Journal of Agricultural Science; Vol. 11, No. 13; 2019
ISSN 1916-9752 E-ISSN 1916-9760
Published by Canadian Center of Science and Education

Hydraulic Traits Performances of Three Pine Species in Tunisia

Sameh Cherif[1,2], Olfa Ezzine[3], Mohamed Larbi Khouja[3] & Zouhaier Nasr[2]

[1] Faculty of Sciences of Bizerte, University of Carthage, Zarzouna, Tunisia

[2] Laboratory of Management and Valorization of Forest Resources, National Institute for Research in Rural Engineering Water and Forest, University of Carthage, Ariana, Tunisia

[3] Laboratory of Forest Ecology, National Institute for Research in Rural Engineering Water and Forest, University of Carthage, Ariana, Tunisia

Correspondence: Sameh Cherif, Faculty of Sciences of Bizerte, University of Carthage, 7021, Zarzouna, Tunisia; LR161INRGREF01 Laboratory of Management and Valorization of Forest Resources, National Institute for Research in Rural Engineering Water and Forest, University of Carthage, Bp 10, 2080 Ariana, Tunisia. Tel: 216-9713-5047. E-mail: sameh.cherif@gmail.com

Received: April 1, 2019 Accepted: June 27, 2019 Online Published: August 15, 2019

doi:10.5539/jas.v11n13p20 URL: https://doi.org/10.5539/jas.v11n13p20

Abstract

Mediterranean forests including Tunisian pine species are threatened by the rising of temperature and decreasing of precipitation. The impact of the increase of aridity differs across species depending on their stomatal and hydraulic responses. In this paper, three pine species: *P. halepensis*, *P. brutia* and *P. canariensis* growing in three different climatic zones: humid, sub-humid and semi-arid, were studied to detect their different responses to drought and guide their selection for reforestation program. Measurements carried out are hydraulic conductivity at point P_{50}, specific conductivity (Ks), midday stem water potential and hydraulic safety margins. Results showed that during summer, vulnerability to embolism, estimated by water potential inducing 50% loss of xylem hydraulic conductivity (P_{50}), is strongly associated with the capacity for drought resistance. *Pinus halepensis* (P_{50} = -4.19 MPa) was found to be more resistant to drought than *P. brutia* and *P. canariensis* in the semi-arid climate, whereas *P. brutia* tolerated the humid climate (P_{50} = -3.7 MPa) and *P. canariensis* seems more adapted to the sub-humid climate (P_{50} = -4.08 MPa). Hydraulic safety margins confirmed the conservative behavior of pine species to avoid drought and for maintaining relatively high water potential in dry conditions. These findings help to assess the impact of mid-summer water deficit on pine species in the context of climate change and to select among these species the most resistant for future reforestation programs.

Keywords: drought, vulnerability to cavitation, inter-specific and intra-specific variability

1. Introduction

Global warming is rapidly changing climatic conditions worldwide, hotter drought periods are inducing tree mortality (Allen et al., 2015) and, by the year 2050, there is likely to be a substantial reorganization of vegetation (McDowell & Allen, 2015). Mediterranean forests are the most affected by these selective pressures (Ramirez-Valiente et al., 2010). Mainly, Mediterranean pinewoods are subject to severe droughts (Martinez-vilalta & Pinol, 2002). In this 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). Drought stress vulnerability has been shown to correlate with site water availability (Nardini et al., 2012), with mean annual rainfall (Maherali et al., 2004), and with the dry-end rainfall boundaries of species distributions (Blackman et al., 2012).

Increasing tension in the water column may eventually lead to cavitation within the xylem by promoting the seeding of air bubbles into water-filled conduits (Sperry et al., 2002). Cavitation reduces total plant hydraulic conductance, it limits the ability to transport water and nutrients to sites of growth and productivity and ultimately may lead to death (Sala et al., 2010). P_{50} is the xylem pressure corresponding to a 50% loss of conductivity, and it is a proxy of cavitation resistance. It is widely used as a comparative index of xylem hydraulic safety, within different parts of the same individual and within species across environmental gradients (Maherali et al., 2004). However, reaching P_{50} indicates that a hydraulic failure has already occurred (Tyree & Sperry, 1988).

Species have been shown to vary considerably in P_{50}, ranging from -0.18 MPa (highly vulnerable) to -14.1 MPa (highly resistant) (Maherali et al., 2004). Much of this variation has been explained by a safety-efficiency trade-off because xylem conduits (tracheids in conifers) offer greater resistance to embolism (Burgess et al., 2006).

Hydraulic safety margins (HSMs) were calculated as the difference in water potential between the minimum value experienced in the field and the value at either 50% loss of xylem hydraulic conductivity (P_{50stem}) (Meinzer et al., 2009).

