Juniperus communis populations exhibit low variability in hydraulic safety and efficiency

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Abstract

The performance and distribution of woody species strongly depend on their adjustment to environmental conditions based on genotypic and phenotypic properties. Since more intense and frequent drought events are expected due to climate change, xylem hydraulic traits will play a key role under future conditions, and thus knowledge of hydraulic variability is of key importance. In this study, we aimed to investigate the variability in hydraulic safety and efficiency of the conifer shrub *Juniperus communis* based on analyses along an elevational transect and a common garden approach. We studied i) juniper plants growing between 700 and 2000 m a.s.l. Innsbruck, Austria, and ii) plants grown in the Innsbruck botanical garden (Austria) from seeds collected at different sites across Europe (France, Austria, Ireland, Germany and Sweden). Due to contrasting environmental conditions at different elevation and provenance sites and the wide geographical study area, pronounced variation in xylem hydraulics was expected. Vulnerability to drought-induced embolisms (hydraulic safety) was assessed *via* Cavitron and ultrasonic acoustic emission technique, and the specific hydraulic conductivity (hydraulic efficiency) *via* flow measurements. Contrary to our hypothesis, relevant variability in hydraulic safety and efficiency was neither observed across elevations, indicating a low phenotypic variation, nor between provenances, despite expected genotypic differences. Interestingly, the provenance from the most humid and warmest site (Ireland) and the northernmost provenance (Sweden) showed the highest and the lowest embolism resistance, respectively. The hydraulic conductivity was correlated with plant height, which indicates that observed variation in hydraulic traits was mainly related to morphological differences between plants. We encourage future studies to underly anatomical traits and the role of hydraulics for the broad ecological amplitude of *J. communis*.

Introduction

Distribution and performance of woody species strongly depend on their ability to cope with the environment. Individuals adjust their traits on long and short term (adaptation and acclimation processes), whereby potential adjustments range according to both genotypic and phenotypic characteristics (Sultan 2000, Nicotra et al. 2010). To investigate variation of functional traits in a selected species, analysis of environmental transects (e.g. elevational transects) and common-garden experiments are powerful approaches. While an environmental transect highlights the phenotypic differences of populations growing in the wild (Bresson et al. 2011, Kremer et al. 2014; e.g. due to temperature differences in the case of elevational transects; Körner 2003, King et al. 2013), the common-garden approach highlights the intraspecific genetic differences of populations growing under the same and partially controlled (e.g. soil, watering) conditions (Frei et al. 2012, David-Schwartz et al. 2016, Xiankui and Chuankuan 2018). The combinations of these two approaches has the potential to deepen the understanding of the variability in species' functional traits (Vitasse et al. 2010, Lamy et al. 2014). Adaptation and acclimation processes are important in plant water relations, and especially relevant for slow growing and long-living woody species (Mencuccini 2003, Pittermann et al. 2012). A successful adaptation in hydraulic traits will play a key role with respect to climate change, as the intensity and frequency of drought events is expected to increase (IPCC 2018), resulting in increasing mortality risk as well as in distribution shifts across many plant communities (Allen et al. 2010, Carnicer et al. 2011, Choat et al. 2012). Susceptibility to drought is strongly related to plant hydraulic traits, and embolism formation was recognised as a major cause for drought-induced mortality (Anderegg et al. 2015, 2016, Hartmann et al. 2015, Pellizzari et al. 2016, Choat et al. 2018). To avoid embolism, plant xylem requires sufficient hydraulic safety (i.e. resistance to formation of embolism) and hydraulic efficiency (i.e. hydraulic conductivity; e.g. Gleason et al. 2016, Prendin et al. 2018). According to the cohesion-tension theory, water is pulled up from soil to leaves in the xylem as a consequence of transpiration (Tyree and Dixon 1983). When the tension (i.e. negative water potential, P) in the water column exceeds critical, species-specific thresholds, water columns can be interrupted by embolism formation (drought-induced embolism; Tyree 2003, Cochard et al. 2009). As described by the air-seeding theory (Zimmermann 1983), this occurs via the expansion of air bubbles to adjacent conduits over the pits. Embolised conduits cannot transport water and, consequently, impair the hydraulic conductivity and thus the water supply of distal plant parts. Conductivity losses can lead to further increase of tensions in the xylem sap and, in worst case, to fatal run-away embolism (Sperry et al. 1998, Tyree and Zimmermann 2002, Gleason et al. 2016). Plants may avoid critical tensions via stomata control, sufficient root water uptake and water storage capacity, and by high hydraulic conductivity (Javot and Maurel 2002, Maseda and Ferna 2006, von Arx et al. 2012). At least in some plant species, there seems to be a trade-off between hydraulic safety and efficiency (Hacke et al. 2000, Martínez-Vilalta et al. 2002, Lens et al. 2011).

There are numerous studies on the variability in hydraulic safety and efficiency across species (e.g. Pockman and Sperry 2000, Lopez et al. 2005, Bouche et al. 2014, Li et al. 2018), while less is known about intra-specific variability in trees (Wortemann et al. 2011, Gea-Izquierdo et al. 2012, López et al. 2013, Lamy et al. 2014, Aranda et al. 2017, Losso et al. 2019) and even less in shrubs (Beikircher and Mayr 2009, Mayr et al. 2010, Lamy et al. 2014, Ganthaler and Mayr 2015, González-Muñoz et al. 2018). In a provenance experiment on *Pinus pinaster*, Lamy et al. (2014) found that cavitation resistance is a genetically based trait, robust to genetic and environmental perturbations (i.e. mutation, hybridization, recombination, etc.). The authors also suggested that xeric *genera*, such as *Juniperus* or *Cupressuss*, may show higher variation in hydraulic safety between populations from contrasting climates.

The genus *Juniperus* is hydraulically interesting as this species exhibits extraordinary high hydraulic safety (Mayr et al. 2006, Willson and Jackson 2006, Beikircher and Mayr 2008). Willson et al. (2008) even found two tropical juniper species (*J. lucayana* and *J. barbadensis*) with high embolism resistance. In the Holarctic, the coniferous shrub *Juniperus communis* L., which is characterized by slow growth rate, high longevity and high ability to cope with low temperatures, water stress, strong wind and soil nutrient scarcity (Thomas et al. 2007, Adams 2014), shows the widest distribution. It grows from sea level at coastal areas up to the krummholz belt above the treeline and forms two subspecies, ssp. *communis* and ssp. *nana* (though, subspecies lack sharp genetic and anatomical differences; Filipowicz et al. 2006, Thomas et al. 2007, Adams 2014). The broad distribution indicates that *J. communis* adapts and/or acclimates easily to a wide range of conditions.

