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Abstract

The recent massive dieback of forest trees due to drought stress makes assessment of the variability of physiological traits that might be critical for predicting forest response and adaptation to climate change even more urgent. We investigated xylem vulnerability to cavitation and xylem specific hydraulic conductivity in seven species of three principal conifer genera (*Juniperus monticola*, *Juniperus deppeana*, *Juniperus flaccida*, *Pinus pseudostrobus*, *Pinus leiophylla, Pinus devoniana*, and the endangered *Picea chihuahuana*) of the Mexican mountains in order to identify the species most vulnerable to future warmer and drier climates. Hydraulic traits were examined using the *in situ* flow centrifuge technique (Cavitron) on branches collected from adult trees of natural populations and seedlings growing in a common garden. We found evidence of significant differences in xylem safety between genera (P_{50}: pressure inducing 50% loss of hydraulic conductance): the three juniper species exhibited low P_{50} values (ranging from -9.9 to -10.4 MPa), relative to the much more vulnerable pine and spruce species (P_{50} ranging between - 2.9 to - 3.3 MPa). Our findings also revealed no variation in P_{50} between adult trees assessed in the field and seedlings growing in a common garden. We therefore propose that if, as projected, climate change makes their natural habitats much warmer and drier, populations of Mexican pines and the studied spruce will be likely to decline severely as a result of drought-stress induced cavitation, while the juniper species will survive.

Introduction

Concerns are increasing because of the mounting evidence of forest decline related to drought stress, apparently linked to ongoing climatic change (Breshears *et al.,* 2005; Peñuelas *et al.,* 2007; Mátyás, 2010; Allen *et al.,* 2010). Hotter drought periods are inducing massive tree mortality (Allen *et al.,* 2015) and, by year 2050, there is likely to be a substantial reorganization of vegetation (McDowell and Allen, 2015), with a plant community composition unfamiliar to modern civilization (Williams *et al.,* 2013). In such a context, the study of variation among and within forest species in terms of cavitation resistance is very important in order to predict the potential of adaptation to climatic change (Choat *et al.,* 2012). Resistance to cavitation has been shown to be a good estimator of tolerance to drought in vascular plant species (Brodribb and Cochard, 2009; Brodribb *et al.,* 2010). Previous studies have reported the high variability of P_{50} (a proxy of cavitation resistance, corresponding to the xylem pressure inducing a 50% loss of hydraulic conductance) among conifer species, ranging from -3 to -19 MPa (Delzon *et al.,* 2010; Pittermann *et al.,* 2010; Larter *et al.,* 2015).

There are indications that many forest tree species possess a very narrow hydraulic safety margin (< 1 MPa) and therefore they will potentially face long-term reductions in productivity and survival in a drier world (Choat *et al.,*

2012). However, large differences in hydraulic safety margins have been observed among species growing in the same habitat and one species can therefore be favored over another under certain conditions (Breshears *et al.,* 2005; Urli *et al.,* 2015). Conifers of genera *Juniperus*, *Picea* and *Pinus* frequently co-occur in the highly biodiverse Mexican mountains (Quiñones-Perez *et al.,* 2014; Figure 1), since they share similar climatic habitat conditions. Previous studies of cavitation resistance in conifer forest communities of southwestern USA (Arizona, New Mexico, Utah and Colorado states, Breshears *et al.,* 2005) have shown large differences in P_{50} values between *Pinus edulis* and *Juniperus monosperma,* even where both species co-occur in that region.

The differences among conifer genera and species for cavitation resistance sharing similar climatic habitats have not been explored for Mexico in great detail, despite the very wide biodiversity of conifers in Mexico (Styles 1993). A previous study, focused on differences within *Pinus hartwegii* along an altitudinal gradient, showed no population-level genetic differentiation for cavitation resistance (Sáenz-Romero *et al.,* 2013). That trend is consistent with much broader studies that indicate remarkably low variation among populations within conifer species (i.e. *Pinus pinaster*, Lamy *et al.,* 2011). At the genus level, pines and spruces seem to be moderately resistant to cavitation (P_{50}: -3 to -4.7 MPa and -3.7 to -5.2 MPa, respectively; Bouche *et al.,* 2014). This pattern contrasts strongly with the more cavitation-resistant genus *Juniperus* (*Cupressaceae*) that also shows much more variation across species, with P_{50} values ranging from around -6 to -14 MPa (Bouche *et al.,* 2014; Willson *et al.,* 2008).