HSMs reflect the degree of hydraulic conservatism of a plant or a given organ (Meinzer et al., 2009; Johnson et al., 2016). HSMs have been used to estimate the water potential threshold leading to catastrophic hydraulic failure in leaves and stems (Meinzer et al., 2009).

The safety margin and efficiency increase with climate but it could arise from the design properties of the xylem tissue itself (Allen et al., 2010). However, large differences in hydraulic safety margins have been noticed among species growing in the same habitat and one species can, therefore, be favored over another under certain conditions (Urli et al., 2015). Tunisian forest covers different species of *Pinus*, three of pine species are the subject of our study.

Aleppo pine (*Pinus halepensis* Mill.) is an important forest tree in the Mediterranean region (Klein et al., 2011). It is native and the most abundant pine species in Tunisia (You et al., 2016). The ability of Aleppo pine to survive and grow in various environments indicates that it is a highly tolerant species (Klein et al., 2012).

Calabrian pine (*Pinus brutia* Ten.), native to the eastern Mediterranean region, can be found in many southern Mediterranean countries. Because of its drought tolerance, it is well adapted to dry summer conditions. The species was widely planted from the '30s to the'70s in Mediterranean areas for soil protection and windbreaks near the coast (Lopez et al., 2016). In Tunisia, this species was introduced in 1960.

Canary pine (*Pinus canariensis*) is an endemic species of the Canary Islands. Current environmental conditions are very different from those in which this species evolved a much wetter climate even during the late Holocene (De Nascimento et al., 2009). Despite its small distribution area, the species grows across a wide climate (from xeric conditions to mixed forest). In Tunisia this species was introduced since 1965.

A better evaluation of the impact of drought on pine species in Tunisia is important for successful forest management and for new plantations.

Based on a functional link between stem hydraulic vulnerability and drought resistance, across species. The aim of the study was to assess and compare the level of variability of P_{50} within-pine species in stem and across sites in summer months 2016; (2) to detect the interaction between species and climate; (3) to examine the relationship between water transport efficiency and P_{50} and (4) to select the most droughts tolerant pine species through comparing the P_{50} and measuring the safety margin.

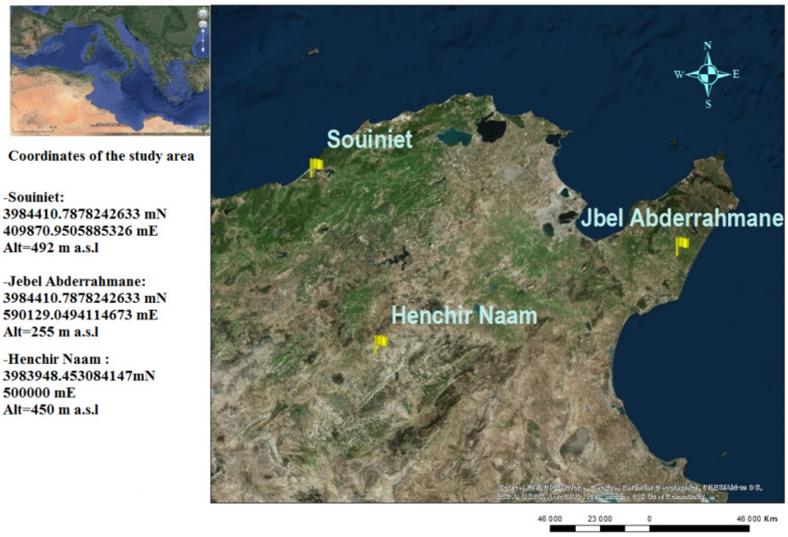
2. Method

2.1 Study site

The study was carried out in three arboreta (Figure 1) on three pine species (*Pinus halepensis*, *P. brutia* and *P. canariensis*). The first, Souiniet "SNT", is located in northwest Tunisia: 3984410.7878242633 mN, 409870.9505885326 mE, Alt = 492 m a.s.l. in the mountainous region of Kroumirie which is characterized by a humid climate (Figure 2). The shrub layer is composed of *Arbutus unedo*, *Erica scoparia*, *Erica arborea*, *Myrtus communis*, *Phillyrea media*, *Halimium halimofolium*, and *Cistus salvifolius* and trees of *Quercus suber*.

The second, Jebel Abderrahmane "JAB", is located in northeast Tunisia 3984410.7878242633 mN, 590129.0494114673 mE, Alt = 255 m a.s.l. and has a sub-humid climate (Figure 2) associated species are mainly composed of Mediterranean maquis with *Quercus coccifera*, *Erica arborea*, *Calycotome intermedia*, *Halimium halimofolium*, *Pistacia lentiscus* and *Phillyrea media*.