In this study, we investigated the variability in hydraulic safety and efficiency of J. *communis*. We studied (i) junipers growing along an elevational transect in the Central European Alps and (ii) five different European provenances grown in a common garden experiment. We hypothesized significant variability in the hydraulic traits considered, both along the elevational transect and across provenances. Higher hydraulic safety and lower hydraulic efficiency (due to suggested trade-offs) were expected at higher elevation, where winter drought is most pronounced, and in provenances from drier regions.

Material and methods

Study sites and plant material

For the elevational transect, samples were collected along the south slope (about 30°) of Nordkette, a mountain range north of Innsbruck (Austria; N47°17’E11°22’). Sampling points were located along the same slope at four elevations: 700, 1200, 1700 and 2000 m a.s.l. (ca. 1 km distance between sampling sites). Along this transect, mean annual temperature decreases by about 0.5°C per 100 m, providing a difference between the lowest and highest sampling points of ca. 6.5 °C (8.5°C and 2°C at 700 and 2000 m a.s.l. respectively). In contrast, mean annual precipitation does not show an elevational trend (ca. 1000 mmy^{-1}; Auer et al. 2007). The substrate is identical at all sampling sites (limestone), though soil at higher elevation is shallower and richer in skeletal material (Wieser 2012). We selected healthy shrubs, ca. 0.5 m tall, with straight main stems, ca. 2.5 cm in basal diameter. For the common garden experiment, seeds were collected from a 3000 km wide area in latitude and longitude, including Sault (South France), Innsbruck (Austria), Sellendorf (North-East Germany), Bundoran (Ireland) and Svartberget (North Sweden; Fig. 1). Seeds were provided by the Forest and Nature Lab of Ghent University (Gruwez et al. 2014). Seedlings germinated between 2013 and 2014 in the Botanical Garden of Innsbruck (N47°16' E11°22; 600 m a.s.l.), where plants grew under identical conditions. All plants grown in the common garden were between 4 and 5 years old. For each plant we recorded total height and diameter at the root collar, and calculated the height to diameter ratio (HDR; Tab. S1 and Fig. S1), as indicator of growth investment (Henry and Aarssen 1999, Anten and Schieving 2010).

For measurements in the transect and common garden approach, the main stem of plants was cut at the base, placed in a black plastic bag and brought to the laboratory. The stem base was recut (2 cm) under water to remove potentially embolised sections. Samples were then covered by black plastic bags and stored at 5°C for 24h in a bucket filled with water to allow for saturation.

Hydraulic safety

Hydraulic safety was analysed by measuring the percentage loss of hydraulic conductance (PLC, %) at different *P* (MPa) and constructing vulnerability curves (*VC*). In the transect approach, *VCs* were measured with the Cavitron centrifugation technique (Cochard 2002). Therefore, a Sorvall RC-5 centrifuge (Thermo Fisher Scientific, Waltham, MA, USA) with a small rotor (15 cm of diameter; Alder-design, see Torres-Ruiz et al. 2014) was used, following the measurement protocol for conifers to avoid pit aspiration (Beikircher et al. 2010). For measurements, 14 cm long stem segments were cut from basal main stem under cold water (distilled water cooled in an ice bath). Use of cold water during the sample preparation increased the viscosity of resin (contained in the bark) and thus reduced outflow of resin at the cut ends. At both sample ends, the bark was removed (ca. 4 cm), and thin slices were re-cut several times with a sharp wood-carving knife to avoid squeezing of conduits. Samples were mounted in the rotor between two cuvettes, which were then filled with distilled, filtered (0.22 µm) and degassed water containing 0.005 % (v/v) "Micropur" (Katadyn Products, Wallisellen, Switzerland), at room temperature (ca. 23 °C). Increasing the rotational speed allowed to stepwise lower *P* in the sample (at intervals of 2000 rpm from ca. 3200 rpm to 20000 rpm, corresponding to ca. -0.25 MPa to -10 MPa,). Respective hydraulic conductance (*K*) was then measured according to Beikircher et al. (2010) and PLC was calculated as:

$$PLC = 100 * (1 - \frac{Ka}{Kmax}) \qquad \text{(eq. 1)}$$

where *Ka* and *Kmax* are the actual and the maximal (initial) conductance ($m^3 s^{-1} MPa^{-1}$), calculated from the measured water flow (*F*, mmol s^{-1}) and the respective hydrostatic pressure difference between cuvettes (ΔP) as:

$$K = \frac{F}{\Delta P} \qquad \text{(eq. 2)}$$

P was computed as:

$$P = -0.25 * \rho\omega^2(R^2 + (R - r)^2) \qquad \text{(eq. 3)}$$

where ρ is the water density (1000 kg*m^{-3}) corrected by the chamber's internal temperature (measured using an infrared thermometer), ω the angular velocity (rad*s^{-1}), R the distance between the rotational axes and the downstream reservoir (m) and r the distance between the two water levels in the reservoirs (m).

In the common garden approach, we used the ultrasonic acoustic emission method. This technique detects and logs acoustic signals emitted during embolism formation (Tyree and Dixon 1983, Mayr and Zublasing 2010). This method is more time consuming than the Cavitron technique but not limited by sample size; as some provenances were too small for the Cavitron method, the ultrasonic technique was used for all plants of the common garden approach. For measurements, a ca. 1x1 cm square of the bark was removed in the centre of the main stem. The debarked area was covered with silicone grease (to ensure optimal acoustic coupling and avoid transpiration from the xylem), and the ultrasonic sensor was attached with a spring clamp. Subsequently, samples were dehydrated on the bench, while ultrasonic acoustic emissions were continuously registered. Measurements were carried out with a Micro-II Express-Digital AE system (Physical Acoustics, Wolfegg, Germany) and 150 kHz ultrasonic resonant sensors (R15/C, 80–400 kHz) connected to a preamplifier set to 40dB. Detection threshold was set to 45 dB, peak definition time, hit definition time and hit lockout time were 200, 400 and 2 µs, respectively. Data were recorded with the AE win software (Mistras Holdings Corp., Princeton,USA; Mayr and Zublasing 2010). At intervals (ca. 6 hours), small side branches, ca. 4 cm in length, close to the sensor were cut and P determined with a pressure chamber (Model 1000 Pressure Chamber, PMS Instrument Company, Corvallis, OR, USA; Scholander et al. 1965). PLC (estimated from the relative number of acoustic emissions) was calculated as:

$$\text{PLC} = 100 * \left(\frac{AEP}{AEtotal}\right) \qquad \text{(eq. 4)}$$

Where *AEP* is the cumulative number of acoustic events registered until a given *P*, and *AEtotal* is the cumulative number of acoustic events after complete dehydration. *VCs* were constructed by plotting PLC *versus* corresponding *P*.