In the present study, we aim to assess differences in hydraulic safety (drought-induced cavitation resistance) and conductivity (water-transport efficiency) among seven Mexican conifer species belonging to three genera: *Juniperus*, *Pinus* and *Picea*. Some of these frequently co-occur in the highly biodiverse Mexican mountains (Quiñones-Perez *et al.,* 2014; Figure 1) and thus share similar climatic habitat conditions. The mountain conifer forests of Mexico are expected to experience a drier climate with more frequent droughts, which may lead to a 92 % loss of their suitable climatic habitat along the Trans-Mexican Volcanic Belt by the end of this century (Rehfeldt *et al.,* 2012). Under this scenario, we hypothesize highly species-specific responses, with a high risk of mortality for species of greater vulnerability to cavitation as a response to drought events.

Materials and Methods

Study area and study species

We focused on seven conifer species, six of which occur across a wide altitudinal gradient along the central Mexican mountains (Trans-Mexican Volcanic Belt, TMVB) and one in the Sierra Madre Occidental (Figure 1). The species were:

(a) Three juniper species: *Juniperus monticola* (high elevation, cold and humid environments, including sites within the Monarch Butterfly Biosphere Reserve overwintering sanctuaries), *J. deppeana* (intermediate elevations between 2200-2900 m a.s.l., temperate climate, occurring in the pine-oak forest, wide distribution in Mexico) and *J. flaccida* (occurring at lower elevations, in environments with marked drought/rainy seasonality and savanna-like vegetation with frequent natural or induced fires, at the lowest altitudinal distribution of the genus in the studied region, overlapping with the upper altitudinal limit of the tropical dry forest) (Carranza and Zamudio, 1994).

(b) Three pine species, selected among the most abundant pine species of the pine-oak forest at the TMVB in Michoacán state, with partially altitudinal overlapping distributions: *Pinus pseudostrobus* (intermediate to high elevations, the most abundant and economically important species), *P. leiophylla* (intermediate altitudes, appearing on poorer sites than *P. pseudostrobus*) and *P. devoniana* (low altitudinal limit of the pine-oak forest, close to the upper altitudinal limit of the tropical dry forest). The distributions of the three pine species overlap at the mid-altitudinal range of the pine-oak forest, approximately at 2200 to 2300 m asl in altitude (Castellanos-Acuña *et al.,* 2015; Table 1)