The third arboretum, Henchir Naam "HNM", is located in northwest Tunisia 3983948.453084147 mN, 500000 mE, Alt = 450 m a.s.l. and is characterized by a semi-arid climate with moderate winters and hot dry summers (Figure 2). Pine trees: *P. halepensis*, *P. brutia* and *P. canariensis* are found in forest mosaics along with other tree species, including *Picris echioides*, *Phalaris truncata*, *Brassica amplexicaulis*, *Euscari comosum* and *Centaurea nicaensis.*



Coordinates of the study area

-Souiniet:
3984410.7878242633 mN
409870.9505885326 mE
Alt=492 m a.s.l

-Jebel Abderrahmane:
3984410.7878242633 mN
590129.0494114673 mE
Alt=255 m a.s.l

-Henchir Naam :
3983948.453084147mN
500000 mE
Alt=450 m a.s.l

Figure1. Regions of three experimental stations

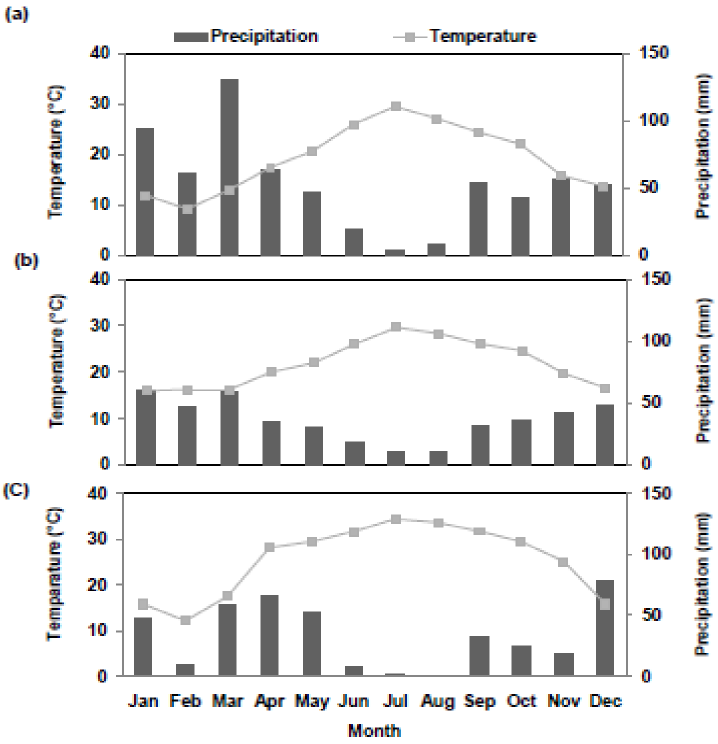


Figure 2. Climatograph of study site: (a) Souiniet site (humid climate), (b) Jbel Abderrahmane (sub-humid) and (c) Henchir Naam (semi-arid). The climatograph illustrates the monthly distribution of precipitation (P) and temperature (T) in 2016

2.2 Sampling

Drought-induced resistance to cavitation and hydraulic conductivity were evaluated in branches collected from three trees studied. For each pine species, we collected three branches of three trees with a mean diameter at breast height (DBH) = 16±0.3 cm and high 13.5±2.5 m. As a total nine branches of each pine species were considered for hydraulic measurement.

Hydraulic experiments started with the collection of samples from three different sites during the summer of 2016 (June, July and August). The hydraulic measurements of the species in the three sites were carried out separately during three days for each month starting from the initial day of collection. Then, the average of three measurements was taken, in order to represent the hydraulic status in the summer period.

Twig water potential and midday water potential were measured with a pressure chamber (Scholander et al., 1965) to construct the vulnerability curves and to measure safety margin, respectively. Three twigs were measured from each tree. Measurements were taken on the same date as the hydraulic measurements.

2.3 Native Embolism

Native embolism (% of the loss of conductivity) and specific conductivity were measured on stem segments using XYL'EM, a xylem embolism meter (Bronkhorst, Montigny-les-Cormeilles, France) (Cruiziat et al., 2002). The technique involves measuring the hydraulic conductance of segments before and after water refilling (Ki and Kmax, respectively). The samples were selected from the upper part of the crown using a pool-pruner. Branches collected early in the morning from each site then bagged and kept in a cooler until they could be transported to the lab (Wheeler et al., 2013). Once in the lab, they were conserved in a cold room and immediately the measurements had begun on the same day for the three sites.