Hydraulic efficiency

The hydraulic efficiency (i.e. specific hydraulic conductivity *ks*) was measured with a modified Sperry apparatus (Sperry et al. 1988) on additional specimens. Samples were cut under water, the needles and bark were removed, and the sample was re-cut several times with a sharp wood-carving knife. Segments, ca. 5 cm in length, were then sealed (under water) into silicon tubes of the measurement system, which was filled with distilled, filtered (0.22 µm) and degassed water containing 0.005 % (v/v) "Micropur" (Katadyn Products, Wallisellen, Switzerland). Flow measurements were made with a digital mass flow meter (Mini CORI-FLOW, Digital Mass Flow Meter, Bronkhorst High-tec, Ruurlo, NL) and corrected for pressure (obtained with a ca. 60 cm pressure head) and sample dimensions. Furthermore, *ks* measurements were corrected for temperature to account for viscosity effects.

Since a significantly positive correlation between *ks* and plant height in the common garden experiment was observed, we introduced an index representative of *ks* rescaled by specimen's height (*ks_h*):

$$ks\_h = ks * \frac{\bar{h}}{hi} \qquad \text{(eq. 5)}$$

Where hi and $\bar{h}$ are the individual and the overall mean stem height (m) of all plants belonging to the common garden experiment. Thus, this index accounts for plant height similarly to the hydraulic conductance, but with hydraulic conductivity units.

Data analysis

VC of each specimen was fitted by an exponential sigmoidal equation (Pammenter and Willigen 1998):

$$PLC = \frac{100}{(1 + \exp(a(P - P50)))} \qquad \text{(eq. 6)}$$

where a is a constant related to the curve slope, *P* the water potential and *P50* the water potential at which 50% of conductivity loss was reached. Besides *P50*, *P12* and *P88* (representing *P* at 12 and 88 loss of conductivity) were extracted from every single curve. Vulnerability parameters (*P12, P50, P88, a*) of single specimens were then used to calculate mean ± SE and coefficient of variation values of each elevation and provenance, and a mean VC was built from pooled data points. Accordingly, also *ks* values of single specimens were used to calculate the mean ± SE and coefficient of variation values for each elevation and provenance. Number of replicates ranged between 4 and 10 (Tab. 1; 2). Due to low germination rates and the slow growth of the seedlings, only few plants reached the sufficient size for experiments, and thus, the number of samples available in the common garden experiment was limited.

Differences between groups were tested with one-way ANOVA and Tukey post-hoc tests, after testing for normal distribution (Shapiro–Wilk test) and homoscedasticity (Levene test). Tukey post-hoc test was run to detect potential differences among group pairs. All statistical tests were run based on measures for individual specimens. We also fitted linear regression between parameters with respect to plant size in the common garden experiment (height, diameter, height to diameter ratio; independent variable), *P50* and *ks* (dependent variable) at individual level. Non-normal distributed data were logarithmically transformed to meet normality and homoscedasticity assumptions (Zar 2010, Zuur et al. 2010). All statistical analysis were conducted with R software (R Core Team 2018) at a probability level of 5%.

To confirm our results, differences between *ks_h* in the common garden experiment were tested through one-way ANOVA and Tukey, as for the other parameters.

All values are given as mean ± SE.

Results

Vulnerability to drought induced embolism

All *VCs* followed a sigmoidal shape with *P50* ranging between -6.57 ± 0.31 (700 m a.s.l.) and -7.02 ± 0.26 MPa (1700 m a.s.l.) in the elevational transect approach (Fig. 2; Tab. 1) and between -5.56 ± 0.30 (Svartberget, S) and -7.15 ± 0.47 MPa (Bundoran, IRL) in the common garden approach (Fig. 3; Tab. 2). Mean SE of *P50* was 0.27 MPa across elevations (Tab. 1) and 0.35 MPa across provenances (Tab. 2). Coefficient of variation of *P50* was highest at 700 m a.sl. (14%; Tab. S2) and for the French and Irish populations (15 %; Tab.S3).

No significant differences in vulnerability parameters (*P12*, *P50*, *P88*, *a*; ANOVA) were found, neither across the elevational transect (Fig. 2; Tab. 1) nor across European provenances (Fig. 3; Tab. 2). However, there was a non-significant trend of less steep curves (parameter *a*) towards higher elevation, and Tukey post-hoc test revealed significant differences between *P50* of Irish *versus* Swedish provenances as well as between *P88* of Irish *versus* the Swedish and Austrian provenances (Tab. 2). Within studied provenances, Irish junipers showed the most negative *P50* and *P88* and thus the highest resistance to embolism formation, while the Swedish provenance was the most vulnerable one. *P50* and plant size parameters (height, diameter and HDR) were not significantly correlated (height: *p-value*=0.48; diameter: *p-value* 0.73; *HDR*: *p-value*=0.35).

Hydraulic conductivity

Hydraulic conductivity (*ks*) of plants collected at different elevations ranged between 4.9 ± 0.43 and 6.0 ± 0.50 $cm^2s^{-1}MPa^{-1}$ at 1200 and 700 m a.s.l., respectively, with mean SE of 0.45 $cm^2s^{-1}MPa^{-1}$ (Fig. 4; Tab. 1). Coefficient of variation was highest at 700 and 1200 m a.s.l. (26 and 27% respectively, Tab. S2). No significant differences were observed, neither from ANOVA neither from Tukey post-hoc test (Tab. 1).

ks of European provenances ranged between 1.9 ± 0.11 and 4.7 ± 0.65 $cm^2s^{-1}MPa^{-1}$ with mean SE of 0.32 $cm^2s^{-1}MPa^{-1}$ (Fig. 5; Tab. 2). Coefficient of variation was highest for the Austrian population (31%; Tab. S3). Since *ks* of provenances was not normally distributed, log(*ks*) was considered for statistical tests. No significant differences emerged from ANOVA test. However, Tukey post-hoc tests indicated higher *ks* values of the Austrian than Irish, Swedish and German provenances. Further, the French and Irish provenances differed significantly (Tab. 2). According to the significantly positive correlation between plant height and *ks*, considering all single specimens (*Pearson coefficient* = 0.81; *p-value*= 1.05e-06; Fig. 6), no correlation between *ks_h* and plant height was present (*p-value*=0.21; Fig. S2). ANOVA and Tukey post-hoc tests also indicated lack of significant differences between *ks_h* of provenances (ANOVA: *p-value*=0.14; Tukey post-hoc test: all *p-values* > 0.05; Fig S3). The HDR of the Austrian provenance (68.65 ± 3.87 m/m) was significantly higher than of the Swedish provenance (49.38 ± 2.83 m/m; Tab. S1, Fig. S4), while other provenances showed a similar ratio.