(c) A very rare, endangered, endemic spruce, *Picea chihuahuana*, with fragmented and endogamic populations, occurring at high elevations, at the cold and humid sites of the Sierra Madre Occidental, in northwestern Mexico. *Picea chihuahuana* is the most abundant spruce among the only three species of this genus that exists in Mexico (the others are *Picea martinezii* and *P. mexicana*), where spruces are postglacial relicts (Ledig *et al.,* 2010; Wehenkel and Sáenz-Romero, 2012; IUCN 2015).
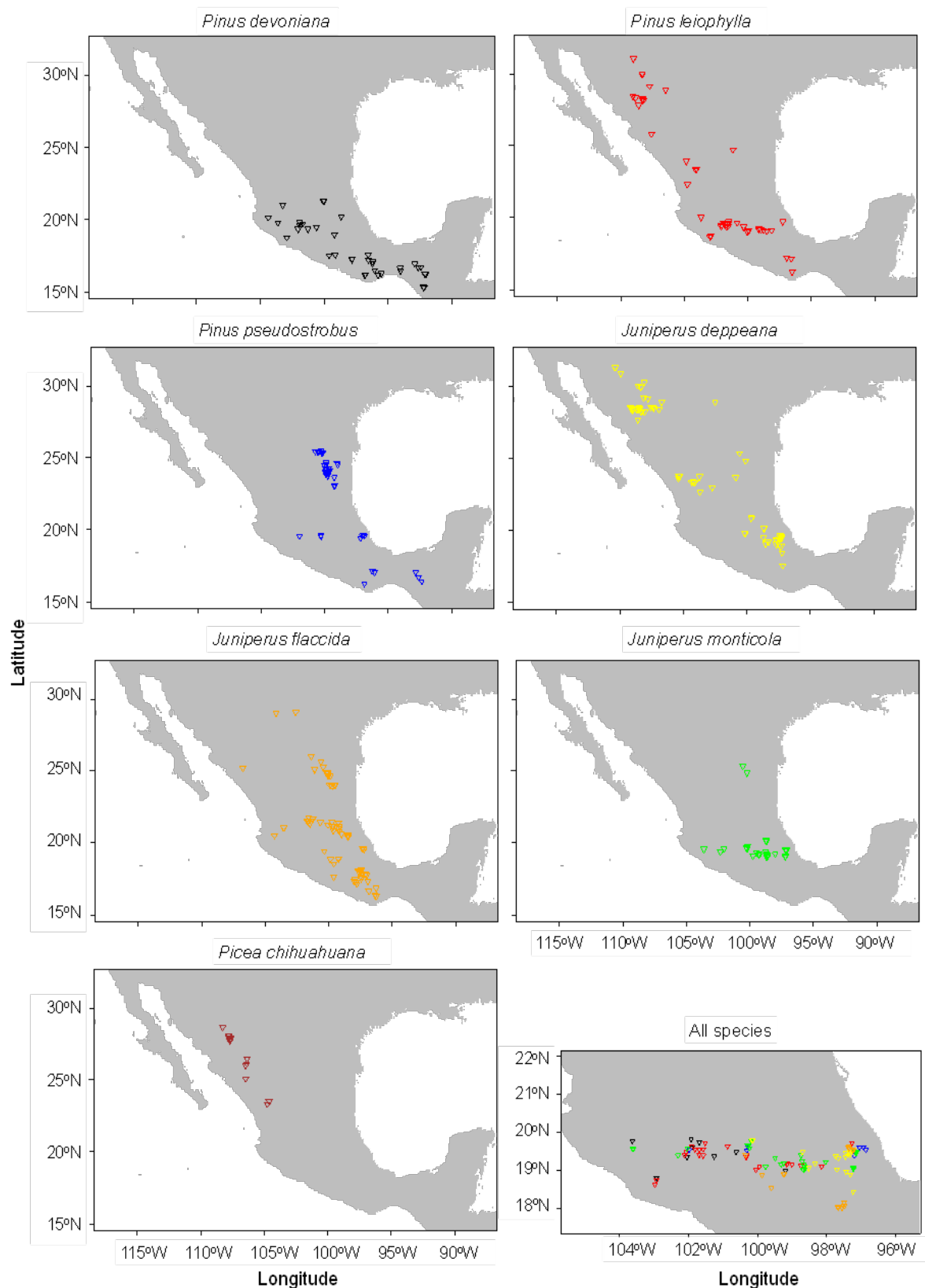
Figure 1. Distribution of the seven studied conifers in Mexico.
Sites correspond to plots recorded by the Mexican National Forest Inventory, for which climatic and aridity index data are available from http://www.worldclim:bioclim and http://www.cgiar-csi:data/global-aridity-and-pet-database, respectively. The final insert shows a close-up of the Trans-Mexican Volcanic Belt.

3

Sampling procedures

Drought-induced resistance to cavitation and hydraulic conductivity were evaluated in branches collected from natural populations of the seven conifer species studied. For each juniper species, we collected branches of seven to eight trees belonging to one population representative of the distribution range of the species, in zones with high conifer diversity (Table 1). For each pine species, six to seven trees from two to four populations were collected, aiming to represent the altitudinal distribution range of each species (Table 1). Fifteen individuals were sampled from *Picea chihuahuana* Santa Barbara population (also known as Arroyo El Infierno; Ledig *et al.,* 2000), at a high elevation (2725 m a.s.l.) site of the Sierra Madre Occidental, Durango State, in northwestern Mexico.

As a complementary sampling to explore variability in hydraulic traits within species, we collected branches of the three pine species from individuals growing in a common garden test at Morelia, Michoacán (Lat. 19.69 N, Lon. 101.25 W, altitude 1.900 m a.s.l.). These trees were grown from seeds obtained from natural populations of the same pine species and region, aiming to represent the altitudinal gradient on which each species occur. However, due to the minimum branch size requirement for xylem cavitation analysis (see details below), only a reduced number of individuals were sampled: two to five seedlings (exceptionally one seedling, in one case) from two populations of each pine species (Table 1). This additional common garden sampling was not possible for the rest of the species studied here, as provenance tests were unavailable. The site of the common garden test has a much warmer and drier climate (mean annual temperature 17.0 ºC, mean annual precipitation 871 mm) than that of the sites of the studied natural populations (although watering was provided when required in order to ensure seedling survival).

