulnerability to cavitation (Tyree & Ewers 1991; Tyree & Zimmermann 2002). Hydraulic efficiency can be characterized by the leaf-specific hydraulic conductivity (k_l) and the specific hydraulic conductivity (k_s). The k_l is a measure of a xylem segment's 'sufficiency' to supply distal leaves with water (Tyree & Ewers 1991; Tyree & Zimmermann 2002), and results from k_s and the ratio of conducting xylem area per supported leaf area (Huber value, HV; Tyree & Ewers 1991; Tyree & Zimmermann 2002). The k_s is related to the sapwood cross-sectional area, and is a measure of a xylem segment's 'efficiency' in conducting water (Tyree & Zimmermann 2002). The k_s is high when conducting elements are wide, the resistance in the conduit lateral connections (pits) is small, and the number of conducting elements per unit stem cross section is high. Conducting elements normally make up only a small proportion of the cells visible in any cross section and this proportion can vary (Tyree & Ewers 1991; Tyree, Davis & Cochard 1994; Tyree & Zimmermann 2002; Hacke, Sperry & Pittermann 2004;

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Mcculloh & Sperry 2005; Pittermann *et al.* 2006; Sperry, Meinzer & McCulloh 2008).

Embolism is induced by drought and/or by freeze-thaw events (e.g. Tyree & Sperry 1989; Sperry & Tyree 1990; Sperry & Sullivan 1992; Mayr, Rothart & Dämon 2003b) and vulnerability to embolism plays a major role in the water relations of woody plants (Tyree & Ewers 1991; Tyree & Zimmermann 2002). Many conifers are known to be very resistant to drought-induced embolism (Sperry & Tyree 1990; Cochard 1992; Brodribb & Hill 1999; Mayr, Wolfschwenger & Bauer 2002; Mayr *et al.* 2006) and also to freeze-thaw-induced embolism (Sperry & Sullivan 1992; Sperry *et al.* 1994; Davis, Sperry & Hacke 1999; Feild & Brodribb 2001; Sperry & Robson 2001; Mayr, Gruber & Bauer 2003a). The genus *Juniperus* (Cupressaceae) exhibits an extraordinarily high resistance to drought-induced embolism (Pockman & Sperry 2000; Martinez-Vilalta, Sala & Pinol 2004; Mayr *et al.* 2006; Willson & Jackson 2006; West *et al.* 2007; Willson, Manos & Jackson 2008). Furthermore, *J. communis* is known to be very frost tolerant and so is able to grow on poor soils and in harsh environments (Zoller 1981; Garcia *et al.* 2000; Thomas *et al.* 2007). It is among the most widely distributed gymnosperms in the Holarctic.

Shrubs are multi-stemmed woody plants with basitonic growth while trees exhibit a single, uniform stem and acrotonic growth (Sitte *et al.* 1998). The large transport distances in trees pose a hydraulic challenge; as the cumulative hydraulic resistance increases with path length (height of tree, length of branches; Ryan & Yoder 1997; Burgess, Pittermann & Dawson 2006), leading to a base-up decrease in Ψ . In addition, Ψ decreases with height because of gravity so that lower vulnerability thresholds, as well as reinforced conduit walls to prevent collapse, are required (Hacke & Sperry 2001; Hacke *et al.* 2001; Burgess *et al.* 2006; Pittermann *et al.* 2006). These aspects led to the hypothesis that height growth of trees may be limited hydraulically (e.g. Ryan & Yoder 1997; Delzon *et al.* 2004; Koch *et al.* 2004; Burgess *et al.* 2006; Ryan, Phillips & Bond 2006; Niklas 2007; Sperry *et al.* 2008). In shrubs, transport distances are normally shorter, although the branching system can be complex (Tyree & Ewers 1991). There are several studies demonstrating pronounced differences in the hydraulic architecture of different growth forms (Ewers & Fisher 1991; Gartner 1991; Tyree & Ewers 1991; Patiño *et al.* 1995). While most of these studies compare different species, only Gartner (1991) presented an intraspecific comparison of shrubs and vines. The author demonstrated differences in k_s and HV between unsupported (shrubs) and supported (vines) stems of *Toxicodendron diversilobum*, while k_t was similar in the two growth forms. In the present study, the variable growth habit of *J. communis* enabled an intraspecific comparison of shrubs and trees. Measurements were made on a study site where both growth forms occur together and thus individuals are subject to similar environmental conditions. We focused on the following questions: Are there differences in hydraulic efficiency and vulnerability to cavitation between shrubs and trees of *J. communis*? Is the hydraulic architecture of juniper trees similar to that

of other tree species? Are differences in the measured hydraulic parameters related to xylem anatomy?

To answer these questions, we studied growth form (length and diameter, mean leaf area, branching patterns, age, annual ring width), hydraulic traits (k_t , k_s , HV, vulnerability to drought-induced embolism) and related anatomical parameters (mean and hydraulic tracheid diameter, cell wall thickness, cell wall reinforcement) of shrubs and trees of *J. communis*. Measurements were made on main shoots of shrubs (referred to as shrub shoots) and also on stems (referred to as tree stems) and branches (referred to as tree branches) of dendriform individuals.

MATERIAL

Juniper plants (*J. communis*) that grew in a natural Scots pine forest near Telfs (600 m a.s.l., Tyrol, Austria, Central European Alps) were selected. The sample area was about 2500 m². Individuals occurred mainly in groups, which were randomly distributed in the sample area. Within groups, both growth forms occurred side by side. Several growth parameters were measured on shrub shoots and on trees up to 3.2 m tall *in situ*. The whole plants were cut down, wrapped in dark plastic bags and transported to the laboratory. There, they were re-cut twice under water, altogether removing a proximal section of about 3 cm and were saturated for 24 h.