Discussion

In this study, we compared the hydraulic safety and efficiency of *J. communis* shrubs growing along an elevational transect and from different European provenances growing in a common garden experiment. Surprisingly, neither the vulnerability to drought-induced embolism (Fig. 2, 3; Tab 1, 2) nor the hydraulic efficiency (Fig. 4, 5; Tab. 1, 2) reflected the pronounced differences in environmental conditions across elevations or across the diverse origin of provenances (Fig. 1).

Vulnerability analysis was based on two techniques because of different plant size in the transect and the common garden approach (see methods). As the ultrasonic method enables only an indirect estimation of PLC (which might be biased by e.g. different energy of ultrasonic signals; see Mayr and Rosner 2011), a comparison with vulnerability thresholds measured by the Cavitron technique might be critical. However, parameters related to *VCs* (*P12, 50, 88*) of samples harvested at 700 m in the transect approach (measured via Cavitron) were only slightly more negative than the ones of young plants grown from seeds harvested at similar sites (Innsbruck provenance; measured via ultrasonic acoustic emissions; Tab. 1, 2). In each case, the analysis within the elevational and the common garden experiment is possible and reliable, as they were based on the same method, respectively. Junipers growing along the elevational transect showed a *P50* down to -7 MPa (Fig. 2; Tab. 1) and thus impressively high embolism resistance. According to values published in previous studies, *J. communis* belongs to a group of rather drought resistant species (Mayr et al. 2006, Beikircher and Mayr 2008, Choat et al. 2012). As high hydraulic safety enables plants to operate at lower *P* (Gleason et al. 2016), low *P50* may be advantageous on drought-prone sites with poorly developed soils (Beikircher et al. 2010) or on sites exposed to harsh winter conditions. At higher elevation, plants have to withstand extreme winter conditions (Körner 2003), and pronounced impairments in xylem hydraulics were reported (Mayr et al. 2020). In *J. communis* growing at the alpine timberline, Mayr et al. (2006) found a minimum *P* of -6.3 MPa and a native PLC of 80% during winter, demonstrating that this species indeed has to deal with extreme stress. Yet, the small elevational variation in vulnerability thresholds observed in the present study indicates that *J. communis* may have a genetically determined high hydraulic safety but restricted genotypic or phenotypic variability. In contrast, Mayr et al. (2006) reported significantly lower *P50* at low compared to high elevation. Though, this study was not based on an elevational transect but on a comparison between plants growing under optimal conditions in the Botanical Garden and plants growing in natural sites at high elevation. The present study further indicates that, besides variability in hydraulic safety, also the potential for adjustments in hydraulic efficiency was limited, as *ks* was similar across elevations (Fig. 4; Tab. 1). We suppose that other xylem traits, such as mechanical support, storage capacities or carbon costs of xylogenesis limit the variability in xylem hydraulic traits of *J. communis* (Myburg et al. 2013, Badel et al. 2015).

Plants in the common garden experiments represented provenances from contrasting European regions, with pronounced differences in climatic and environmental characteristics (e.g. water availability and mean temperature; Fig. 1), which were expected to also influence xylem traits (Maherali et al. 2004, Fonti et al. 2010, Fonti and Jansen 2012, Gea-Izquierdo et al. 2012). Due to the wide geographical area covered by the provenances under study, ranging from South France to Central Sweden, we also expected a strong genetic differentiation. The expansion of *J. communis* in Eurasia (e.g. North Europe and Siberia) started in the Alps (Hantemirova et al. 2016). During the last glaciation, only few populations survived in Central Europe due to peculiar micro-refugia, leading to a genetic differentiation between European populations (Michalczyk et al. 2010). Accordingly, our provenances differed in growth habit, plant size (Fig. S1; Tab. S1) and growth investment patterns (Fig. S4; Tab. S1) although grown in the common garden. Thus it was surpising that these plants, despite obvious phenotypic differences and likely high genetic variability, did not show any relevant variation in xylem hydraulics. We consider the overall homogeneity not just as an effect of the limited sample size, as performed ANOVA analysis has proved to be robust in case of reduced sample size (Sokal and Rohlf 2012). Interestingly, Tukey post-hoc test revealed few significative difference between vulnerability parameters of provenances (Tab. 2), but these were opposite to what we expected: the Irish provenance, which derived from the most humid and warmest site (Fig. 1), had the lowest *P50* (Fig. 3; Tab. 2) and thus was most embolism resistant. In contrast, highest *P50* was observed in the Swedish provenance and thus the northernmost site showed the lowest embolism resistance. Notably, this provenance showed the smallest height and the smallest HDR (Fig. S1; Fig. S4; Tab. S1). We assume that the small size of Swedish junipers is advantageous, as plants will be protected from harsh conditions during winter by the snow cover. This might allow a slightly reduced hydraulic safety. Indeed, tree-ring studies demonstrated that juniper profits from prostrate growth and the corresponding snow cover protection (Pellizzari et al. 2014, Carrer et al. 2019). Overall, our common garden experiment confirms the findings of Willson et al. (2008), who compared hydraulic traits of 14 North American junipers species and found root and stem embolism resistance to be highly conserved traits. Regarding hydraulic efficiency, similar to other conifers (Mayr et al. 2003, Froux et al. 2005, Charra-Vaskou et al. 2012), we did not observe significant differences among provenances through ANOVA test, despite the large variation detected from 1.94 (Irish provenance) to 4.71 $cm^2s^{-1}MPa^{-1}$ (Austrian provenance; Fig. 5; Tab. 2). In general, the low variability in xylem hydraulic traits is in accordance with Rosas et al. (2019), who found a limited intraspecific variability in xylem efficiency (and safety) along a humidity gradient in six tree species. The low hydraulic variability is striking considering the high variability in the growth rates between provenances.

Observed differences in hydraulic efficiency, disclosed through the Tukey post-hoc test, were related to differences in the habitus of Juniper provenances as we found *ks* to be significantly correlated with plant height (Fig. 6; also see Fig. S1). It is known that hydraulic efficiency is adjusted with plant height, and according to the model of West, Brown and Enquist (WBE; West et al. 1999), diameter of xylem conduits and pits increase exponentially downwards with the distance from the apex (Anfodillo et al. 2006, Lazzarin et al. 2016). Smaller plants thus have narrower conduits and pit apertures, which, negatively influences hydraulic efficiency (Hacke and Sperry 2001, Bouche et al. 2014). This explains why tallest plant in our common garden experiment exhibited highest *ks*. The variation in *ks* between plants within and between provenances thus was related to differences in plant size, while the hydraulic efficiency was not directly influenced by the provenance. In agreement to this allometric relationship, we did not detect any significant differences in efficiency between provenances, when measures were rescaled with respect to plant height (Fig. S3).