Each branch was re-cut under water with a razor blade into three stems 30 cm long with a 5-7 mm vessel diameter ($n = 27$) to remove artificial embolism and to release tension gradually. The solution used was a mixture of 10 mM KCl and 1 mM $CaCl_2$. Ki and Kmax (kg s^{-1} MPa^{-1}) were measured at low pressure (60 kPa). Before measuring Kmax, vacuum rehydration was used in our measurements to avoid vessel embolism.

2.4 Vulnerability Curves

Vulnerability to xylem cavitation was assessed using the bench dehydration technique (Cochard et al., 2005). The observed curve was fitted to a logistic function (Pammenter & Vanderwillingen, 1998):

$$PLC = \%100/\{1 + \exp[S/25(P - P_{50})]\} \tag{1}$$

From the equation of the curve, we could determine a xylem water potential causing 50% loss of hydraulic conductivity at point P_{50} (Spark & Black, 1999), and S is related to the slope of the vulnerability curve at P_{50}.

2.5 Specific Conductivity

Hydraulic conductivity (Kh, kg s^{-1} m^{-1} MPa^{-1}) was measured according to the method described by (Sperry & Tyree, 1988). Segments were perfused with a degassed diluted solution of water and HCl (pH = 2) filtered with a 0.1 µm filter. Specific conductivity (Ks, kg s^{-1} m^{-1} MPa^{-1}) was determined for each segment:

$$Ks = Kh/Sa \tag{2}$$

Where, Sa (mm^2) is the sapwood transverse area of the segment (excluding the central pith).

2.6 Twig Water Potential (TWP) and Midday Water Potential

Three small twigs (5-7 cm long) from the considered trees were removed to measure the vulnerability curves using a Scholander pressure chamber (SKPM 1400®, Skye Instruments Ltd., Powys, UK), (Scholander et al., 1965). Midday water potential was measured between 12:00 and 14:00 a.m. in dry months of 2016 to represent the hydric status in this period.

2.7 Safety Margins

According to Meinzer et al. (2009), hydraulic safety margins of each species were estimated using the proxy between midday water potential (P_{min}) and xylem dysfunction (P_{50}). $HSM_{(stem)}$ = minimum $\Psi_{stem} - P_{50stem}$. In order to reflect the intrinsic drought tolerance abilities under summer drought of plants in the field, we used the mean of minimum values Ψ_{stem} in the dry summer.

2.8 Statistical Analysis

Statistical results were obtained in two steps. The first step was a combined analysis with three factors of classification. The second step consists on a simple analysis by a single factor of classification considering species, or site. The latter step was done since there are interactions between (species × site).Generalized linear models (GLMs) were applied to the following dependent variables: (1) P_{50}; (2) specific conductivity (Ks); and safety margin. A Normal distribution model best fitted the variables. Results are presented in the form of the Fisher test value (F), parameter estimates and respective P value. Correlations between the two variables ks and P_{50} were tested by Pearson correlation test.

3. Results

3.1 Vulnerability to Cavitation

All vulnerability curves (VCs) for pine species in this experiment had a sigmoid shape. Statistically significant differences were obtained in cavitation resistance between species ($p < 0.001$) and sites ($p = 0.039$). For any given species, there were differences between sites ($p < 0.001$) and for any given site; there were differences between species ($p < 0.001$).

For *P. halepensis* P_{50} was reached at -3.62 MPa, -3.57 MPa to -4.19 MPa in humid, sub-humid and semi-arid climates, respectively. While for *P. brutia*, P_{50} was reached at -3.69 MPa, -3.88 MPa to -3.81 MPa in a humid, sub-humid and semi-arid climates, respectively. However, for *Pinus canariensis*, P_{50} was varied between -3.05 MPa, -4.09 MPa and -2.65 MPa in humid, sub-humid and semi-arid climates, respectively (Table 1).

Table 1. Comparison of cavitation resistance parameters for three pine species in different sites SNT" (Souiniet), "JAB" (Jebel Abderrahmane) and "HNM" (Henchir Naam)

Species	**Site**	**P_{50}(MPa)**	**Ks (kg m^{-1} s^{-1} MPa^{-1})**
P. canariensis	HNM	-2.65 ± 0.15^a	0.03 ± 0.003^b
P. halepensis		-4.19 ± 0.169^c	0.09 ± 0.165^a
P. brutia		-3.81 ± 0.09^b	0.20 ± 0.019^b
P. canariensis	JAB	-4.08 ± 0.06^c	0.17 ± 0.072^b
P. halepensis		-3.57 ± 0.086^a	0.08 ± 0.016^a
P. brutia		-3.88 ± 0.086^b	0.58 ± 0.017^c
P. canariensis	SNT	-3.05 ± 0.15^a	0.035 ± 0.103^b
P. halepensis		-3.62 ± 0.23^c	0.123 ± 0.025^a
P. brutia		-3.69 ± 0.23^b	0.084 ± 0.038^b

Note. Within each sites, values labeled with different superscript letters are significantly different ($P < 0.05$).