Morphological, hydraulic and anatomical analyses were performed on shrub shoots and also on tree stems and branches. The latter were classified either as lower branches (inserted between 0 to 0.7 m in height), middle branches (1 to 2 m) or upper branches (higher than 2 m). Tree stems were subdivided into middle stem (middle third of the whole stem) and upper stem (upper third of the whole stem, including the top). The lower third of the stem could not be used because of its large diameter and numerous branches. Sample sections were taken every 3 to 10 cm along shrub shoots and middle stem, upper stem, lower, middle and upper branches of trees. We also measured pathway length from the base to each sample section.

METHODS

Growth form and growth rate

The growth habit of all plants used was sketched in the field and several parameters relating to their growth form were recorded and later analysed. The lengths of shrub shoots and the heights of trees were measured from the ground to the tips, and so was the length of the tree branches from the point of insertion to the tips. Diameters of shrub shoots and tree stems were measured 15 cm above the ground, and of branches 2 cm distal to the insertion site. Mean numbers of shoots per shrub could only be estimated as shrubs were growing in dense populations, and shoots often emerged and branched subterraneously. The angle between the horizontal soil surface and the basal section of shrub shoots or of tree stems was also measured *in situ*. Leaf area per shrub

shoot, whole tree or tree branch, was measured in the course of making conductivity measurements (see further discussion). To calculate the ratio of terminal to lateral shoot length, the length of the terminal and of the longest lateral shoot was measured at the distal ends of shrub shoots, branches and the treetops, respectively. For growth rate analyses, age and annual ring width were measured on samples of shrub shoots and of tree stems taken between 5 and 15 cm above ground. In contrast to some other juniper species, *J. communis* has distinct latewood–earlywood boundaries and no false rings (see also Greguss 1955; Grosser 1977; Schweingruber 1992). Therefore, analyses along the whole cross section were feasible.

Hydraulic conductivity

Conductivity measurements were made on fully saturated samples with a modified Sperry apparatus (Sperry, Donnelly & Tyree 1988; Chiu & Ewers 1993; Vogt 2001) without flushing. Samples, up to 10 cm long, were immersed in distilled water, decorticated, re-cut with a sharp wood carving knife and sealed in the silicone tubes of the apparatus (see Mayr *et al.* 2002). Measurement pressure was set to 4 kPa. The flow rate was determined with a PC-connected balance (Sartorius BP61S, 0.1 mg precision; Sartorius AG, Göttingen, Germany) by weight registration every 10 s and linear regression over 200 s. For measurements, distilled, filtered (0.22 µm) and degassed water containing 0.005% (v/v) ‘Micropur Forte MF 1000F’ (a mixture containing Ag⁺ and sodium hypochlorite sold for water sterilization and preservation; Katadyn Products Inc., Wallisellen, Switzerland) to prevent microbial growth (Sperry *et al.* 1988) was used (also see methods sections in Mayr, Schwienbacher & Bauer 2003c; Mayr *et al.* 2006; Mayr & Charra-Vaskou 2007).

The leaf-specific conductivity k_1 (m² s⁻¹ Pa⁻¹) was calculated as

$$k_1 = \frac{Ql}{A_1\Delta P} \quad (1)$$

where Q is the volume flow rate (m³ s⁻¹), l is the segment length (m), A_1 is the supplied leaf area (m²) and ΔP is the pressure difference between the segment ends (Pa). Calculations were corrected to 20 °C to account for changes in the viscosity of water with temperature.

For the determination of A_1 , twigs were dipped into liquid nitrogen for a few seconds and frozen needles were detached manually. For each sample, about 50 needles were taken to measure A_1 with a digital video camera (Leaf Area and Analysis System SI 721; Skye Instruments Ltd., Llandrindod Wells, UK) as well as dry weight (80 °C, 24 h). Based on the ratio of area to dry weight, A_1 was calculated from the dry weight of all needles taken from a sample.

The specific hydraulic conductivity (k_s) was measured similarly to k_1 , but related to the xylem cross-sectional area (A_c ; sapwood less heartwood; m²; Eqn 2). To distinguish

heartwood from sapwood, dye experiments were made with Phloxine B (2% w/v; Sigma, St. Louis, MO, USA; see Mayr & Cochard 2003):

$$k_s = \frac{Ql}{A_c\Delta P} \quad (2)$$

The Huber value (HV; m²/m²) is the ratio of the sapwood cross sectional (A_c) to the leaf area (distal) supported (A_1) as given in Eqn 3 (Tyree & Ewers 1991):

$$HV = \frac{A_c}{A_1} \quad (3)$$

Vulnerability analysis

Vulnerability curves were obtained by dehydrating samples to differing extents and plotting the fractional (%) loss of conductivity versus the water potential (Ψ). Curves were fitted using an exponential sigmoidal equation (Eqn 4) given in Pammenter and Vander Willigen (1998):

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

where PLC is the percent loss of conductivity, Ψ is the corresponding water potential (MPa) and a is related to the slope of the curve. Ψ_{50} is the Ψ value corresponding to 50% loss of conductivity.

The water potential was measured with a Model 1000 Pressure Chamber (PMS Instrument Company, Corvallis, OR, USA). Measurements were made on up to 10-cm-long end segments of side twigs. Loss of hydraulic conductivity was quantified by measuring the increase in hydraulic conductivity after removal of xylem embolisms by repeated high-pressure flushes with a modified Sperry apparatus. Flushing (80 kPa, 20 min) was repeated until measurements showed no further increase in conductivity. PLC was calculated from the ratio of initial to maximal conductivity (Sperry *et al.* 1988).

