

Insights into xylem vulnerability to cavitation in *Fagus sylvatica* L.: phenotypic and environmental sources of variability

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Summary Xylem vulnerability to cavitation is a key parameter in understanding drought resistance of trees. We determined the xylem water pressure causing 50% loss of hydraulic conductivity (P_{50}), a proxy of vulnerability to cavitation, and we evaluated the variability of this trait at tree and population levels for *Fagus sylvatica*. We checked for the effects of light on vulnerability to cavitation of stem segments together with a time series variation of P_{50} . Full sunlight-exposed stem segments were less vulnerable to cavitation than shade-exposed ones. We found no clear seasonal change of P_{50} , suggesting that this trait was designed for a restricted period. P_{50} varied for populations settled along a latitudinal gradient, but not for those sampled along an altitudinal gradient. Moreover, mountainside exposure seemed to play a major role in the vulnerability to cavitation of beech populations, as we observed the differences along north-facing sides but not on south-facing sides. Unexpectedly, both north-facing mountainside and northern populations appeared less vulnerable than those grown on the southern mountainside or in the South of France. These results on beech populations were discussed with respect to the results at within-tree level.

Keywords: drought tolerance, European beech, hydraulic, phenotypic plasticity, populations, xylem embolism.

Introduction

Global warming models predict that drought will become an increasingly important factor limiting tree growth and survival. Knowledge of factors enabling tree species to occupy different habitats is therefore important. According to Bazzaz (1996), a high degree of ecological variation, i.e., a wide range of different habitats potentially occupied by a species, can be achieved by various means: the species can show a

high degree of genetic variability, comprising genotypes especially adapted to different habitats, or the tree can exhibit phenotypic plasticity in different environments. European beech (*Fagus sylvatica*) is a widespread species of the European temperate forest with a natural range of distribution extending from southern Sweden to central Italy, western France, northern Portugal and central Spain and eastern to north-western Turkey. It dominates natural forests in dry to humid conditions and requires a humid atmosphere and a well-drained soil (Rose et al. 2009). In the Mediterranean basin, beech grows in mountainous regions where rainfall is high, just barely within the limit of its requirements (Garcia-Plazaola and Becerril 2000). In France, beech forests and/or stands occupy broad geographic and altitudinal ranges from plains at sea level up to 1700 m a.s.l. Because of its broad ecological amplitude, European beech is expected to contain variability for many traits such as resistance to cavitation events by its xylem.

It is now clear that xylem dysfunction induced by drought is a serious threat to plant productivity and survival. Comparisons of species growing in contrasting environments suggest that increased cavitation resistance is a key component of species growing in drought-prone habitats (Tyree and Ewers 1991, Pockman and Sperry 2000, Cochard et al. 2008). Correlations between drought resistance and xylem vulnerability to cavitation have been found in groups of woody species with contrasting ecological preferences (Nardini et al. 2000, Sperry and Hacke 2002, Pita et al. 2003, Tyree et al. 2003, Maherali et al. 2004). Xylem vulnerability to cavitation is usually described through vulnerability curves, i.e., the plot of percent loss of xylem hydraulic conductivity against xylem tension. For more than two decades, vulnerability to cavitation has been seen as an intrinsic property of the conductive elements of the xylem (Tyree and Ewers 1991, Tyree et al. 1994, Cochard 2006) and can be evaluated without submitting the plant material to a long period of drought. Consequently, xylem

vulnerability to cavitation has widely been documented across species and has been shown to vary greatly between species (Tyree and Ewers 1991, Maherali et al. 2004, Bréda et al. 2006, Cochard 2006, Froend and Drake 2007, Brodribb and Cochard 2009). To date, reports at the intra-specific level are much scarcer, but resistance to cavitation can vary significantly between populations of the same species (Alder et al. 1996, Sparks and Black 1999, Choat et al. 2007) or between closely related genotypes (Vander Willigen and Pammenter 1998, Sangsing et al. 2004, Cochard et al. 2007), and between organs of the same plant (Tyree et al. 1993, Sperry and Saliendra 1994, Hacke and Sauter 1995, Cochard et al. 1999).

We hypothesized that vulnerability to cavitation varies in tree populations according to their water availability. Recently, we demonstrated in a poplar clone that this trait acclimates to drier soil conditions (Awad et al. 2010). Here, we examined the variability of vulnerability to cavitation in beech at the within-tree level and between in situ populations. First, we assessed the within-tree variation in vulnerability to cavitation due to light and seasonal effects. Then, we compared in situ populations along altitudinal and latitudinal gradients for their vulnerability to cavitation. We hypothesized that vulnerability to cavitation should vary in beech forests both with elevation and along a latitudinal gradient as mountains are steep climate gradients, the altitudinal gradient is often claimed to mirror the latitudinal one (Rahbek 1995, Fosaa 2004).