Overall, it is remarkable that variation in hydraulic traits was small with respect to the broad elevational and geographical range of studied populations. According to previous studies, variability in hydraulic traits may be most pronounced in rear edge populations, especially those living at southern, dryer margins (Wortemann et al. 2011, Stojnić et al. 2018). Our study populations grow in temperate areas, which may show generally lower variability than populations at lower latitude (Vitasse et al. 2014). Thus, we cannot exclude that more marginal juniper populations may exhibit adjustments in hydraulic traits, despite the low variability observed in the current study.

Conclusion

In contrast to our hypothesis, hydraulic safety and hydraulic efficiency of *J. communis* were found to be strikingly homogenous, both along the elevational gradient and across different European provenances grown in the common garden. This indicates a low variability in xylem hydraulic traits. Future studies should focus on the anatomical traits underlying the overall high embolism resistance, and, in consequence, the broad ecological amplitude of this species, despite its limited potential for hydraulic adjustment. Moreover, the analysis of additional parameters, such as resources allocation, may help discovering subtle intraspecific variations, currently undetectable. This will also enable an estimation of this species performance under future climatic conditions.

Conflict of Interest

None declared

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List of figures

Figure 1: Geographical location and climate at the provenance sites for *Juniperus communis* L. grown in the Innsbruck Botanical garden, Austria (N47°16' E11°22; 600 m a.s.l.). Origin locations are indicated in the map and climate conditions are summarized by Walter-Lieth climatographs, showing mean monthly precipitation (blue, mm), mean monthly temperature (red, °C), months in which frost events are likely to occur (light blue boxes) and wet periods (dark blue filled areas).

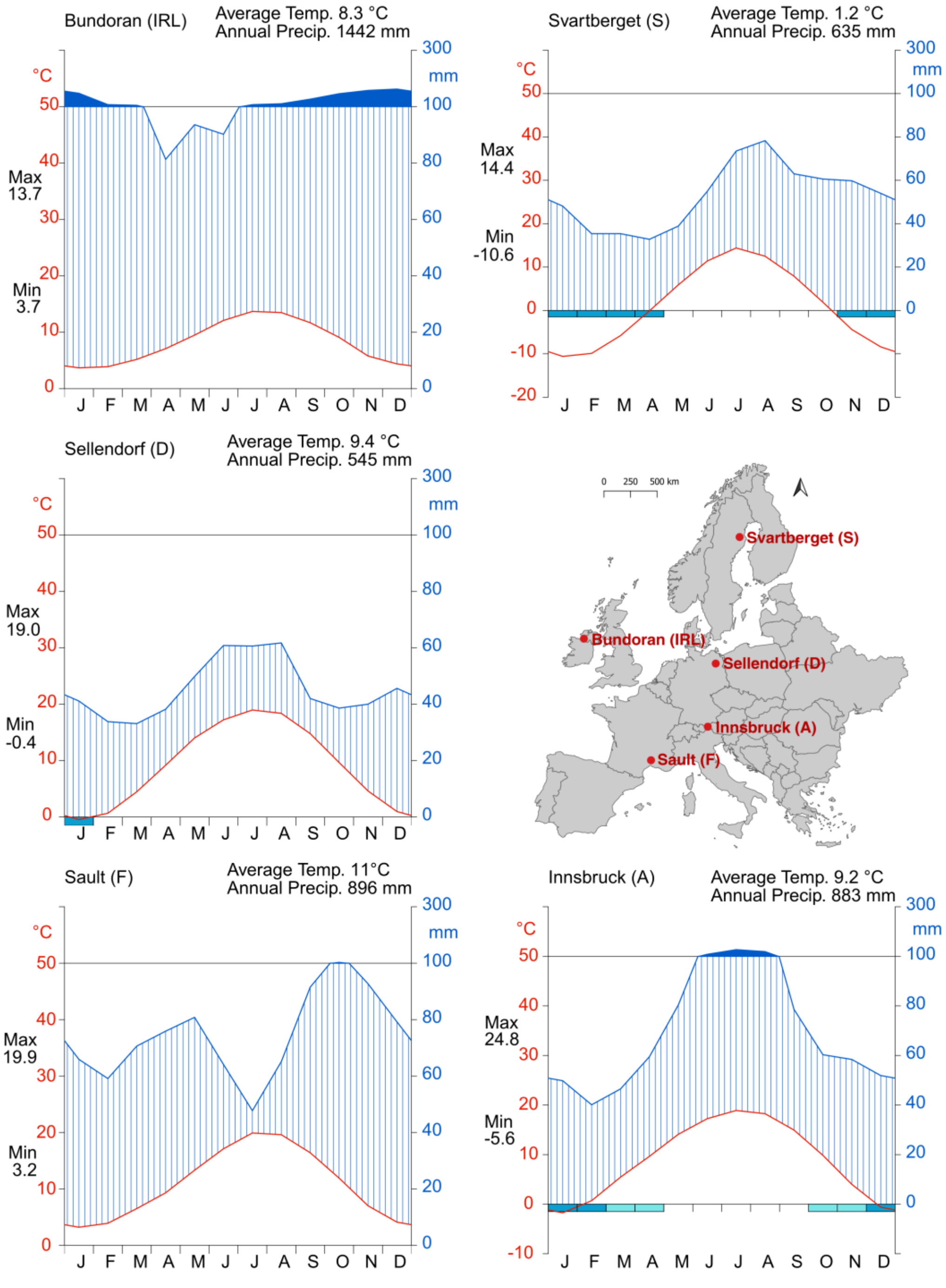

Bundoran (IRL)
Average Temp. 8.3 °C
Annual Precip. 1442 mm
Max 13.7
Min 3.7
Svartberget (S)
Average Temp. 1.2 °C
Annual Precip. 635 mm
Max 14.4
Min -10.6
Sellendorf (D)
Average Temp. 9.4 °C
Annual Precip. 545 mm
Max 19.0
Min -0.4
Sault (F)
Average Temp. 11°C
Annual Precip. 896 mm
Max 19.9
Min 3.2
Innsbruck (A)
Average Temp. 9.2 °C
Annual Precip. 883 mm
Max 24.8
Min -5.6
°C
mm
J F M A M J J A S O N D
0 250 500 km
Svartberget (S)
Bundoran (IRL)
Sellendorf (D)
Innsbruck (A)
Sault (F)

Figure 2: Vulnerability curves of *Juniperus communis* L. growing at different elevations (m). Curves representative of each elevation (continuous line) are the average curves calculated from all measured points (dots). Mean ± SD values of water potential at 12, 50 and 88% loss of hydraulic conductivity (*P12*, *P50* and *P88;* upper panels) were calculated from individual curves (see Material and Method section).