Table 1. Population origin of the branch samples analyzed for cavitation, either from collection of field samples, or from populations represented in a common garden test.

With the exception of *Picea chihuahuana*, collected in Durango state (Dgo.), northwestern Mexico, all others come from Michoacán state (Mich.), central-western Mexico. Sample size indicates the number of trees from which samples were collected.

Locality and State	Elevation (m a.s.l.)	Lat (N)	Lon (W)	Species	Sample size (individuals)	
					Field	Common garden
Santa Bárbara, Dgo.	2.725	23.66	105.44	*Picea chihuahuana*	15	-
Sierra Chincua, Mich.	3.142	19.65	100.25	*Juniperus monticola*	8	-
Tlalpuhahua, Mich.	2.575	19.80	100.17	*Juniperus deppeana*	8	-
Tuxpan, Mich.	1.870	19.60	100.48	*Juniperus flaccida*	7	-
Cerro Pario (High), Mich.	2.746	19.47	102.18	*Pinus pseudostrobus*	6	-
Cerro Pario (Int.), Mich.	2.600	19.47	102.19	*Pinus pseudostrobus*	7	-
Cerro Pario (Low), Mich.	2.520	19.46	102.20	*Pinus pseudostrobus*	-	3
La Pila (High), Mich.	2.422	19.45	102.18	*Pinus pseudostrobus*	7	-
				Pinus leiophylla	7	-
La Pila (**Low**), Mich.	2.310	19.44	102.17	*Pinus pseudostrobus*	-	3
				Pinus leiophylla	6	2
				Pinus devoniana	-	5
El Rosario (High), Mich.	2.217	19.43	102.17	*Pinus leiophylla*	-	**2**
				Pinus devoniana	6	**-**
El Rosario (Int.), Mich.	2.110	19.43	102.16	*Pinus leiophylla*	-	2
				Pinus devoniana	6	1
El Rosario (Low), Mich.	2.034	19.42	102.15	*Pinus devoniana*	7	-
Jicalán, Mich.	1.650	19.38	102.08	*Pinus devoniana*	6	-

Sample processing

Branches were collected early in the morning to avoid high temperatures and all needles were immediately removed to prevent desiccation. The samples were then wrapped in wet paper towels, placed in black bags, and immediately posted to France for analysis. Vulnerability to drought-induced cavitation was determined**,** at the high-throughput phenotyping platform for hydraulic traits (CavitPlace, University of Bordeaux, Talence, France; http://sylvain-delzon.com/caviplace). The samples were kept wet and cool (3°C) until cavitation resistance was measured within three weeks of collection. Prior to measurement, all branches were cut with a razor blade under water to a standard length of 27 cm, the bark was removed and they were fully rehydrated before further processing.

Measurement of resistance to cavitation

Xylem cavitation was assessed with the CAVITRON, a flow centrifuge technique, following the procedure described in Cochard (2002) and Cochard *et al.,* 2005. In the CAVITRON, a centrifugal force establishes a negative xylem pressure, inducing a loss of conductance by cavitation. Samples are inserted into a custom-built rotor (Precis 2000, Bordeaux, France) mounted on a high-speed centrifuge (Sorvall RC5, USA). Xylem pressure (P_i) is first set to a reference pressure (-0.5 MPa) and hydraulic conductivity (ki) is determined by measuring the flux through the sample. The centrifugation speed is then set to a higher value for 3 minutes to expose the sample to more negative pressure.

The conductance was measured three to four times, and the average was used to compute the percentage loss of xylem conductance (PLC in %) at that pressure (see Delzon *et al.,* 2010 for details). This procedure was repeated for at least eight pressure steps with a -0.5 MPa step increment until the PLC reached at least 90%. Rotor velocity was monitored with a 10 rpm resolution electronic tachymeter and xylem pressure was adjusted to about -0.02 MPa. Conductance measurements were taken using the Cavisoft software (version 2.0, BIOGECO, University of Bordeaux).