Materials and methods

Vulnerability to xylem cavitation

We used the Cavitron technique (Cochard et al. 2005) to measure vulnerability to cavitation of stem segments. This technique uses centrifugal force to increase tension in a calibrated stem segment, while variations in its xylem hydraulic conductance are measured. Samples (0.7–0.8 cm in diameter and 28 cm in length) were cut in the air from 50-cm-long stem segments, placed on a custom-built rotor and spun at set velocities. Maximal conductance (k_{\max}) was determined by setting the xylem pressure to a reference value of -1.00 Mpa, without having flushed them previously. Xylem pressure was then set to gradually more negative values by 0.50 MPa steps. For each new xylem pressure, a hydraulic conductance (k_{ψ}) value was measured at equilibrium and the percent loss of conductance (PLC) per sample was computed as $PLC = 100 \times (1 - k_{\psi}/k_{\max})$. This procedure was repeated until PLC reached at least 90%. The rotor velocity was monitored with an electronic tachometer (10 r.p.m. resolution) and xylem pressure was adjusted to approximately ± 0.02 MPa. The dependence of PLC on xylem pressure was used to generate vulnerability curves for each stem segment, which were fitted to the following sigmoid function (Pammenter and Vander

Willigen 1998):

$$PLC = \frac{100}{1 + \exp(s/25(P - P_{50}))},$$

where P is the water potential, PLC is the corresponding percent loss of conductivity, P_{50} is the negative pressure causing 50% loss of conductance and s is the slope of the curve at its inflection point.

Plant material

Current year plant material from differently aged European beech trees grown in different, contrasting environments were used, according to the questions addressed. Except where specified, we used full sunlight stem segments. They were collected between 9:00 a.m. and 12:00 noon. We used a pruning pole to sample stem segments 50 cm long in the top half of each branch or shoot, according to the tree height. These stem segments were promptly defoliated, wrapped in a wet soft tissue and enclosed in a humid black plastic bag to minimize dehydration and prevent non-steady-state embolism occurring. We brought the stem segments to the laboratory and stored them at 5 °C for up to 30 days, i.e., until measurements were completed.

In August 2006, we collected samples within 2 h from a single 7-m-high tree growing in a deciduous Allagnat forest location, to evaluate the length of time stem segments could be stored without impacting on their P_{50} value. To avoid light acclimation effects, we harvested only full sunlight-exposed branches. The samples were wrapped in humid paper and kept at 5 °C in a sealed black plastic bag. We used a set of five to six stem segments stored for 0, 3, 6, 7, 8 and 10 weeks to determine P_{50} values in this experiment.

To analyse the effects of light together with seasonal variations in vulnerability to cavitation, four mature trees were chosen in a deciduous forest at the Allagnat location (Table 1). The selected trees grew at the edge of the forest with southern branches fully exposed to sunlight, whereas

Table 1. Name, geographical location and elevation of the study sites.

Name of the forest site, location in France	Global positioning	Altitude (m)/ mountainside	Reference for the study sites
Allagnat, centre	45°45'N, 2° 54'E	1000	Cochard et al. (2005)
Graouilly, north-east	49°04'N, 6° 01'E	300	Piboule et al. (2005)
Hesse, north-east	48°40'N, 7° 03'E	330	Granier et al. (2000)
Mount Ventoux, south-east	44°10'N, 5° 14'E	950/North 1260/North 1520/North 930/South 1250/South 1565/South	Dreyfus (2008)

northern ones were deeply shaded by upper branches and (or) surrounding trees during the growing season. For each light exposure condition, three to five stem segments were collected at different locations in each tree to avoid spatial positioning effects between sampling periods. In these experiments, we used segments that were more than 1 or 2 years old, as the current year shoots were too short to fit the customized centrifuge rotor, especially the shade-exposed ones. P_{50} data collected from the four trees were pooled, and their means and standard errors (SEs) were calculated. For two out of the four trees, we carried out a survey of vulnerability to cavitation for both light- and shade-exposed stem segments ($n = 4$ or 5) for 11 sampling dates between April 2007 and August 2008. The mean and SEs of their P_{50} values were calculated for each tree on each sampling date.