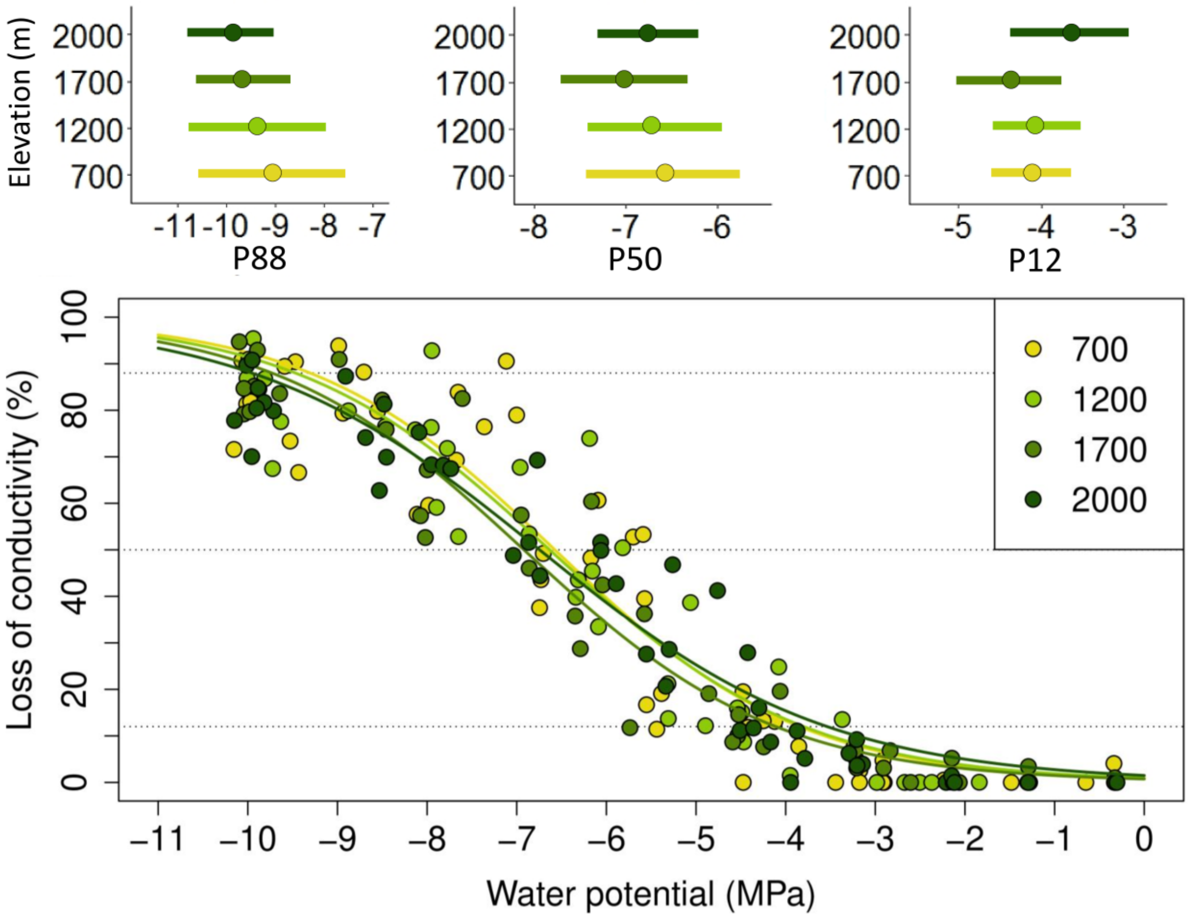


Figure 3: Vulnerability curves of *Juniperus communis* L. from different European provenances grown in the Innsbruck botanical garden, Austria (N47°16' E11°22; 600 m a.s.l.). Curves representative of each provenance (continuous line) are the average curves calculated from all measured points (dots). Mean ± SD values of water potential at 12, 50 and 88% loss of hydraulic conductivity (*P12*, *P50* and *P88;* upper panels) were calculated from individual curves (see Material and Method section).