Percentage loss of conductance in the xylem as a function of xylem pressure (MPa) represents the vulnerability curve (VC) of the sample. A standard sigmoid function (Pammenter and Van der Willigen, 1998; Cochard *et al.,* 2005) was fitted to the VC of each sample, using SAS v 9.1 (SAS Institute 2004) and the following equation:

$$PLC = \frac{100}{1 + e^{(\frac{S}{25}*(P-P_{50})})}$$

where P_{50} (MPa) is the xylem pressure that induces 50% loss of conductance and S (% MPa^{-1}) is the slope of the vulnerability curve at the inflexion point. The specific hydraulic conductivity (k_s, m² MPa^{-1}s^{-1}) of the xylem was calculated by dividing the maximum hydraulic conductivity measured at low speed by the sapwood area of the sample.

More negative P_{50} (xylem pressure inducing 50% loss of conductance) values indicate higher resistance to cavitation, while the slope of the vulnerability curve (S) indicates how fast cavitation progresses at P_{50}.

Statistical analysis

We tested differences in xylem pressure inducing 50% loss of conductance (P_{50}), slope of the vulnerability curve at the inflexion point (S) and xylem specific hydraulic conductivity (k_s) among species and genera by conducting a two-way nested ANOVA followed by a *post-hoc* Tukey test (α = 0.05). The ANOVAs were performed using the Procedure GLM of SAS (SAS Institute, 2004). Variance components were estimated using the Procedure VARCOMP with the method of restricted maximum likelihood (REML) of SAS (SAS Institute, 2004).

In order to find possible evolutionary associations between increasing cavitation resistance and increasing aridity, we conducted a regression analysis between the means of the hydraulic traits of each species (all species, field data only) against the median of three climate variables along each species distribution range: Mean Annual Temperature (MAT), Mean Annual Precipitation (MAP), Annual Aridity Index (AAI: Mean Annual Precipitation/ Mean Annual Potential Evapotranspiration). We also regressed the means of the hydraulic traits of each species against the extreme values of the climatic variables, calculated as the median of the 5% of highest MAT (MAT_max), lowest MAP (MAP_min) and more arid AAI (AAI_max) values. Climatic and aridity index values averaged per species were estimated from presence points covering the full distribution range of the species (illustrated on Figure 1 for Mexico) and obtained from http://www.worldclim:bioclim and http://www.cgiar-csi:data/global-aridity-and-pet-database, respectively. For *Juniperus* and *Pinus* genera, we explored the relationship between the intraspecific variability in hydraulic traits and the climate of each population by regressing the means per population against the provenance climate variables for those two genera.

In the specific case of the genus *Pinus*, we also explored the plasticity in hydraulic safety and conductivity. To do so, we compared the P_{50}, S and k_s of field versus common garden samples using a two-way ANOVA, in which the species and the study (field/common garden) were included as factors.

Results

Differences among genera and species

Hydraulic traits varied widely across the studied species, with P_{50} values ranging from -2.94 MPa (*Pinus pseudostrobus*) to -10.37 MPa (*Juniperus monticola*). The slope of the vulnerability curve varied from extremely steep (87.78 % MPa^{-1} for *Pinus leiophylla*) to very flat (i.e. less than 20 % MPa^{-1} for each juniper species).

Most of this variation occurred at the genus level since, for example, juniper P_{50} was on average about 7 MPa more negative than the pine and spruce P_{50} values (see Figure 2). Similarly, we found large differences in the slope of the vulnerability curve at the inflexion point (*S*) between the juniper species in comparison to the pines and the spruce. The three *Pinus* species had *S* values well above 50 % MPa^{-1}, *Picea chihuahuana* was close to this (47), but the *Juniperus* species had *S* values of between 16 and 20. We evidenced significant differences among genera in P_{50} (xylem pressure inducing 50% loss of conductance, $P < 0.0001$) and *S* (slope of the vulnerability curve at the inflexion point, $P = 0.0013$). Differences among genera explained 98 % and 67 % of the total variation for P_{50} and *S*, respectively (Table 2). In contrast, differences between species within genera accounted for a marginal 0.2%, and 1.9% for P_{50}, and *S*, respectively (Table 2).