During the 2006 growing season, we selected four beech populations located along a latitudinal gradient from northern to southern France (Graouilly, Hesse, Allagnat and Mount Ventoux; Table 1) to investigate the difference in vulnerability to cavitation between in situ populations. The samples, collected from 10 adult tree branches and 9 stems from juveniles in Allagnat, were also used to check for the effects of tree stature on vulnerability to cavitation. As no difference was found between juvenile and adult plants, we pooled the data. We also pooled the data for the Mount Ventoux populations, as a comparison of vulnerability to cavitation made at five elevations along a northern altitudinal gradient revealed no difference in P_{50} for the whole set of samples. One stem segment per tree from 8, 9, 19 and 50 trees in the Graouilly, Hesse, Allagnat and Mount Ventoux sites were, respectively, sampled (Table 1) and the mean P_{50} values with their SEs were calculated. These mean and SE values were used as a proxy for each given site. On 14 June 2008, we again harvested six stem segments from different trees at three elevations on north-facing and south-facing mountainsides at the Mount Ventoux site to check for mountainside exposure effects in variability in vulnerability to cavitation. In this site, the sampling was carried out >900 m a.s.l. because only scattered beech trees were available below this baseline.

Statistical analysis

We carried out analysis of variance (ANOVA) to determine whether P_{50} means are significantly different between populations settled along latitudinal and altitudinal gradients. In case of significant differences, we refer to the Tukey's multiple range test at $P < 0.05$ to compare the mean values. To analyse the light effects together with intra-annual variations in P_{50} , a repeated ANOVA was performed based on the factors such as 'light' and 'time'. Then, for each factor, the mean values were compared using the Tukey's multiple range test at $P < 0.05$. We carried out regression analysis to check whether the slope is significantly different from zero at $P < 0.05$ to test samples for any age effect and the conservation delay.

All the measured and derived data underwent statistical analysis using the Statgraphics plus 4.1 software package.

Results

Age effect and conservation delay of severed samples

No significant difference in P_{50} values was observed regarding the age effect of the stem segments (Figure 1a). We also found that beech stem segments stored for 10 weeks at 5 °C in humid dark conditions were still suitable for P_{50} determination (Figure 1b), probably because xylem conduits and the bulky xylem tissue are made of dead cells. Thus, storing stem segments for weeks at low temperature constitutes a great issue for large-scale screening campaigns of vulnerability to cavitation, such as those carried out in this study.

Phenotypic variation of vulnerability to cavitation

Figure 2 shows that the full sunlight-exposed stem segments were significantly less vulnerable to cavitation than the shade-exposed ones. When both types of stem segment of a given tree were considered separately, they differed significantly in their vulnerability to cavitation over the timespan of the survey, except for a few sampling dates (Figure 3). Nevertheless, the full sunlight-exposed stem segments

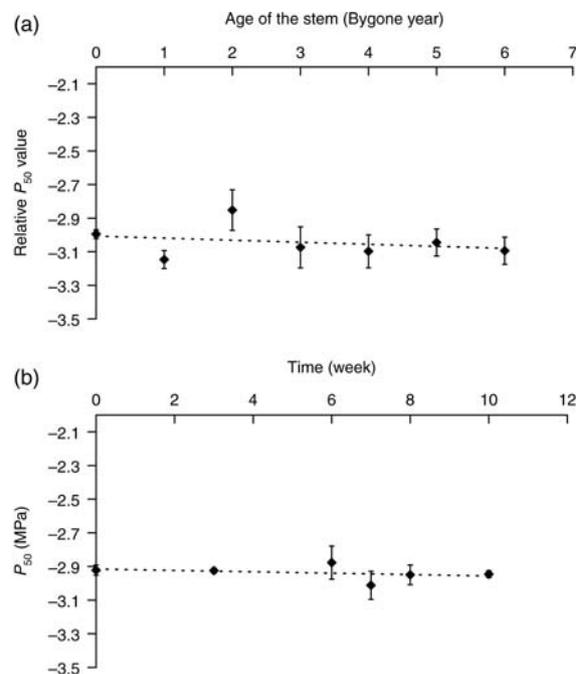


Figure 1. Effects of age of the stem (a) and the conservation time of samples at 5 °C (b) on their vulnerability to cavitation. (a) x-Axis represents the age class of the stem segments (0 is for current year stem, 1 is for stems of more than 1 year old, etc.) and the y-axis represents the P_{50} of the samples relative to the P_{50} mean value of the trees from a given in situ population. Data are means (\pm SE) of 6–131 stem segments. (b) The P_{50} value of stem segments from a single beech tree was determined after 0, 3, 6, 7, 8, 10 weeks of storage at 5 °C wrapped in humid paper. The samples were collected from a single tree within 2 h. Data are means (\pm SE) of four to six stem segments. The lines are linear regressions. Their slopes are not significantly different from 0, with $P = 0.6719$ and 0.6264 , respectively, for (a) and (b).