Anatomical measurements

Samples previously used for conductivity measurements or vulnerability analysis were soaked in an ethanol/glycerol/water solution (1:1:1, v/v/v) for 2 weeks. Cross sections were cut with a microtome (Schlittenmikrotom OME, Reichert, Vienna, Austria) and stained with phloroglucinol-HCl (stains lignin bright red). Anatomical parameters were analysed with a light microscope (Olympus BX41; Olympus Austria, Vienna, Austria) interfaced with a digital camera (Cyber-shot DSC-W17; Sony, Vienna, Austria) and image analysis software (ImageJ 1.37; public domain, National Institutes of Health, Bethesda, MD, USA). Individual conduit areas were measured in radial sectors of the youngest three annual rings (2004–2006) to analyse a representative area within the sapwood. Radial sectors were located opposite to any compression wood, which is hydraulically of minor importance (see also Mayr & Cochard 2003). The

mean hydraulic conduit diameter (d_h) was calculated according to Eqn 5 (Sperry & Hacke 2004):

$$d_h = \frac{\sum d^5}{\sum d^4} \quad (5)$$

where d is the side (μm) of the tracheids analysed, calculated from the tracheid area and assuming a square shape.

To characterize conduit wall reinforcement, we measured the 'thickness-to-span ratio' $(t/b)_h^2$ (Hacke *et al.* 2001). The wall thickness between conduits (t) was measured directly in the tangential walls, while the conduit wall span (b) was assumed equal to the side of a square with an area identical to the conduit lumen area. Measurements were made on tracheid pairs, whereby the tracheids analysed showed a diameter similar to d_h ($\pm 1 \mu\text{m}$; see also Hacke & Sperry 2001; Hacke *et al.* 2001).

Number of samples and statistics

Conductivity measurements were made on three to five individual plants per growth form. Depending on length and height (samples of 3 to 10 cm), 17 to 112 samples were taken per shrub shoot and also of middle stem, upper stem, lower, middle and upper branches of trees. For vulnerability analyses, 6 to 29 individual plants per growth form were cut, and 43 to 138 samples per group (shrub shoot, middle stem, upper stem, lower, middle and upper branches) were taken.

Of the samples for conductivity and vulnerability analyses, 10 samples per group were chosen for anatomical measurements. Of a total of 6000 to 13 000 conduits per group, mean diameter (d_{mean}), maximum diameter (d_{max}) and mean hydraulic diameter (d_h) were calculated. 'Thickness-to-span ratio' $(t/b)_h^2$ was determined in 50 to 130 tracheid pairs per

group. Growth form parameters were analysed on three different shrubs and three different trees. Age and annual ring width were measured on the most basal sample of each shrub and tree, respectively, taken for conductivity measurements.

Differences between groups were tested with the Welch test (vulnerability thresholds and d_h), analysis of variance and Tamhane test (HV, k_s , k_l and t) or Mann–Whitney U -test with Bonferroni correction [d_{mean} and $(t/b)_h^2$]. Differences between shrubs and trees relating to growth form and growth rate were tested with the Student's t -test. All tests were made at a probability level of 5% (except the Welch test) after first testing for normal distribution and for variance of the data. Correlation coefficients were tested with Pearson's product-moment coefficient.

RESULTS

Growth form and growth rate

The parameters studied revealed pronounced differences in growth form and growth rate of shrubs and trees of *J. communis*: shrubs showed a distinct basitonic, sympodial growth. Individuals were composed of at least eight similar shoots per plant, and shoots often branched into several homologous side branches, leading to a typical shrubby habit. The angles between the soil surface and shrub shoots were less than 70° (Table 1). In contrast, trees were single-stemmed (monopodial) individuals with an acrotonic growth habit. They could clearly be subdivided into a distinct, vertically growing (90°) main axis (stem) and horizontally oriented (plagiotropic) branches. Tree stems and branches differed in length and diameter (Table 1). The ratio of terminal to lateral shoot length corresponded to the acrotonic growth habit of trees: in treetops, terminal shoots were about four times longer than lateral shoots. This ratio

Table 1. Growth form parameters, age and mean annual ring width of shrubs (shoots) and trees (stem, lower, middle and upper branches) of *Juniperus communis* ssp. *communis*

Parameter	Shrub	Tree			
	Shoot	Stem	Lower branches	Middle branches	Upper branches
Growth form and branching pattern	Basiton, sympodial	Acroton, monopodial	–	–	–
Mean ratio terminal to lateral shoot length	$1.4 \pm 0.1^\circ$	$4.2 \pm 0.9^*$	$1.6 \pm 0.3^\circ$	$3.1 \pm 0.8^*$	$3.4 \pm 0.5^*$
Number of shoots/stems per individual	>8	1	–	–	–
Mean angle between soil surface and shoot/stem ($^\circ$)	$42 \pm 18^\circ$	$90 \pm 0^*$	–	–	–
Mean length or height (cm)	$116 \pm 12^\circ$	$280 \pm 72^*$	$115 \pm 13^\circ$	$92 \pm 8^*$	$50 \pm 7^*$
Mean diameter (shrub shoots and tree stems 15 cm above soil, branches 2 cm distal of insertion (cm))	$1.37 \pm 0.25^\circ$	$5.67 \pm 0.16^*$	$1.23 \pm 0.15^\circ$	$1.00 \pm 0.16^\circ$	$0.51 \pm 0.08^*$
Mean leaf area (cm ²)	$2024 \pm 640^\circ$	$27\,631 \pm 2879^*$	$1734 \pm 605^\circ$	$2167 \pm 579^\circ$	$538 \pm 180^*$
Age (years)	11–24 $^\circ$	23–48 *	–	–	–
Mean annual ring width (mm)	$0.330 \pm 0.144^\circ$	$0.757 \pm 0.299^*$	–	–	–

Asterisks indicate significant differences from shrub shoots and circles indicate significant differences from tree stems (mean \pm SE).