Xylem transport efficiency, k_s, varied from 0.0003 m² MPa^{-1} s^{-1} for *Picea chihuahuana* to 0.0021 m² MPa^{-1}s^{-1} for *Pinus leiophylla* (17 % of the total variation is explained by the species), but no significant differences among genera were found for this trait ($P = 0.066$).
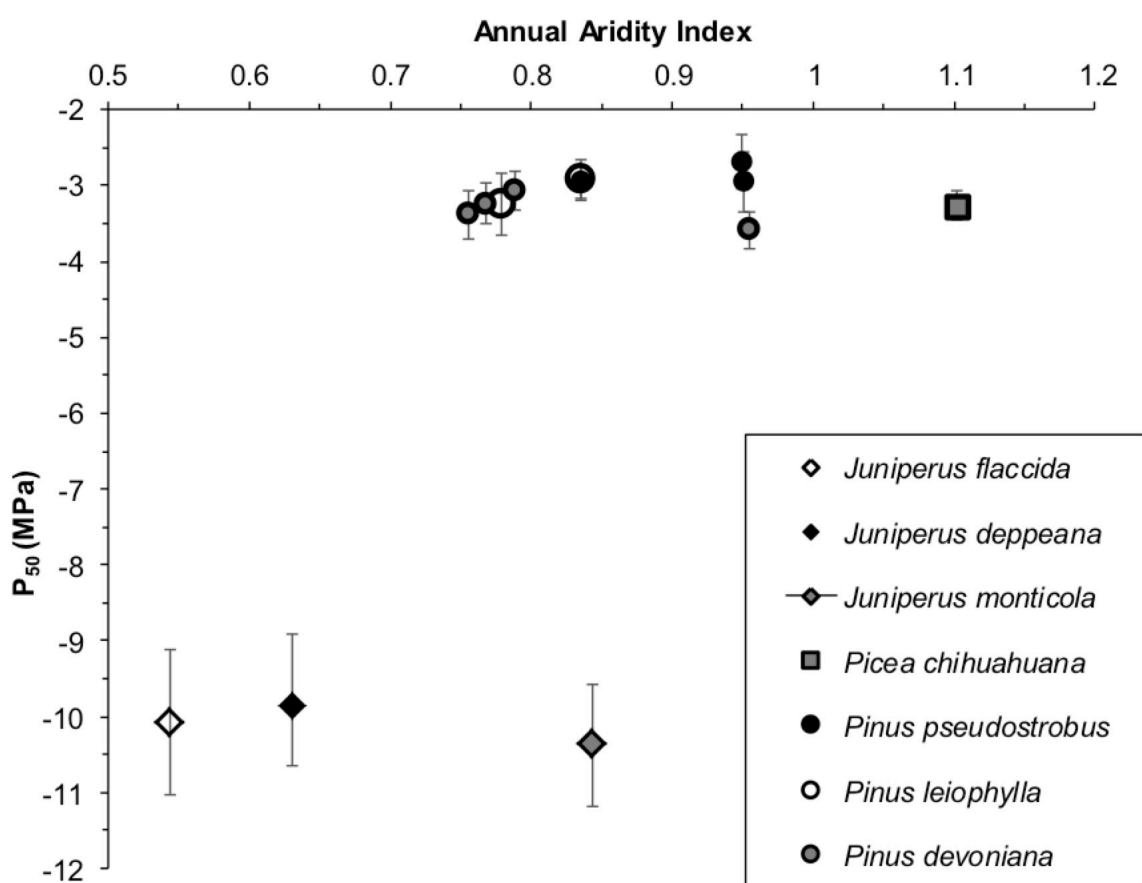

Figure 2. Xylem pressure inducing 50% loss of hydraulic conductance (P_{50}) in MPa.

P_{50} is plotted against the Annual Aridity Index median per species and per population (larger values indicate colder and more humid; smaller values indicate warmer and drier environments). Vertical bars represent 95 % confidence intervals

Association with climatic variables

There is a complete lack of association between P_{50}, *S* and k_s and the six climatic variables (regression: $r^2 < 0.03$; $P > 0.20$). Notice on Figure 2 that *Juniperus monticola*, despite growing in much less arid (more cold and humid) sites than all of the pines and the spruce, shows a P_{50} similar to that of *Juniperus deppeana* and *J. flaccida*, which grow in the warmest and driest sites of this study. Similarly, we found no significant relationship between the hydraulic traits and climate of each population at the genus level (*Juniperus* and *Pinus*; $P > 0.30$).