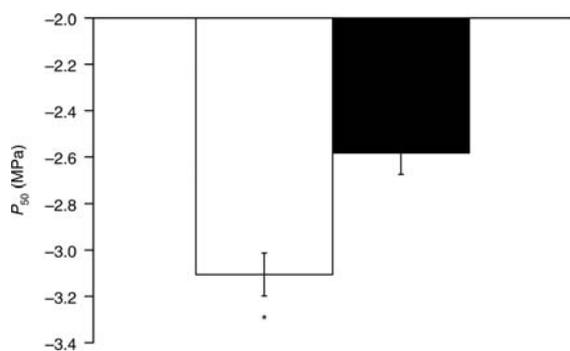


Figure 2. Vulnerability to cavitation of beech shade-exposed (black bars) and full sunlight-exposed stem segments (white bars). The pressure causing 50% loss of conductance (P_{50}) was determined for samples collected from four trees. Data are means (\pm SE) of 16 stems. They were significantly different, $P = 27.3 \times 10^{-6}$.

tended to have more negative P_{50} values compared with those shade exposed. Some significant variations of the vulnerability to cavitation can be observed over time (Figure 3), but these variations were different depending on the tree and no specific seasonal changes were detected. Nevertheless, we observed minor variations in vulnerability to cavitation of the samples during the leafy period, i.e., between June and October, especially in full sunlight-exposed stem segments.

Variability in vulnerability to cavitation between populations along altitudinal and latitudinal gradients

Values of P_{50} differed significantly between most of the populations (Figure 4) growing in France along a north-east to south-east latitudinal gradient (Table 1). The population from the centre of France had intermediate values of P_{50} when compared with both northern (-3.77 MPa) and southern (-2.40 MPa) ones. The largest difference in P_{50} (1.37 MPa) was found between the populations of the Mount Ventoux (southern) and Graouilly (northern) sites. Unexpectedly, the P_{50} values of beech harvested at the northern site were lower than those from the central and southern sites. At the central site, vulnerability to cavitation was similar for stems of juveniles and branches of adult trees. Hence, plant stature probably plays only a minor role in determining beech P_{50} .

Figure 5 shows that populations located on south-facing mountainsides along an altitudinal gradient of Mount Ventoux displayed no statistical changes in their vulnerability to cavitation. In contrast, populations from the north-facing mountainside differed in P_{50} in some cases.

Discussion

Phenotypic plasticity of vulnerability to cavitation

We have shown that vulnerability to cavitation in *F. sylvatica* varies with the exposure of the shoots to sunlight, the shade-exposed stem being more vulnerable to

cavitation than the sun-exposed one (Figures 2 and 3). Our results are in line with those previously reported (Cochard et al. 1999; Barigah et al. 2006). To grow, European beech, as a shade-tolerant tree species, can take advantage of changes in irradiance, such as those associated with mortality of overstory trees (Stickan and Zhang 1992). Consequently, the tree needs to acclimatize its hydraulic features to use the available light efficiently for carbon gain and resume rapid growth. A high transpiration rate requires a hydraulic system able to sustain large water fluxes, together with the ability to tolerate large water potential differences in the xylem conduits (i.e., low xylem vulnerability to cavitation, Tyree and Ewers 1991). Thus, full sunlight-exposed stems need to be designed with low vulnerability to cavitation so as to support increases in the stomatal conductance and transpiration rate of their leaves.

Regarding the seasonal variations in vulnerability to cavitation, we observed many occurrences of differences between stem segments with different light exposure (Figure 3a and b). These observations suggest that the light exposure of the stems and/or branches played a major role in their hydraulic architecture. Full sunlight- and shade-exposed stem segments generally differed in their P_{50} . However, this observation was unexpected given the environmental conditions, which were prone to significant changes between leafy and leafless periods. During leafless periods, the evaporative demand of the air was assumed to be low and the soil water availability was assumed to be high. The changes in xylem anatomy can occur only in the growing season during wood formation, as xylem conduits are made of dead cells with no short-term capacity to acclimatize or adjust to changes in hydraulic demand. This would explain why no variation in vulnerability to cavitation was observed for samples kept for 5 weeks in humid and dark conditions (Figure 1). Thus, an environmental event such as a frost or a spell of drought that occurs in spring at the time of early wood vessel formation can directly impact on cells undergoing differentiation and thus leave an imprint inside xylem conduits.