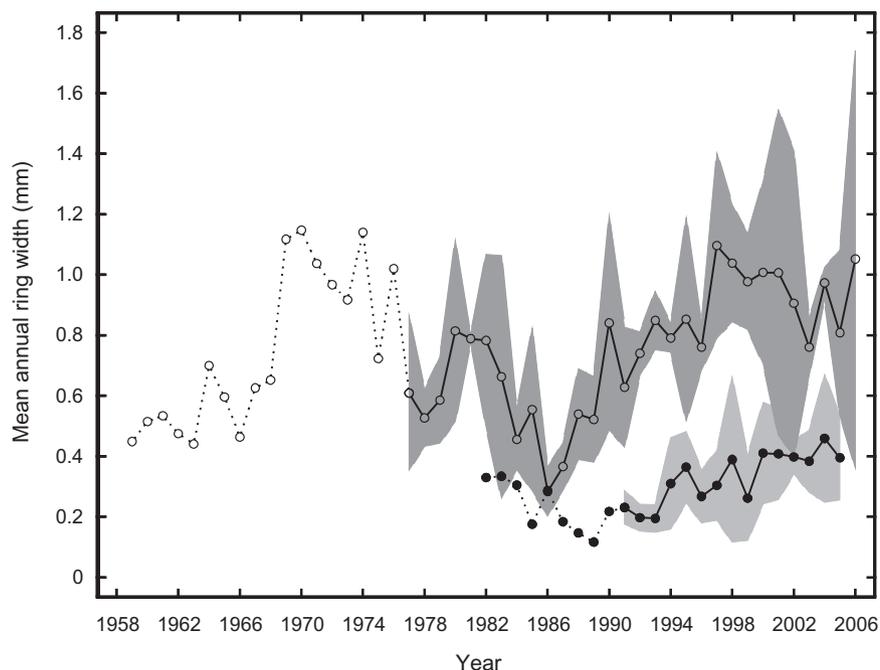


Figure 1. Mean annual ring width (symbols) and SE (grey areas) of shrub shoots (solid circles, light grey area) and tree stems (open circles, dark grey area) of *Juniperus communis* ssp. *communis*. Symbols outside of the grey areas and connected with dashed lines show single values of the oldest individual.

decreased in tree branches from top to base (Table 1). In shrub shoots, the ratio was significantly lower. Shrub shoots were also significantly shorter and smaller in diameter than tree stems, and supplied correspondingly reduced leaf areas (Table 1).

Shrubby individuals were between 11 and 24 years old, and trees were between 23 and 48 years old (Table 1). Annual rings of trees were significantly wider than those of shrubs, which indicates a higher growth rate (Table 1, Fig. 1). Inter-annual ring variations showed similar patterns in shrubs and trees (Fig. 1).

Hydraulic efficiency

The tree stems showed a significantly higher leaf-specific conductivity (k_l) and specific conductivity (k_s) than did shrub shoots (Table 2). Regarding k_l , k_s and HV, shrubby specimens were similar to lower tree branches (no significant differences) and hardly differed (HV) from middle

tree branches. Upper tree branches showed a significant higher HV and lower k_s than did shrub shoots.

Within trees, k_l was highest in the stem (significantly different from branches, Table 2). The k_l of the middle stem was high because the k_s was significantly higher than in other groups (Table 2). In contrast, high k_l in the upper stem resulted from an extraordinarily high HV. Lowest k_l and k_s were found in upper branches (Table 2), and HV increased from lower to upper branches.

Plotting k_l , k_s and HV versus the position within the individual plant (distance from ground) revealed further differences. In shrub shoots, k_l , k_s and HV decreased towards the distal end (Figs 2 & 3). Along the tree stems, k_l and k_s also decreased with height but HV increased (Fig. 2). No trend was found for k_l in any tree branches, or for k_s or for HV in lower and middle tree branches. In upper tree branches, k_s decreased with distance to the ground and HV increased; however, when tree branches were analysed separately, a general decrease in k_l and k_s with distance to the branch base was found (Fig. 3). Only in the most basal

Table 2. Hydraulic efficiency parameters (leaf-specific conductivity, k_l ; specific conductivity, k_s ; and Huber value, HV) of shrubs (shoots) and trees (middle and upper stem, lower, middle and upper branches) of *Juniperus communis* ssp. *communis*

Parameter	Shrub	Tree				
	Shoot	Middle stem	Upper stem	Lower branches	Middle branches	Upper branches
k_l ($\text{m}^2 \text{s}^{-1} \text{MPa}^{-1} \times 10^{-7}$)	$1.93 \pm 0.11^\circ$	$4.46 \pm 0.40^*$	$4.08 \pm 0.24^*$	$2.14 \pm 0.13^\circ$	$2.25 \pm 0.12^\circ$	$1.99 \pm 0.11^\circ$
k_s ($\text{m}^2 \text{s}^{-1} \text{MPa}^{-1} \times 10^{-4}$)	$5.71 \pm 0.19^\circ$	$11.48 \pm 0.45^*$	$7.11 \pm 0.51^\circ$	$5.62 \pm 0.26^\circ$	$5.84 \pm 0.22^\circ$	$4.14 \pm 0.25^{*\circ}$
HV $\times 10^{-4}$	3.31 ± 0.11	3.93 ± 0.35	$6.14 \pm 0.29^{*\circ}$	3.85 ± 0.18	$3.97 \pm 0.18^*$	$4.90 \pm 0.16^*$

Asterisks indicate significant differences from shrub shoots and circles indicate significant differences from tree middle stem (mean \pm SE). For further statistics, see text.