Differences between field and common garden tests

There were no significant differences between the values of the hydraulic traits obtained from trees in the field and common garden tests, denoting a lack of phenotypic variability in the traits measured within species (Table 2). Differences among studies account for a meaningless 0.0 %, 0.9 % and 0.0 % of the total variation for P_{50}, S and k_s, respectively (non-significant; P > 0.45; Table 2). Figure 3 shows how similar are the P_{50} values among studies and also among pine species.

Table 2. Analysis of variance

Analysis of variance (% of contribution to total variance and P, significance) of xylem cavitation resistance traits (P_{50}, xylem pressure inducing 50% loss of conductance and S, slope of the vulnerability curve at the inflexion point) and xylem transport efficiency (k_s, xylem specific hydraulic conductivity). Analyses were conducted: (a) comparing among genera from branches collected from natural populations (three species of *Juniperus monticola*, three *Pinus* and one *Picea*) and (b) comparing among studies (field *vs.* common garden) only for *Pinus* species. Origin of samples as in Table 1.

	df	P_{50} %	P	S %	P	k_s %	P
a) All species, only field samples							
Genus	2	97.9	<0.0001	67.3	0.0013	45.6	0.0661
Species (Genus)	4	0.2	0.0483	1.9	0.1516	16.9	<0.0001
Residual	88	1.9		30.8		37.6	
Total	94	100.0		100.0		100.0	
b) Only *Pinus* species, field *vs.* common garden							
Study	1	0.0	0.7475	0.9	0.5457	0.0	0.4524
Species	2	0.0	0.7957	0.0	0.9145	17.0	0.2763
Study* Species	2	21.5	0.0044	8.5	0.0207	9.2	0.1484
Residual	70	78.5		90.5		73.8	
Total	75	100.0		100.0		100.0	

Discussion

Large differences among genera

We evidenced here that the three juniper species studied are much more resistant to cavitation than the three co-occurring pine species and the Chihuahua spruce examined: P_{50} values of *Juniperus monticola*, *J. deppeana*, and *J. flaccida* were three times more negative than those of *Picea chihuahuana*, *Pinus devoniana*, *P. leiophylla* and *P. pseudostrobus*. Similar differences have been reported among other juniper and pine species that grow in same or similar environments (Linton *et al.,* 1998) and with previous studies focused in species of these two genera (Delzon *et al.,* 2010; Bouche *et al.,* 2014). Although *Picea chihuahuana* was the only *Picea* species examined here, its P_{50} value (- 3.3 MPa) was very close to those reported for other species of this genus (Delzon *et al.,* 2010, Bouche *et al.,* 2014; Nolf *et al.,* 2015). Regarding the slope of the cavitation curve, Delzon *et al.,* 2010 suggested that slopes >50 % MPa^{-1} indicate a very fast rate of embolism. According to our results, the three pines and *Picea chihuahuana* had much larger slope mean values than those of the *Juniperus* species, confirming the greater vulnerability to cavitation in the pine and spruce species compared to the juniper species. These differences can be linked to an evolutionary divergence in hydraulic strategies within conifers when faced with drought (Brodribb *et al.,* 2014).

Lack of correlation with climate and conservatism within genera

We did not find significant correlations between hydraulic safety (P_{50}, S) and efficiency traits (k_s) and climate variables, indicating a trait conservatism within genera. For example, *J. monticola*, which grows in the wettest conditions, shows a P_{50} similar to that of *J. flaccida*, which grows in the driest environments. This result contrasts to previous studies that report positive correlations between P_{50} and MAP or MAT (Maherali *et al.,* 2004; Choat *et al.,* 2012) and suggest evolutionary associations between increasing cavitation resistance and increasing aridity across functional groups of conifers. However, our results must be treated with some caution since not all of the regions occupied by each species are represented in the populations sampled.