We also observed the variations in vulnerability to cavitation in 2007, but the patterns were not similar for the two trees in question (Figure 3). This difference was difficult to explain, as the trees were close to each other and so were assumed to be growing under the same climatic conditions. The observed discrepancy may result from soil heterogeneity, but this did not fit the assumption that in time series of different individuals, the existence of common variability is caused by the influence of a given environmental factor (Fonti et al. 2010).

Phenotypic variability of vulnerability to cavitation in beech populations

In this study, we showed a great variability in the vulnerability to cavitation in *F. sylvatica*, with the greatest difference in the P_{50} values of 1.37 MPa between two populations

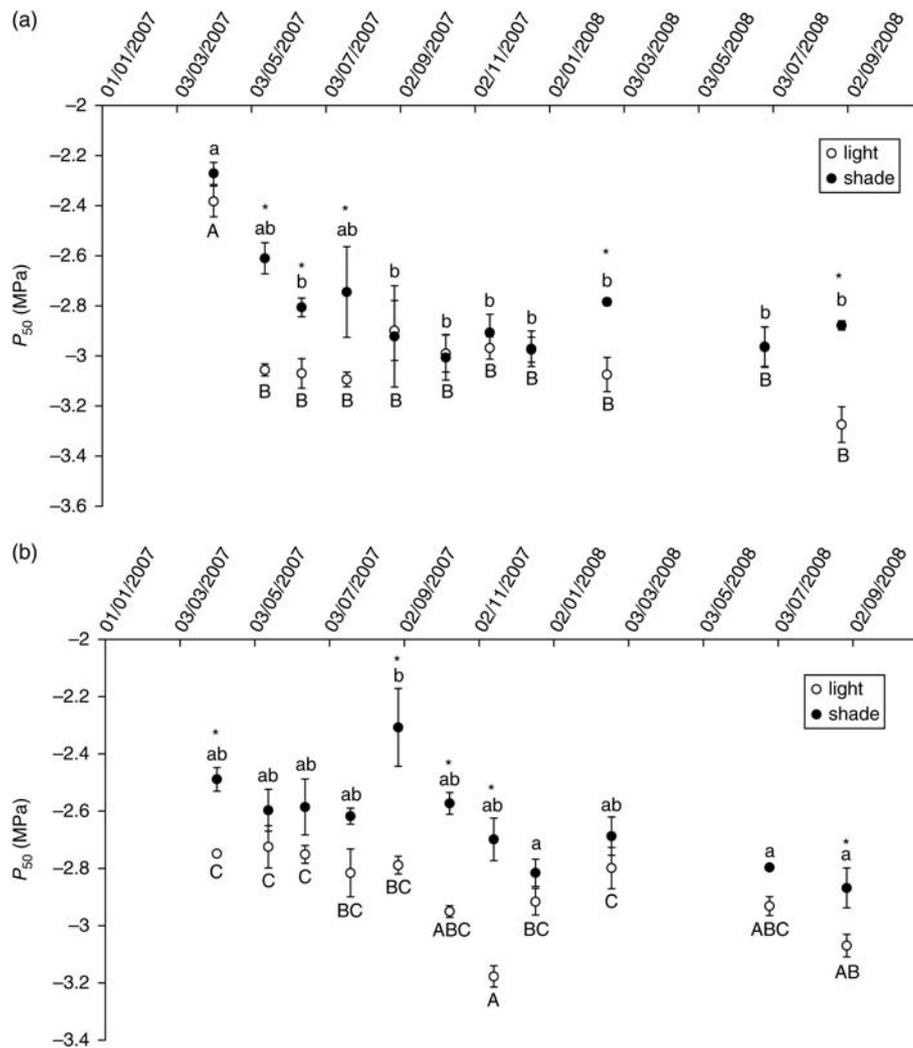


Figure 3. Time course vulnerability to cavitation of shade-exposed (closed circle) and full sunlight-exposed stem segments (open circle) for two trees (a and b). P_{50} values for both shade-exposed and full sunlight-exposed stem segments were determined for 11 sampling days (from April 2007 to August 2008). Data are means (\pm SE) of three to five stems. For each light condition, P_{50} means obtained during the survey were compared. Different upper and lower case letters indicate significant differences for light- and shade-exposed stems, respectively. For each sampling date, P_{50} means were compared between light- and shade-exposed stems and asterisks indicate significant differences, $P < 0.05$.