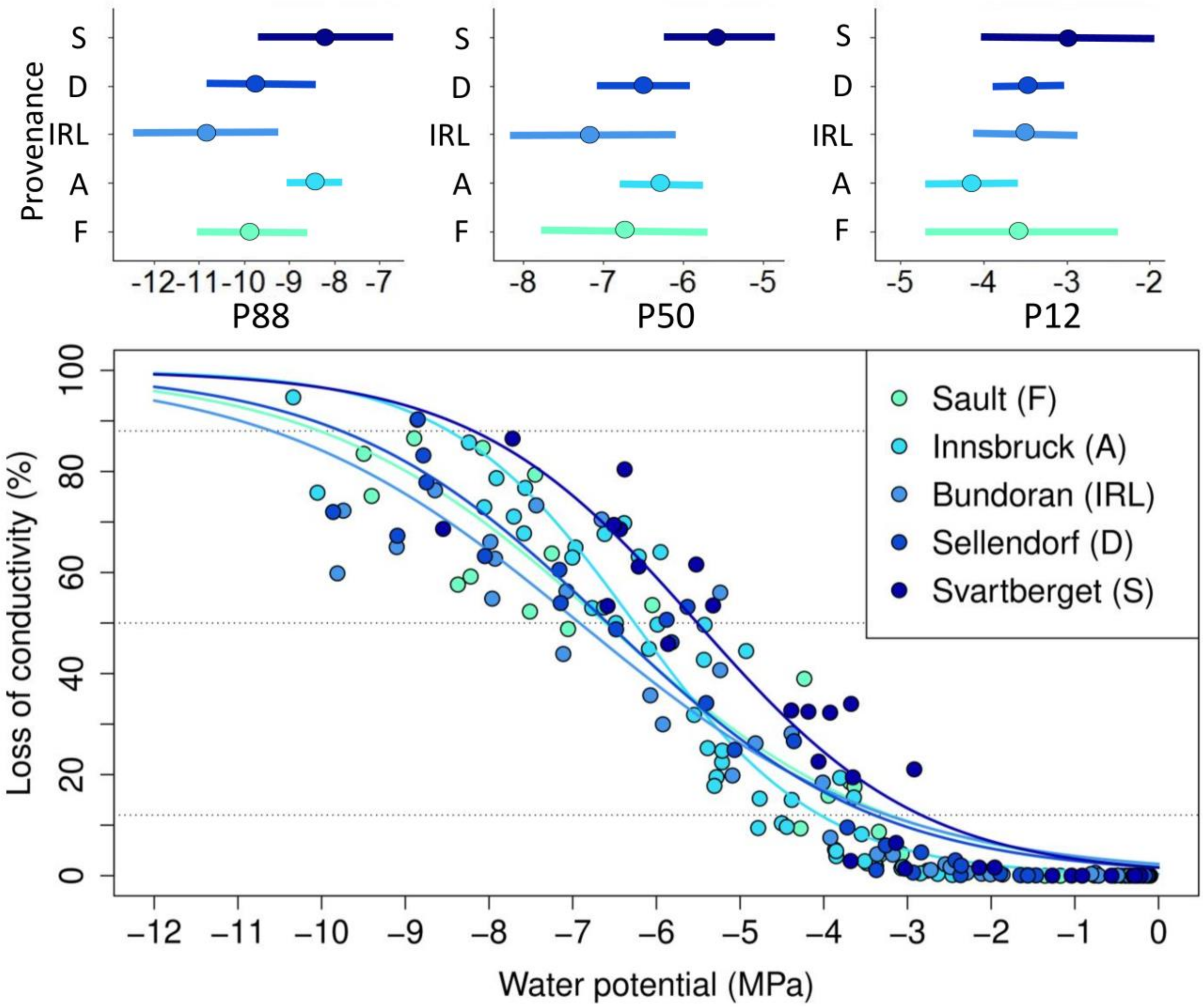


Figure 4: Violin plots of hydraulic conductivity (*ks*; cm^{2}s^{-1}MPa^{-1}) of *Juniperus communis* L. growing at different elevations. Boxplots represent the median, the 25th and 75th percentiles, minimum, maximum and outlying points.

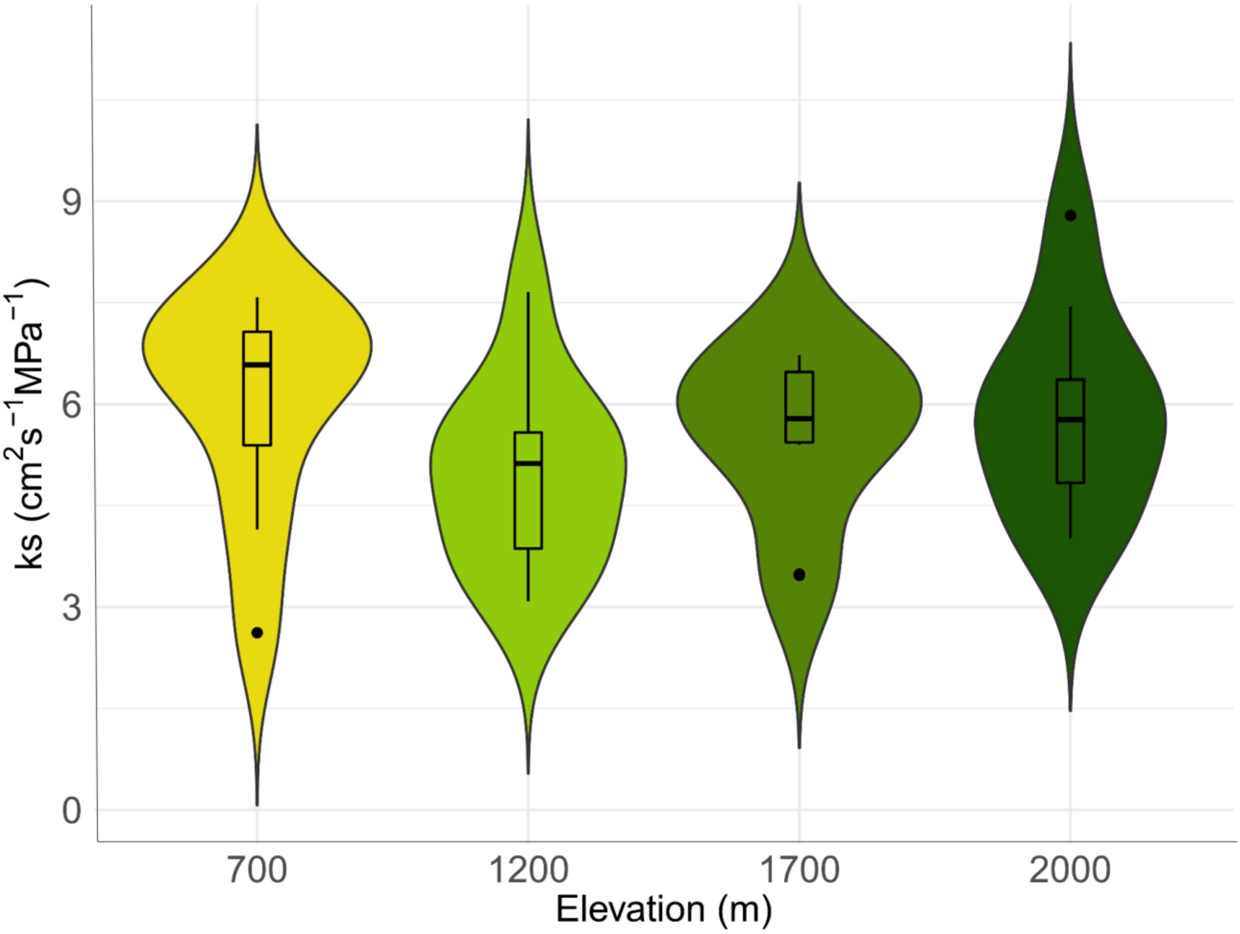


Figure 5: Violin plots of hydraulic conductivity (*ks*; cm^{2}s^{-1}MPa^{-1}) of *Juniperus communis* L. from different European provenances grown in the Innsbruck Botanical garden, Austria (N47°16' E11°22; 600 m a.s.l.). Boxplots represent the median, the 25th and 75th percentiles, minimum, maximum and outlying points.