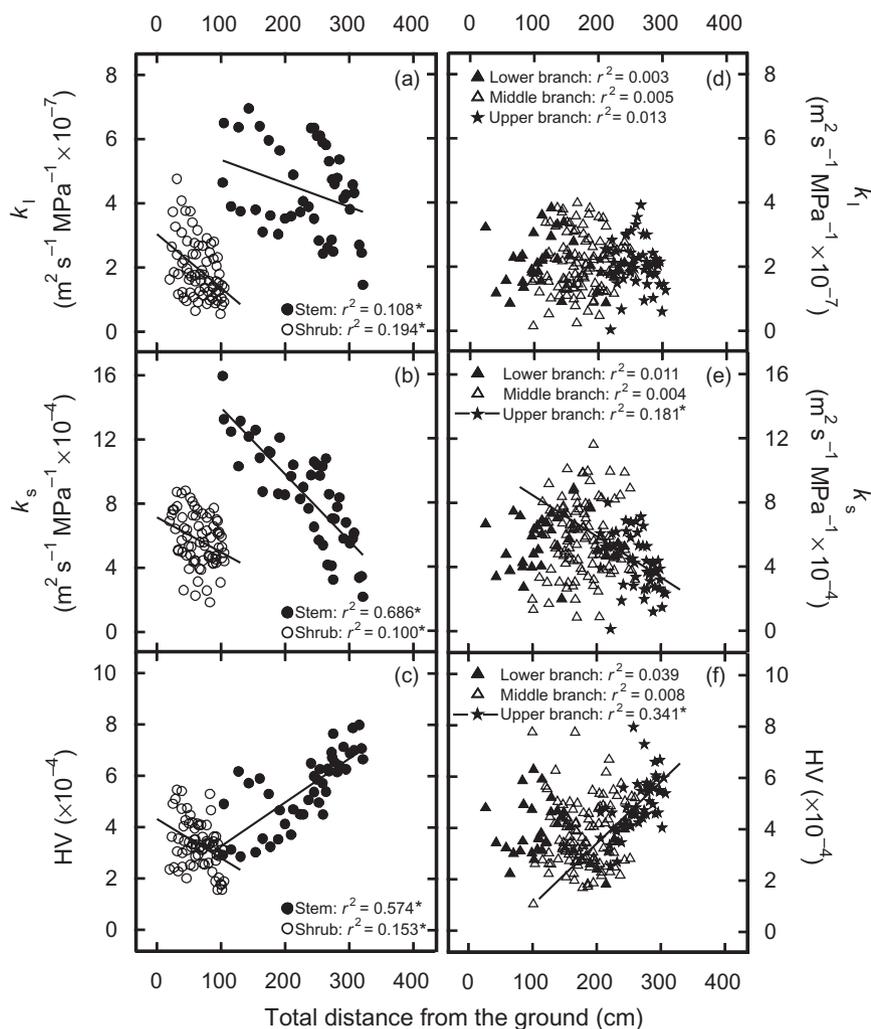


Figure 2. Leaf-specific conductivity (k_l), specific conductivity (k_s) and Huber value (HV) versus the distance from the ground of shrub shoots (a–c), also of stems (a–c), lower branches, middle branches and upper branches (d–f) of trees of *Juniperus communis* ssp. *communis*. Asterisks and lines show significant correlations.

sections were conductivities always lower than in adjacent distal sections.

Vulnerability to cavitation

Vulnerability analyses revealed no significant differences between shrub shoots and the stem and upper branches of trees (Fig. 4). Lower and middle tree branches showed significantly lower Ψ_{50} and Ψ_{90} (water potential at 50 and 90% loss of conductivity, respectively) than did shrub shoots, while no differences were found for Ψ_{10} (water potential at 10% loss of conductivity).

Within trees, drought tolerance was lowest in the stem and highest in branches (Fig. 4). Although differences were small, lower and middle branches showed significantly lower Ψ_{50} than did stems. The Ψ_{50} of branches increased from lower to upper ones (Fig. 4). Again, no significant differences were found for Ψ_{10} , and only middle branches differed in Ψ_{90} .

Anatomy

Tracheid diameters (i.e. d_{mean} , d_{max} and d_h) were highest in the middle stem and lowest in the upper branches of trees

(both significantly different from all other groups; Table 3). For tree branches, a significant decrease in tracheid diameters from lower ones to upper ones was found. Because of the low tracheid wall thickness (t), the middle stem and lower branches of trees showed a significantly lower ‘thickness-to-span ratio’ $(t/b)_h^2$ compared with all other groups (Table 3). Shrub shoots showed a d_h similar to that of lower tree branches, and a $(t/b)_h^2$ similar to those of middle branches, upper branches and upper stem of trees (Table 3). Specific conductivity (k_s) was significantly correlated with d_h , while no significant correlations were observed between k_l and d_h (Fig. 5).

DISCUSSION

J. communis shows remarkable intraspecific variation in its hydraulic architecture, which corresponds to morphological differences observed in its two contrasting growth forms (Table 1, Fig. 1). The most pronounced hydraulic differences were found between shrub shoots and tree stems. The latter showed an improved hydraulic efficiency as leaf-specific conductivity (k_l) was about twice that of shrub shoots, and the specific conductivity (k_s) and the Huber value (HV) were higher overall in tree stems (Table 2).