on two different sites (Figure 5). Such a within-species variability can be attributed to the large ecological amplitude of the beech. In contrast, *Pinus sylvestris*, which is roughly as sensitive as beech, showed limited variability in vulnerability to cavitation between and within populations (Martinez-Vilalta et al. 2009). Such between-population differences in beech can be driven by phenotypic plasticity depending on the environmental conditions and genetic differentiation. According to Hamrick (2004), most of the genetic variation for most traits resides within populations, with few differences between populations. This assumption suggests that environmental factors play a major role in the observed variations between populations for vulnerability to cavitation. We found that beech populations from north-east France were more drought resistant to cavitation than those from the south-east (Figure 4). Although the genetic origins

of our beech populations were not fully known, these results are unexpected. Indeed, the southern French populations occurred at the natural southern limit of beech distribution in a Mediterranean climate (Parelle et al. 2006). This area is characterized by its long droughts, high evaporative demand and energy balance in summer, which would be expected to be detrimental to beech growth and survival. In *P. sylvestris*, the vulnerability to cavitation was not associated with global climate dryness (Martinez-Vilalta et al. 2009). There are two explanations for such a discrepancy between vulnerability to cavitation and the locations of beech populations. First, growth processes may have been favoured for drought resistance instead of vulnerability to cavitation. Many studies have investigated the drought sensitivity of beech populations along geographical gradients of precipitation (Garcia-Plazaola and Becerril 2000, Nielsen and Jorgensen

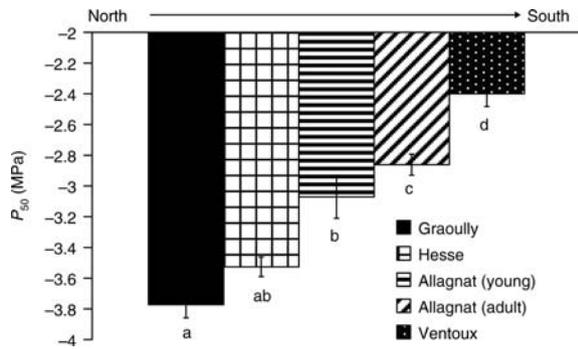


Figure 4. Vulnerability to cavitation in beech populations distributed along a latitudinal gradient. P_{50} values were determined for sampled trees from Graouilly, Hesse, Allagnat and Mount Ventoux forest sites. The arrow indicates the ranking of the populations distributed along the north-to-south direction. For Allagnat site, P_{50} values were determined for juveniles and adult trees. Data are means (\pm SE) of 8–50 stem segments. Only one stem was sampled per tree. Data with sharing different letters are significantly different with $P < 0.05$.

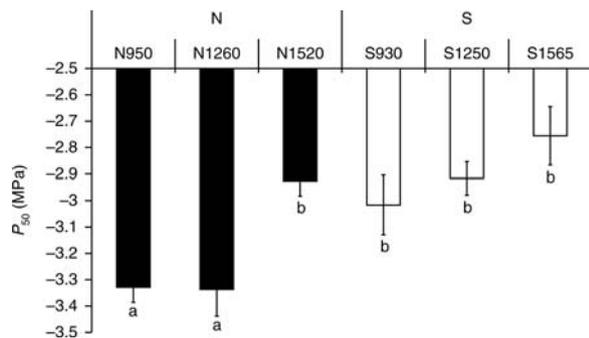


Figure 5. Vulnerability to cavitation in north- and south-facing mountainside beech populations distributed along altitudinal gradients at the Mount Ventoux site. The P_{50} values were determined for trees located on the north (N) side at elevation 950, 1260 and 1520 m, and on the south (S) side at elevation 930, 1250, 1565 m. Data are means (\pm SE) of six stems. Only one stem was sampled per tree. Data with different letters are significantly different with $P < 0.05$.