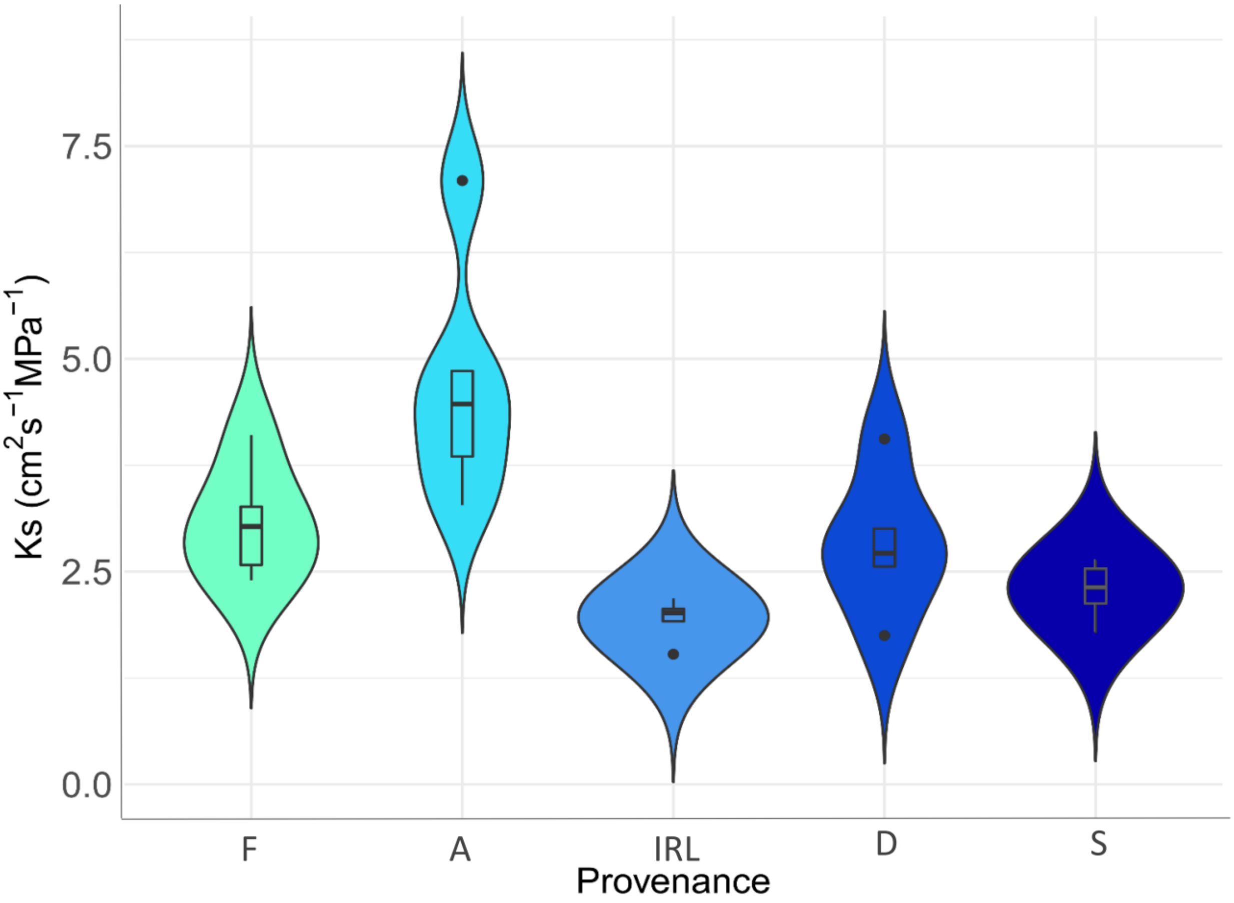
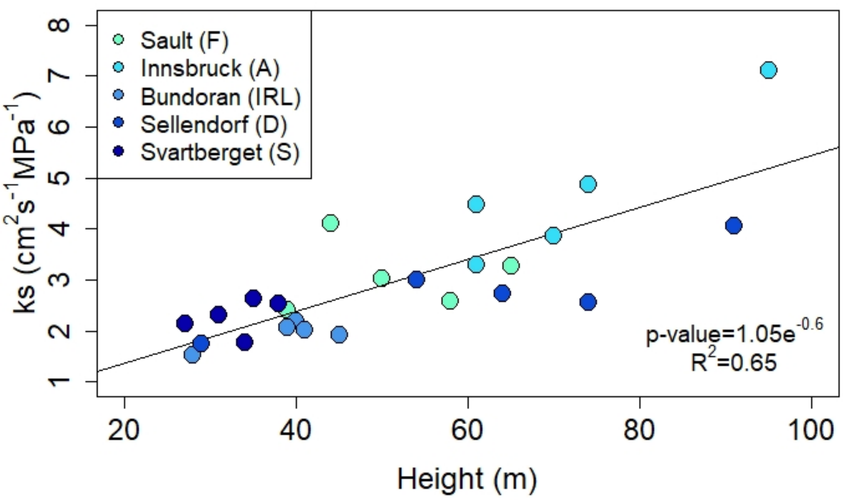


Figure 6: Hydraulic conductivity (*ks*; $cm^2s^{-1}MPa^{-1}$) *versus* plant height (m) of *Juniperus communis* L from different European provenances grown in the Innsbruck botanical garden, Austria (N47°16' E11°22; 600 m a.s.l.). R^2 and p-value refers to the linear model represented by the black line.



	Variable	Elevation (m a.s.l)			
		700	1200	1700	2000
Vulnerability	*P12*	-4.11 ± 0.17^{a}	-4.06 ± 0.20^{a}	-4.35 ± 0.25^{a}	-3.64 ± 0.26^{a}
	P50	-6.57 ± 0.31^{a}	-6.71 ± 0.29^{a}	-7.02 ± 0.26^{a}	-6.76 ± 0.20^{a}
	P88	-9.04 ± 0.53^{a}	-9.35 ± 0.53^{a}	-9.69 ± 0.37^{a}	-9.89 ± 0.32^{a}
	a	0.87 ± 0.10^{a}	0.82 ± 0.11^{a}	0.77 ± 0.05^{a}	0.66 ± 0.04^{a}
	n	8	7	7	8
Efficiency	*ks*	6.02 ± 0.50^{a}	4.94 ± 0.43^{a}	5.55 ± 0.38^{a}	5.86 ± 0.47^{a}
	n	10	10	10	10

	Variable	Provenance				
		Sault (F)	Innsbruck (A)	Sellendorf (D)	Bundoran (IRL)	Svartberget (S)
Vulnerability	*P12*	-3.56 ± 0.58^{a}	-4.14 ± 0.22^{a}	-3.46 ± 0.21^{a}	-3.5 ± 0.29^{a}	-2.97 ± 0.45^{a}
	P50	-6.74 ± 0.51^{ab}	-6.27 ± 0.18^{ab}	-6.51 ± 0.27^{ab}	-7.15 ± 0.47^{a}	-5.56 ± 0.30^{b}
	P88	-9.91 ± 0.56^{ab}	-8.41 ± 0.24^{a}	-9.55 ± 0.54^{ab}	-10.8 ± 0.68^{b}	-8.15 ± 0.60^{a}
	a	0.64 ± 0.05^{a}	0.96 ± 0.07^{a}	0.68 ± 0.08^{a}	0.55 ± 0.03^{a}	0.89 ± 0.18^{a}
	n	4	6	4	5	5
Efficiency	*ks*	3.07 ± 0.30^{ab}	4.71 ± 0.65^{b}	2.82 ± 0.37^{ac}	1.94 ± 0.11^{c}	2.28 ± 0.15^{ac}
	n	5	5	5	5	5