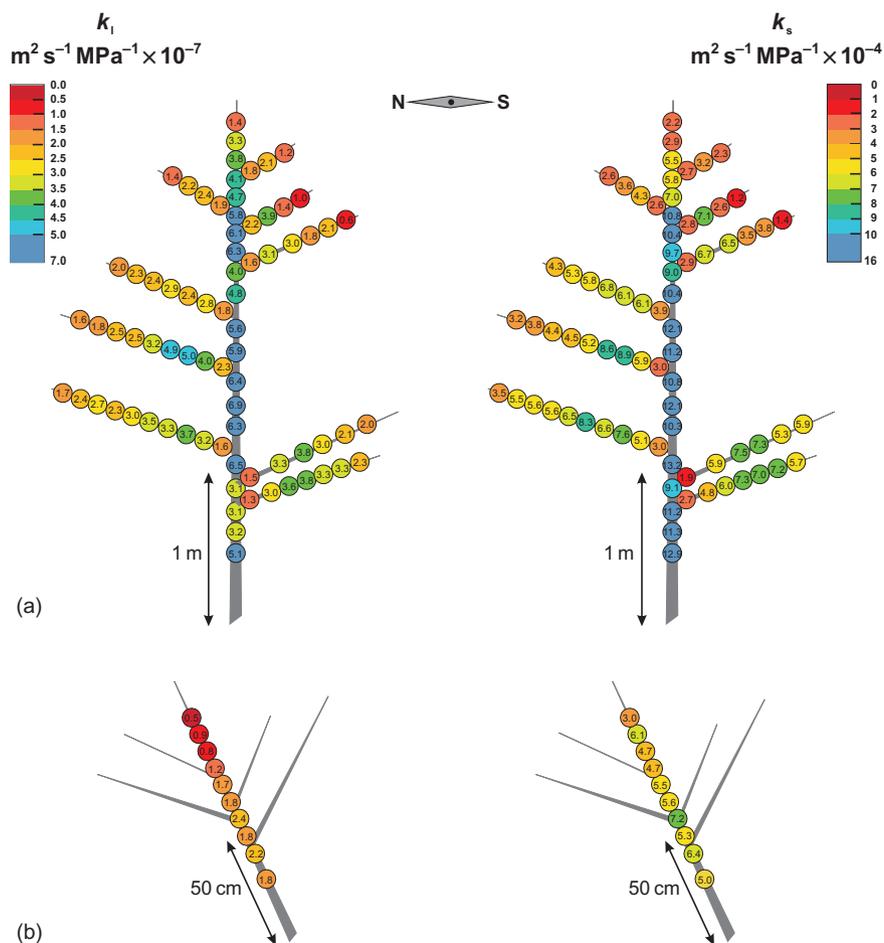


Figure 3. Leaf-specific conductivity (k_l) and specific conductivity (k_s) within (a) trees and (b) shrubs of *Juniperus communis* ssp. *communis*. Drawings show representative individuals. Conductivities given for all positions are indicated by a colour scale (see legend). For trees, north to east exposed branches (N) are drawn on the left, south to west (S) exposed branches on the right side.

Furthermore, HV increased from the stem’s base to the top while it decreased in shrub shoots (Table 2, Fig. 2). This indicates that tree stems of *J. communis* serve an important hydraulic function with increased transport capacities and improved hydraulic supply to distal leaves (Ewers & Zimmermann 1984a; Tyree & Sperry 1989; Tyree & Ewers 1991). In *T. diversilobum*, no differences in k_l between vines and shrubs have been found, but adaptations in HV enabled similar pressure gradients in the stems of different growth forms (Gartner 1991). Ewers and Zimmermann (1984a)

reported that small trees of *Tsuga canadensis* showed hydraulic architecture similar to the top but not to the base of taller trees. In contrast, shrub shoots of *J. communis* were most similar to lower tree branches (Table 2). This can be explained by the observation that young *Tsuga* plants already show a tree-like growth while *J. communis* normally undergoes a transition from a shrub to a tree-like growth form (also see Introduction).

Variation in cavitation resistance was small in *J. communis* (Fig. 4). Both growth forms showed a generally high

Table 3. Anatomical parameters [mean diameter, d_{mean} ; maximum diameter, d_{max} ; mean hydraulic diameter, d_h ; cell wall thickness, t ; and ‘thickness-to-span ratio’ $(t/b)_h^2$] of shrubs (shoots) and trees (middle and upper stem, lower, middle and upper branches) of *Juniperus communis* ssp. *communis*

Parameter	Shrub	Tree				
	Shoot	Middle stem	Upper stem	Lower branches	Middle branches	Upper branches
d_{mean} (μm)	9.49 \pm 0.046°	11.85 \pm 0.039*	9.50 \pm 0.032°	9.83 \pm 0.042*°	8.75 \pm 0.040*°	7.43 \pm 0.042*°
d_{max} (μm)	22.13	25.79	21.22	22.43	20.32	17.42
d_h (μm)	13.42 \pm 0.0003°	15.89 \pm 0.0001*	13.05 \pm 0.0002*°	13.45 \pm 0.0002°	12.62 \pm 0.0003*°	11.05 \pm 0.0004*°
t (μm)	4.62 \pm 0.067°	3.97 \pm 0.105*	4.73 \pm 0.092°	3.69 \pm 0.081*	4.27 \pm 0.071*	4.10 \pm 0.059*
$(t/b)_h^2$	0.13 \pm 0.004°	0.07 \pm 0.004*	0.14 \pm 0.005°	0.08 \pm 0.003*	0.12 \pm 0.004°	0.14 \pm 0.004°

Asterisks indicate significant differences from shrub shoots and circles indicate significant differences from tree middle stem (mean \pm SE; except d_{max}). For further statistics, see text.