2003, Rose et al. 2009). From these studies, it was concluded that a higher tolerance to drought stress in southern populations is based on morphological and growth parameters, such as acorn mass for seedlings and root/shoot ratio for mature trees rather than on a better photoprotective system. This assumption could explain the lack of correlation between vulnerability to cavitation and altitudinal distribution. For example, *Populus euphratica*, one of the tree species most vulnerable to cavitation, is able to grow in arid areas because of its ability to access deep water tables (Hukin et al. 2005). According to Mayr et al. (2007), freezing and drought-induced embolism proceed by the same mechanism. Consequently, we suggest that the low P_{50} values observed in north-east and central populations could result from an acclimation to the occurrences of both low-temperature (winter) and severe drought episodes (summer)

which take place frequently in these areas. Secondly, we observed, on the one hand, that vulnerability to cavitation did not vary much throughout the seasons (Figure 2) and, on the other hand, that no change in vulnerability to cavitation occurs over the 10 weeks the severed stems were stored in humid and dark conditions (Figure 1b). Because vulnerability to cavitation might rely on the environmental conditions prevailing during xylem vessel formation, differences in vulnerability to cavitation between populations depend on environmental conditions of both limited time and their respective phenology. To support this, we recently showed that vulnerability to cavitation acclimates to drier soil conditions if poplar trees are grown under different water regimes (Awad et al. 2010).

Variability in vulnerability to cavitation due to mountainside exposure seemed to be typically higher than that due to altitudinal distribution. Light exposure seemed to play a major role, as populations growing at 1520 m a.s.l. on the north-facing mountainside had a vulnerability to cavitation similar to that of beeches distributed over the entire south-facing mountainside. Both mountainside effects and altitudinal gradients are complex and involve many different co-varying factors, such as topography, soil and climatic variables such as temperature, precipitation, sun and wind (Austin et al. 1996). It emerged from our data sets that European beech was able to display different degrees of phenotypic variability along geographic zones, but to a lesser extent along an altitudinal gradient (Figures 4 and 5).

Conclusions

Our results show that the changes in vulnerability to cavitation occur both within trees and between in situ populations. This trait seems to be at least partially governed by environmental conditions such as light exposure, probably those prevailing during wood formation and xylem conduit differentiation. This hinders the interpretation of the relationship between vulnerability to cavitation and environmental conditions especially the water availability. The correlation between vulnerability to cavitation and drought resilience found between species appears to be less relevant at the within-species level. From a methodological point of view, the weak variations through the seasons and the conservation delay of the samples make large-scale analyses of the vulnerability to cavitation feasible.

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References

- Alder, N.N., J.S. Sperry and W.T. Pockman. 1996. Root and stem xylem embolism, stomatal conductance and leaf turgor in *Acer grandidentatum* populations along a soil moisture gradient. *Oecologia* 105:293–301.