3.2 Midday Water Potential

Midday water potential had statistically significant differences between species ($p < 0.001$), sites ($p < 0.001$) and between dates of measurement ($p < 0.001$), and there is a significant interaction between climate and sites ($p < 0.001$). For any given species, there were differences between sites ($p < 0.001$). For any given site, there were differences between species ($p < 0.001$).

The mean of midday water potential revealed significant differences between species ($p < 0.001$) and sites ($p < 0.001$). For *P. halepensis*, P_{min} was -3.63 MPa, -3.38 MPa and -3.18 MPa in semi-arid, sub-humid and humid climates. While for *P. canariensis*, P_{min} was -2.04 MPa, -3.22 MPa and -2.62 MPa in semi-arid, sub-humid and humid climates. However, for *P. brutia* P_{min} was varied between -3.62 MPa, -2.79 MPa and -2.06 MPa in semi-arid, sub-humid and humid climates (Table 2).

Table 2. Midday water potential (Ψ: MPa) of three pine species in different sites

Pine species	Souiniet	Jebel Abderrahmane	Henchir Naam
P. canariensis	-2.62 ± 0.01^b	-3.22 ± 0.01^c	-2.04 ± 0.01^a
P. halepensis	-3.18 ± 0.04^b	-3.38 ± 0.01^b	-3.63 ± 0.01^c
P. brutia	-2.06 ± 0.01^a	-2.79 ± 0.08^b	-3.62 ± 0.01^c

Note. The values represent the mean with±SE; a, b, c indicate the averages with different upper indices are significantly different ($P < 0.05$).

3.3 Hydraulic Safety Margins

Under dry conditions, the safety margin in *P. halepensis* was 0.44 MPa, 0.19 MPa, and 0.45 MPa in humid, sub-humid and semi-arid climates, respectively. The safety margin in *Pinus brutia* was 1.63 MPa, 0.89 and 0.19 MPa in humid, sub-humid and semi-arid climates, respectively. For *P. canariensis*, the safety margin was 0.43 MPa, 0.87 MPa, and 0.61 MPa in humid, sub-humid and semi-arid climates, respectively.

3.4 Correlation Between Specific Conductivity and P_{50}

The specific hydraulic conductivity was significantly different between species ($p < 0.001$) and sites ($p < 0.001$).The interaction term was also significant ($p < 0.001$). For any given species, there were differences between sites ($p < 0.001$). Furthermore, a positive low weak correlation index was noticed between cavitation resistance P_{50} (safety) and xylem hydraulic conductivity ks (efficiency). The weak correlation was noticed mainly in *P. brutia* at the semi-arid and sub-humid climates with $r^2 = 0.006$ and $r^2 = 0.028$, respectively. In *Pinus halepensis*, the correlation was $r^2 = 0.022$ in a humid climates (Table 3).

Table 3. Correlation indices and their significance level (prob, in italic) between Ks and P_{50} in different pine species at three sites "SNT" (Souiniet), "JAB" (Jebel Abderrahmane) and "HNM" (Henchir Naam)

Site		*P. halepensis*	*P. brutia*	*P. canariensis*
SNT	r^2	0.022^{ns}	0.082^{ns}	0.108^{ns}
	prob	*0.903*	*0.584*	*0.075*
JAB	r^2	0.230^{ns}	0.028^{ns}	0.083^{ns}
	prob	*0.081*	*0.080*	*0.541*
HNM	r^2	0.011^{ns}	0.006^{ns}	0.073^{ns}
	prob	*0.812*	*0.694*	*0.640*

Note. ns: non-significant.

4. Discussion

4.1 Distribution of Pine Species

The pressure inducing 50% loss of xylem hydraulic conductivity is considered a major vulnerability tolerance trait and it varies among pine species. The reason for species distribution seems to be related to cavitation resistance across multiple geographic scales (Delzon et al., 2010). *Pinus halepensis* was much more resistant to cavitation in semi-arid climates. While *Pinus brutia* was more resistant to cavitation in humid climates However, *Pinus canariensis* was more resistant to cavitation and better adapted to sub-humid climates (Table 1). Our results were in agreement with Brodribb et al. (2014) who reported that *P. halepensis* was highly adapted to aridity in a semi-arid study site (Figure 3).