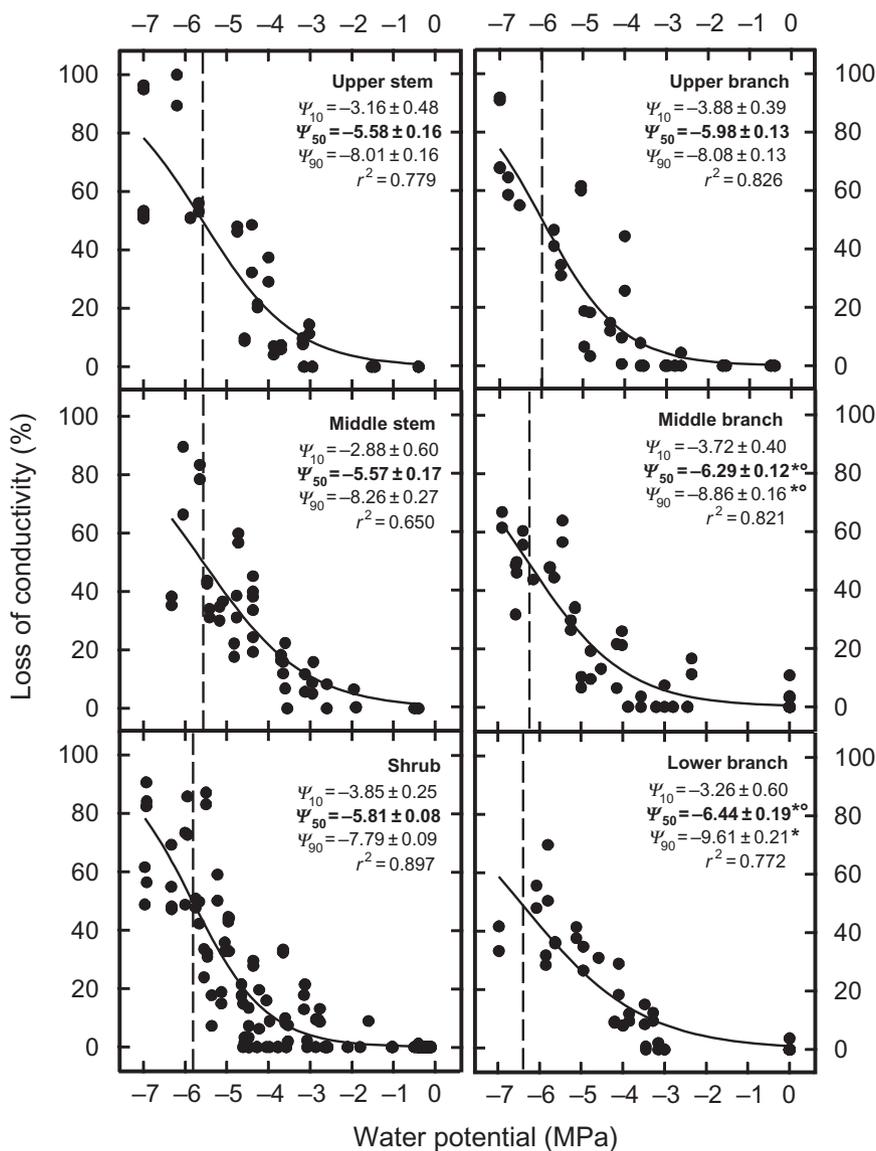


Figure 4. Drought-induced vulnerability (loss of conductivity versus water potential) of shrubs (shoots) and trees (middle and upper stem, lower, middle and upper branches) of *Juniperus communis* ssp. *communis*. Values of Ψ_{10} , Ψ_{50} and Ψ_{90} (water potential at 10, 50 and 90% loss of conductivity) are given \pm SE. Dashed lines show Ψ_{50} . Asterisks and circles indicate significant differences from shrub shoots and tree middle stems, respectively. For further statistics, see text.

resistance to drought-induced embolism. If other species (e.g. *Molinia caerulea*, *Frangula alnus*) at the sample site can be taken as indicator species, these suggest rather mesic conditions for the test area and we can assume that relatively few embolisms would occur in juniper *in situ*. Mayr *et al.* (2006) also reported a midday xylem water potential no more negative than -2 MPa, indicating that embolisms are unlikely at any time during the year in *J. communis* shrubs growing at a similar elevation. Sperry (2004) postulated that many plants maximize gas exchange while avoiding hydraulic failure by operating on the edge of dysfunction. In contrast, *J. communis* showed vulnerability thresholds far more negative than ecologically relevant Ψ values. It remains unclear why the genus *Juniperus* has evolved into having this extraordinarily low vulnerability to embolism, which has been reported for several of its species (Sperry & Tyree 1990; Linton, Sperry & Williams 1998; Pockman & Sperry 2000; Martinez-Vilalta *et al.* 2004; Mayr *et al.* 2006; Willson & Jackson 2006).

Numerous studies on many tree species report the typical properties of a tree's hydraulic architecture (Zimmermann 1978; Tyree *et al.* 1983; Ewers & Zimmermann 1984a,b; Tyree & Ewers 1991; Cruziat, Cochard & Ameglio 2002; Martinez-Vilalta *et al.* 2004; Cochard *et al.* 2005; McCulloh & Sperry 2005; Poyatos, Martinez-Vilalta & Cermak 2007). Juniper trees are here observed to be similar to other trees in many aspects. For example, hydraulic efficiency (i.e. k_1 and k_s) was higher in the stem than in the branches (Table 2). Such a hydraulic hierarchy has been observed in many other conifers (Ewers & Zimmermann 1984a,b; Mayr *et al.* 2003b) and angiosperms (Zimmermann 1978; Tyree & Zimmermann 2002). It allows upper canopy leaves to compete successfully for water and minerals with leaves situated at the base (Zimmermann 1978; Tyree *et al.* 1983; Tyree & Ewers 1991) and it also helps to avoid critical Ψ values arising in the upper parts of trees (Ewers & Zimmermann 1984a; Tyree & Sperry 1989). Within each tree branch (and shrub shoot), k_1 and k_s were low at the base, increased

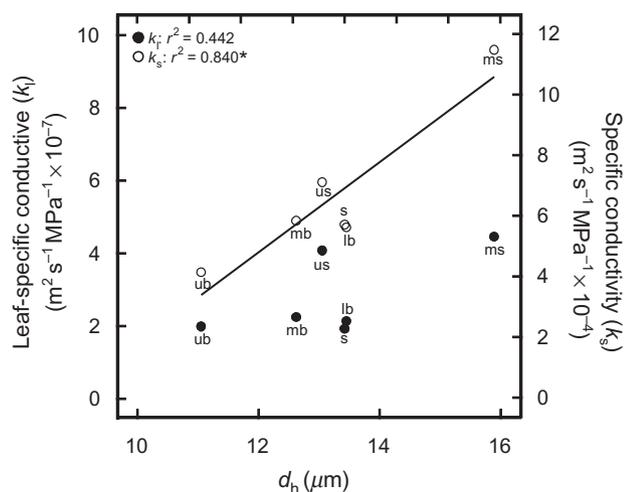


Figure 5. Leaf-specific conductivity and specific conductivity versus mean hydraulic diameter (d_h) of shrub shoots (s) and tree middle stem (ms), tree upper stem (us), tree lower branches (lb), tree middle branches (mb) and tree upper branches (ub) of *Juniperus communis* ssp. *communis*. Asterisk indicates significant correlation.