Lack of phenotypic variability

For the *Pinus* genus, we found no effect of the study, between samples collected from adult trees in natural populations (field) and from seedlings growing in a common garden, in any of the studied hydraulic traits. This low variability has already been observed in pinaceae species. For instance, Lamy *et al.,* 2014 reported no phenotypic variability in P_{50} between maritime pine populations in Europe. On the contrary, Martinez-Vilalta *et al.,* 2009 found a significant between-population variability in Scots pine, with no link to climatic dryness, Very recently, David-Schwartz *et al.,* 2016 reported a significant genetic differentiation between Aleppo pine provenances growing in common garden. Overall, the intra-specific variation in cavitation resistance is much smaller in conifers than in angiosperms (Anderegg, 2014). Taken in conjunction, these studies highlight the fact that more research is needed, especially to quantify the phenotypic plasticity of those traits by conducting reciprocal transplant experiments.

Implications for climate change adaptation

These results (high vulnerability to cavitation and lack of phenotypic variability for pines) suggest a potential drought-induced mortality of pine species with respect to that of *Juniperus*, under the warmer and drier environments predicted for Mexican regions in this century (Sáenz-Romero *et al.,* 2010; Rehfeldt *et al.,* 2012). When species of these two genera co-occur in the same habitats, the pine species more vulnerable to cavitation may show a much narrower safety margin and face a consequently higher risk of hydraulic failure. This has taken place already in the semiarid woodland communities of Utah, Colorado, Arizona and New Mexico, USA, where two consecutive dry and warm years (2000 to 2003) induced a massive forest decline of *Pinus edulis*, while *Juniperus monosperma* survived (Breshears *et al.,* 2005). In Mexico, however, some *Juniperus* can occur in much drier habitats than pines and can therefore experience much lower minimum water potential, leading to a reduced safety margin. To confirm this, water potential would have to be measured during a dry season. However, recent studies show a strong correlation between P_{50} and mortality (not only in safety margin versus mortality) and, therefore, the more vulnerable species (pines and spruce in the case of our study) might be more at risk than juniper (Anderegg *et al.,* 2016).

In the particular case of *Picea chihuahuana*, our results indicate that, at least regarding resistance to cavitation, it is as vulnerable to drought stress as the three pines studied. Under climate change, this will put additional pressure on *Picea chihuahuana*, a species that is already endangered due to its narrow and fragmented distribution (Ledig *et al.,* 2010), with some populations displaying signs of genetic erosion (Wehenkel and Sáenz-Romero, 2012). Severe drought-stress events due to climatic change may thus cause massive mortality in this species, as has already occurred in some spruce-dominated forest of the Rocky Mountains, USA (Bigler *et al.,* 2007) and Norway (Solberg, 2004). However, considering that *Picea chihuahuana* as a whole is already endangered, a climatic change-linked massive mortality might eventually lead to extinction of the species.

Future research needed

Exploring resistance to cavitation in roots and leaves would provide complementary information to support our hydraulic trait results at branch level (see Domec *et al.,* 2009; Domec *et al.,* 2015), as well as examining cavitation resistance in the other two spruces represented in Mexico (*Picea martinezii* and *Picea mexicana*). Moreover, conducting measurements under natural or experimental drought stress conditions, such as over the range of water potentials experienced during critical heat waves and/or drought periods, would be of value to confirm the different abilities of each genus and species in terms of coping with the warmer and drier conditions predicted by the IPCC (2013). For quantifying the phenotypic plasticity of those traits, it would be advisable to conduct experiments including reciprocal transplantation, and to construct a response curve function to the climatic transfer distance (difference between the climate of the test site and climate of the seed source). Finally, the notion that juniper species might be more dominant than pine species in future climates than they are today, highlights the need for studying variability among juniper populations in terms of cavitation resistant traits, which to date have been studied mostly for pine species.

Conclusions

Our results confirm the greater vulnerability of three Mexican pine species and of *Picea chihuahuana* to cavitation compared to three species of the genus *Juniperus*. This higher vulnerability is particularly concerning in the case of *Picea chihuahuana*, an endemic and endangered species that presents a narrow and fragmented distribution. Our results suggest that, if the predicted climatic change does make the natural habitats of this species much warmer and drier, populations of Mexican pines and spruces will be likely to present severe decline, whereas the juniper species may survive. A process that would simplify the ensembles of natural species through a vegetation recomposition that is characterized by a more sparse tree coverage might then endanger the high biodiversity of the Mexican pine-oak and conifer forest, where pine species might die but juniper, which is more resistant to drought, will remain.

Acknowledgements

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