Lopez et al. (2016) found differences in cavitation in vulnerability curves during the wet and dry provenance trials of *P. canariensis* (-3.1 MPa, -4.1 MPa, respectively). The hydraulic conductivity of the xylem is highly variable through species (Brodribb & Feild, 2000; Pockman & Jackson, 2004). The cavitation responses are depending not only on species but also on the climate (site) in which they grow. Corcuera et al. (2011) confirmed that the site was a significant source of variation for cavitation resistance and stem specific conductivity.

These results suggest that cavitation vulnerability limits plant distribution by defining maximum drought tolerance across habitats (Pockman & Sperry, 2000). These differences can be linked to an evolutionary divergence in hydraulic strategies within conifers when faced with drought (Brodribb et al., 2014).

4.2 Hydraulic Safety Margins

The width of the safety margin varies among species and increases with the decline of vulnerability (Martinez-Vilalta et al., 2002). All pine species had the same hydraulic strategies: they were resistant to cavitation, and the hydraulic safety margin was positive and revealed the difference in the degree of resistance to a drought of the species. *Pinus halepensis*, *P. brutia* and *P. canariensis* had a smaller safety margin under different climates.

Pine species adopted an extremely conservative water use mechanism (water saver) to maintain high drought resistance. Species that displayed a conservative xylem safety margin had a low risk of xylem cavitation were also those species that closed their stomata relatively early in response to desiccation. Our interpretation of these results is that isohydric species are more likely to maximize carbon uptake when conditions are favorable, but to do so and to avoid hydraulic failure, they also need to maintain larger safety margins (Skelton et al., 2015). The low overall variation of minimum water potential as a general rule in pine species implies that structural and physiological adjustments take place to maintain water potentials within relatively narrow limits, in agreement with an isohydric behavior.

4.3 Cavitation Resistance (Safety) and Xylem Hydraulic Conductivity (Efficiency)

The relationship between cavitation resistance (safety) and xylem hydraulic conductivity (efficiency) was not significant within pine species in three climates. This result was in agreement with Maherali et al. (2004) (Table 2). Furthermore, safety-efficiency trade-off may not be at all expected in gymnosperms, considering that safety appears to arise mainly from the amount of overlap between the sap-impermeable torus relative to the size of the pit aperture (Delzon et al., 2010,) which may have minimal influence on efficiency. The efficiency or safety thus arises from the design properties of the xylem tissue (membrane thickness, size, and quantity), conduit lumens (size, diameter) as well as inter-conduit (Gleason et al., 2016).

The results of pine species in different climates indicate that high vulnerability to cavitation does not necessarily reflect low levels of resistance to drought, but may be part of the overall optimization of reduced water availability and the requirement for maintaining gas exchange under dry conditions.

The adaptation mechanisms of pine species by means of extremely conservative water use (water saver) contribute to high drought resistance.

Further studies are required to investigate the interaction effects between the responses of pine tree associated with drought resistance and soil physical properties.

5. Conclusions

Vulnerability to xylem cavitation has also been found to vary substantially across species. The responses are depending not only on species but also on the climates in which they grow. Pine species evolve to more negative P_{50} to avoid the risk of xylem embolism during prolonged drought. Under dry conditions, *P. halepensis*, *Pinus canariensis* and *P. brutia* are better adapted to semi-arid, sub-humid and humid climates, respectively.

The findings of these experiments may help to quantify the impact of mid-summer water deficit on south Mediterranean pinewoods and to determine the tolerant pine species to drought. Therefore, this leads to preserving pine species which is a part of a future reforestation program.

Acknowledgements

The authors acknowledge helpful funding from the European Union Horizon 2020 programme, under Faster project, grant agreement N° [810812]. Thanks to Jordi Marinez-vilaltà for his considerable comments for manuscript and thanks to Mediterranean observatory Rural Environment and water for providing meteorological data from different regions.

References

Allen, C. D., Breshears, D. D., & McDowell, N. G. (2015). On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere, 129*, 1-55. https: //doi.org/10.1890/ES15-00203.1

Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., … Cobb, N. (2010). A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management, 259*, 660-684. https://doi.org/10.1016/j.foreco.2009.09.001

Blackman, C. J., Brodribb, T. J., & Jordan, G. J. (2012). Leaf hydraulic vulnerability influences species' bioclimatic limits in a diverse group of woody angiosperms. *Oecologia, 1*68, 1-10. https://doi.org/10.1007/s00442-011-2064-3

Brodribb, T. J., & Field, T. S. (2000). Stem hydraulic supply is linked to leaf photosynthetic capacity: Evidence from New Caledonian and Tasmanian rainforests. *Plant Cell & Environment, 23*, 1381-1381. https://doi.org/10.1046/j.1365-3040.2000.00647.x