towards the distal parts and decreased again near the tip (Fig. 3). A reduced conductivity at the base of branches has been described in many species (Tyree & Zimmermann 2002) and interpreted as a hydraulic bottleneck related to the necessary reorganization of the xylem at branch junctions. We did not observe a clear pattern of k_l and k_s in juniper tree branches when plotted against the pathway length (distance to ground; Fig. 2), which was probably because of variations in hydraulic conductivity due to diameter (e.g. Patiño *et al.* 1995) or sample age. In contrast, along the tree stem, k_l and k_s decreased while HV increased with height (Fig. 2, Table 2). Similar trends were reported for *T. canadensis* (Ewers & Zimmermann 1984a), *Abies balsamea* (Ewers & Zimmermann 1984b), *Abies concolor* (Huber 1928) and *Betula papyrifera* (Zimmermann 1978), and these trends are consistent with correlations observed in hydraulic conductivity and stem diameter (Tyree *et al.* 1983; Patiño *et al.* 1995; Cochard, Lemoine & Dreyer 1999; Mencuccini 2002). In contrast, no particular pattern for k_l was found along the main axes in *Populus grandidentata* or adult *Acer saccharum*, while in young maple, k_l even increased from the stem base to the top (Zimmermann 1978; Tyree & Zimmermann 2002).

The distribution of k_l , k_s and HV within a tree provides important information on the extent of apical dominance. According to Ewers and Zimmermann (1984a), Tyree and Ewers (1991) and Tyree and Zimmermann (2002), trees with strong apical dominance also tend to have a hydraulic dominance, which is characterized by large increases in conductivity and HV towards the dominant apex compared with primary and secondary branches. In *A. balsamea* individuals with strong apical dominance, k_l near the tip of the leader was up to 17 times greater than in lateral branches and HV increased from the base upwards.

However, in individuals with weak apical dominance, k_l tapered off near the top of the tree, and HV decreased with height (Ewers & Zimmermann 1984b). In juniper trees, HV increased with height, but k_l and k_s in the upper stem were only slightly higher compared with the upper branches (Table 2), which indicates a rather weak hydraulic dominance. Adams and Pandey (2003) reported that the genes for apical dominance are not well regulated in *J. communis*.

The patterns of cavitation resistance in juniper trees (Fig. 4) contrast with the safety architecture of other tree species, which protect important parts like the stem and the upper branches by low vulnerability thresholds (vulnerability segmentation; Tyree & Sperry 1989; Tyree & Zimmermann 2002). For example, leader shoots of *Picea abies* were less vulnerable to drought-induced embolism than twigs (Mayr *et al.* 2003b), and in *Sequoia sempervirens*, the upper branches were less vulnerable to drought-induced embolism than the lower branches (Burgess *et al.* 2006). In contrast, and as mentioned earlier, juniper is probably well adapted by its generally high resistance to drought-induced embolism so that further vulnerability segmentation is not necessary. Similarly, in *Juniperus osteosperma*, no significant differences in drought tolerance between juvenile and old branches were found (Linton *et al.* 1998).

In keeping with the Hagen–Poiseuille equation (Tyree & Zimmermann 2002), k_s and d_h of juniper xylem were significantly correlated, and also k_l increased with d_h (Fig. 5). It has to be considered that conductivity parameters do not only depend on conduit diameter, but also on the resistance of pit connections, the number of conducting elements and, in the case of k_l , on the leaf area supplied (Tyree & Ewers 1991; Tyree *et al.* 1994; Tyree & Zimmermann 2002; Hacke *et al.* 2004; McCulloh & Sperry 2005; Pittermann *et al.* 2006; Sperry *et al.* 2008). Our findings show that hydraulic adaptations were based on anatomical differences leading, for example, to the improved hydraulic efficiency of the stem.

Resistance to drought-induced embolism is related to pit properties (e.g. size, permeability, stability of the torus) and to wall reinforcement (Sperry & Tyree 1990; Sperry & Saliendra 1994; Sperry *et al.* 1994; Hacke & Sperry 2001; Hacke *et al.* 2001) rather than to conduit diameter; however, recent studies revealed an indirect impact of conduit diameter at least in some species ('pit area hypothesis'; Wheeler *et al.* 2005; Hacke *et al.* 2006; Sperry *et al.* 2007). While Willson and Jackson (2006) found a significant correlation between Ψ_{50} and d_h in four other juniper species, in our study, neither d_h nor cell wall thickness (t) or cell wall reinforcement [wall 'thickness-to-span ratio' $(t/b)_h^2$] was correlated with the water potential at 50% loss of conductivity (Table 3, Fig. 4). Our values, however, fit with the general $(t/b)_h^2$ versus Ψ_{50} relationship of conifers (Hacke & Sperry 2001; Hacke *et al.* 2001, 2004). We reason that different mechanical requirements masked the correlation of $(t/b)_h^2$ and Ψ_{50} , as shrub shoots, tree stems and branches are subjected to different mechanical demands.

CONCLUSION

J. communis can grow like a shrub or a tree, but the tree-like forms do not reach the height of other conifers. We found these growth forms to differ in their hydraulic architecture, such that shrub shoots are similar to lower tree branches and differ most from tree stems. This indicates an altered hydraulic function in the latter. Some aspects of the hydraulic architecture of tree-like *J. communis*, for example, the formation of highly conductive xylem in the stem and optimized patterns in HV, are similar to other tree species. Other aspects of tree-like juniper are more similar to shrubby junipers as differences between the hydraulics of tree branches and of shrub shoots are small, and the hydraulic dominance in juniper trees is weak. Thus, changes in xylem anatomy and, consequently, adaptations in hydraulic architecture in juniper trees are still probably insufficient to allow for the development of taller growth forms.

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