Brodribb, T. J., McAdam, S. A. M., Jordan, G. J., & Martins, S. C. V. (2014). Conifer species adapt to low-rainfall climates by following one of two divergent pathways. *Proceedings of the National Academy of Sciences USA, 111*, 14489-93. https://doi.org/10.1073/pnas.1407930111

Burgess, S. S. O., Pittermann, J., & Dawson, T. E. (2006). Hydraulic efficiency and safety of branch xylem increases with height in *Sequoia sempervirens* (D. Don) crowns. *Plant Cell & Environment, 29*(2), 229-239. https://doi.org/10.1111/j.1365-3040.2005.01415.x

Choat, B., Jansen, S., Brodribb, T. J., Cochard, H., Delzon, S., Bhaskar, R., …. Zanne, A. E. (2012). Global convergence in the vulnerability of forests to drought. *Nature, 491*, 752-755. https://doi.org/10.1038/nature11688

Cochard, H., Damour, G., Bodet, C., Tharwat, I., Poirier, M., & Améglio, T. (2005). Evaluation of a new centrifuge technique for rapid generation of xylem vulnerability curves. *Physiologia Plantarum, 124*, 410-418. https://doi.org/10.1111/j.1399-3054.2005.00526.x

Corcuera, L., Cochard, H., Gil-Pelegrin, E., & Notivol, E. (2011). Phenotypic plasticity in mesic populations of *Pinus pinaster* improves resistance to xylem embolism (P_{50}) under severe drought. *Trees, 25*, 1033-1042. https://doi.org/10.1007/s00468-011-0578-2

Cruiziat, P., Cochard, H., & Améglio, T. (2002). Hydraulic architecture of trees: Main concepts and results. *Annals of Forest Science, 59*, 723-752. https://doi.org/10.1051/forest:2002060

De Nascimento, L., Willis, K. J, Fernández-Palacios J. M., Criado, C., & Whittaker R. J. (2009). The long-term ecology of the lost forests of La Laguna. Tenerife (Canary Islands). *Oxford Neuroscience Journal of Biogeography, 36*, 499-514. https://doi.org/10.1111/j.1365-2699.2008.02012.x

Delzon, S., Douthe, C., Sala, A., & Cochard, H. (2010). Mechanism of water-stress induced cavitation in conifers: Bordered pit structure and function support the hypothesis of seal capillary-seeding. *Plant, Cell and Environment, 33*, 210-2111. https://doi.org/10.1111/j.1365-3040.2010.02208.x

Gleason, S. M., Westoby, M., Jansen, S., Choat, B., Hacke, U. G.., Pratt, R. B., ... Zanne, A. E. (2016). Weak tradeoff between xylem safety and xylem-specific hydraulic efficiency across the world's woody plant species. *New Phytologist, 209*, 123-136. https://doi.org/10.1111/nph.13646

Johnson, D. M., Wortemann, R., McCulloh, K. A., Jordan-Meille, L., Ward, E., Warren, J. M., … Domec J. C. (2016). A test of the hydraulic vulnerability segmentation hypothesis in angiosperm and conifer tree species. *Tree Physiology, 36*, 983-993. https://doi.org/10.1093/treephys/tpw031

Klein, T., Cohen, S., & Yakir, D. (2011). Hydraulic adjustments underlying drought resistance of *Pinus halepensis*. *Tree Physiology, 31*, 637-648. https://doi.org/10.1093/treephys/tpr047

Klein, T., Di Matteo, G.., Rotenberg, E., Cohen, S., & Yakir, D. (2012). Differetial ecophysiological response of a major Mediterranean pine species across a climatic gradient. *Tree Physiology, 33*, 26-36. https://doi.org/10.1093/treephys/tps116

López, R., Cano, F. G., Choat, B., Cochard, H., & Gil, L. (2016). Plasticity in Vulnerability to Cavitation of *Pinus canariensis* Occurs only at the Driest End of an Aridity Gradient. *Frontiers in Plant Science, 7*, 769. https://doi.org /10.3389/fpls.2016.00769

Maherali, H., Pockman, W. T., & Jackson, R. B. (2004). Adaptive variation in the vulnerability of woody plants to xylem cavitation. *Ecology, 85*, 2184-2199. https://doi.org / 10.1890/02-0538

Martínez-Vilalta, J., & Piñol, J. (2002). Drought-induced mortality and hydraulic architecture in pine populations of the NE Iberian Peninsula. *Forest Ecology and Management, 161*, 247-256. https://doi.org/10.1016/S0378-1127(01)00495-9

McDowell, N. G.., & Allen, C. D. (2015). Darcy's law predicts widespread forest mortality under climate warming. *Nature Climate Change, 5*, 669-672. https://doi.org/10.1038/nclimate2641

Meinzer, F. C., Johnson, D. M., Lachenbruch, B., McCulloh, K. A., & Woodruff, D. R. (2009). Xylem hydraulic safety margins in woody plants: Coordination of stomatal control of xylem tension with hydraulic capacitance. *Functional Ecology, 23*, 922-930. https://doi.org/10.1111/j.1365-2435.2009.01577.x

Nardini, A., Pedà, G., & La Rocca, N. (2012). Trade-offs between leaf hydraulic capacity and drought vulnerability: morpho-anatomical bases, carbon costs and ecological consequences. *New Phytologist, 196*, 788-798. https://doi.org/10.1111/j.1469-8137.2012.04294.x

Pammenter, N. W., & Van der Willigen, C. (1998). A mathematical and statistical analysis of the curves illustrating vulnerability of xylem to cavitation. *Tree Physiology, 18*, 589-593. https://doi.org/10.1093/treephys/18.8-9.589

Pockman, W. T., & Sperry, J. S. (2000). Vulnerability to xylem cavitation and the distribution of Sonoran desert vegetation. *American Journal of Botany, 87*, 1287-1299. https://doi.org/10.2307/2656722

Ramirez-Valiente, J. A., Sánchez-Gómez, D., Aranda, I., & Valladarres, F. (2010). Phenotypic plasticity and local adaptation in leaf ecophysiological traits of 13 contrasting cork oak populations under different water availabilities. *Tree Physiology, 30*, 618-627. https://doi.org/10.1093/treephys/tpq013

Sala, A., Piper, F., & Hoch, G. (2010). Physiological mechanisms of drought-induced tree mortality are far from being resolved. *New Physiologist, 186*, 274-281. https://doi.org/10.1111/j.1469-8137.2009.03167.x

Scholander, P. F., Bradstreet, E. D., Hemmingsen, E. A., & Hammel, H. T. (1965). Sap pressure in vascular plants. *Science, 148*, 339-346. https://doi.org/10.1126/science.148.3668.339

Skelton R. P., West A. G., & Dawson, T. E. (2015). Predicting plant vulnerability to drought in biodiverse regions using functional traits. *Proceedings of the National Academy of Sciences USA, 112*, 5744-5749. https://doi.org/10.1073/pnas.1503376112

Sparks, J. P., & Black, R. A. (1999). Regulation of water loss in populations *of Populus trichocarpa*: The role of stomatal control in preventing xylem cavitation. *Tree Physiology, 19*, 453-459. https://doi.org/10.1093/treephys/19.7.453

Sperry, J. S., & Tyree, M. T. (1988). Mechanism of water stress-induced xylem embolism. *Plant Physiology, 88*, 581-587. https://doi.org/10.1104/pp.88.3.581

Sperry, J. S., Donnelly, J. R., & Tyree, M. T. (1988). A method for measuring hydraulic conductivity and embolism in xylem. *Plant, Cell and Environment, 11*, 35-40. https://doi.org/10.1111/j.1365-3040.1988.tb01774.x

Sperry, J. S., Hacke, U. G., Oren, R., & Comstock, J. P. (2002). Water deficits and hydraulic limits to leaf water supply. *Plant Cell& Environment, 25*, 251-263. https://doi.org/10.1046/j.0016-8025.2001.00799.x

Tyree, M. T., & Sperry, J. S. (1988). Do woody plants operate near the point of catastrophic xylem dysfunction caused by dynamic water stress? Answers from a model. *Plant Physiology, 88*, 574-580. https://doi.org/10.1104/pp.88.3.574

Urli, M., Lamy, J. B., Sin, F., Burlett, R., Delzon, S., & Porté, A. J. (2015). The high vulnerability of *Quercus robur* to drought at its southern margin paves the way for *Quercus ilex*. *Plant Ecology, 216*, 177-187. https://doi.org/10.1007/s11258-014-0426-8

Wheeler, J. K., Huggett, B. A., Tofte, A. N., Rockwell, F. E., & Holbrook, N. M. (2013). Cutting xylem under tension or supersaturated with gas can generate PLC and the appearance of rapid recovery from embolism. *Plant, Cell and Environment, 36*, 1938-1949. https://doi.org/10.1111/pce.12139

You, H., Jinb, H., Khaldi, A., Kwaka, M., Lee, T., Khainea, I., … Woo, S. (2016). Plant diversity in different bioclimatic zones in Tunisia Journal of Asia-Pacific. *Biodiversity, 9*, 56-62. https://doi.org/10.1016/j.japb.2016.01.002

Copyrights