- Austin, M.P., J.G. Pausas and A.O. Nicholls. 1996. Patterns of tree species richness in relation to environment in south-eastern New South Wales, Australia. *Aust. J. Ecol.* 21:154–164.
- Awad, H., T.S. Barigah, E. Badel, H. Cochard and S. Herbette. 2010. Poplar vulnerability to xylem cavitation acclimates to drier soil conditions. *Physiol. Plant.* 139:280–288.
- Barigah, T.S., T. Ibrahim, A. Bogard, B. Faivre-Vuillin, L.A. Lagneau, P. Montpied and E. Dreyer. 2006. Irradiance-induced plasticity in the hydraulic properties of saplings of different temperate broad-leaved forest tree species. *Tree Physiol.* 26:1505–1516.
- Bazzaz, F.A. 1996. *Plants in changing environments*. Cambridge University Press, Cambridge.
- Bréda, N., R. Huc, A. Granier and E. Dreyer. 2006. Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. *Ann. For. Sci.* 63:625–644.
- Brodribb, T.J. and H. Cochard. 2009. Hydraulic failure defines the recovery and point of death in water-stressed conifers. *Plant Physiol.* 149:575–584.
- Choat, B., L. Sack and N.M. Holbrook. 2007. Diversity of hydraulic traits in nine *Cordia* species growing in tropical forests with contrasting precipitation. *New Phytol.* 175:686–698.
- Cochard, H. 2006. Cavitation in trees. *C. R. Physique* 7:1018–1026.
- Cochard, H., D. Lemoine and E. Dreyer. 1999. The effects of acclimation to sunlight on the xylem vulnerability to embolism in *Fagus sylvatica* L. *Plant Cell Environ.* 22:101–108.
- Cochard, H., G. Damour, C. Bodet, I. Tharwat, M. Poirier and T. Améglio. 2005. Evaluation of a new centrifuge technique for rapid generation of xylem vulnerability curves. *Physiol. Plant.* 124:410–418.
- Cochard, H., E. Casella and M. Mencuccini. 2007. Xylem vulnerability to cavitation varies among poplar and willow clones and correlates with yield. *Tree Physiol.* 27:1761–1767.
- Cochard, H., S.T. Barigah, M. Kleinhentz and A. Eshel. 2008. Is xylem cavitation resistance a relevant criterion for screening drought resistance among *Prunus* species? *J. Plant Physiol.* 165:976–982.
- Dreyfus, P. 2008. Dynamiques du Sapin, du Hêtre et des Pins dans l'arrière-pays méditerranéen: de la modélisation à l'aide à la gestion. Atelier REGEFOR 2007 - Forêts mélangées: quels scénarios pour l'avenir? *Rev. For. Fr.* 60:233–249.
- Fonti, P., G. von Arx, I. Garcia-Gonzalez, B. Eilmann, U. Sass-Klaassen, H. Gartner and D. Eckstein. 2010. Studying global change through investigation of the plastic responses of xylem anatomy in tree rings. *New Phytol.* 185:42–53.
- Fosaa, A.M. 2004. Biodiversity patterns of vascular plant species in mountain vegetation in the Faroe Islands. *Diver. Distrib.* 10:217–223.
- Froend, R. and P. Drake. 2007. Defining phreatophyte response to reduced water availability: preliminary investigations on the use of xylem cavitation vulnerability in *Banksia* woodland species. *Austr. J. Bot.* 54:173–179.
- García-Plazaola, J.I. and J.M. Becerril. 2000. Photoprotection mechanisms in European beech (*Fagus sylvatica* L.) seedlings from diverse climatic origins. *Trees Struct. Funct.* 14:339–343.
- Granier, A., E. Ceschia, C. Damesin, E. Dufrêne, D. Epron, P. Gross, E. Lebaube, V. Le Dantec, N. Le Goff, D. Lemoine, E. Lucot, J. Ottorini, J. Pontailler and B. Saugier. 2000. The carbon balance of a young Beech forest. *Funct. Ecol.* 14:312–325.
- Hacke, U. and J. Sauter. 1995. Vulnerability of xylem to embolism in relation to leaf water potential and stomatal conductance in *Fagus sylvatica*, *F. purpurea* and *Populus balsamifera*. *J. Exp. Bot.* 46:1177–1183.
- Hamrick, J.L. 2004. Response of forest trees to global environmental changes. *For. Ecol. Manag.* 197:323–335.
- Hukin, D., H. Cochard, E. Dreyer, D. Le Thiec and M.B. Bogeat-Triboulot. 2005. Cavitation vulnerability in roots and shoots: does *Populus euphratica* Oliv., a poplar from arid areas of Central Asia, differ from other poplar species? *J. Exp. Bot.* 56:2003–2010.
- Maherali, H., W.T. Pockman and R.B. Jackson. 2004. Adaptive variation in the vulnerability of woody plants to xylem cavitation. *Ecology.* 85:2184–2199.
- Martinez-Vilalta, J., H. Cochard, M. Mencuccini, et al. 2009. Hydraulic adjustment of Scots pine across Europe. *New Phytol.* 184:353–364.
- Mayr, S., H. Cochard, T. Améglio and S.B. Kikuta. 2007. Embolism formation during freezing in the wood of *Picea abies*. *Plant Physiol.* 143:60–67.
- Nardini, A., S. Salleo, M. Lo Gullo and F. Pitt. 2000. Different responses to drought and freeze stress of *Quercus ilex* L. growing along a latitudinal gradient. *Plant Ecol.* 148:139–147.
- Nielsen, C.N. and F.V. Jorgensen. 2003. Phenology and diameter increment in seedlings of European beech (*Fagus sylvatica* L.) as affected by different soil water contents: variation between and within provenances. *For. Ecol. Manag.* 174:233–249.
- Pammenter, N. and C. Vander Willigen. 1998. A mathematical and statistical analysis of the curves illustrating vulnerability of xylem to cavitation. *Tree Physiol.* 18:589–593.
- Parelle, J., J.P. Roudaut and M. Ducrey. 2006. Light acclimation and photosynthetic response of beech (*Fagus sylvatica* L.) saplings under artificial shading or natural Mediterranean conditions. *Ann. For. Sci.* 63:257–266.
- Piboule, A., C. Collet, H. Frochot and J.F. Dhote. 2005. Reconstructing crown shape from stem diameter and tree position to supply light models. I. Algorithms and comparison of light simulations. *Ann. For. Sci.* 62:645–657.
- Pita, P., A. Gasco and J. Pardos. 2003. Xylem cavitation, leaf growth and leaf water potential in *Eucalyptus globulus* clones under well-watered and drought conditions. *Funct. Plant Biol.* 30:891–899.
- Pockman, W.T. and J.S. Sperry. 2000. Vulnerability to cavitation and the distribution of sonoran desert vegetation. *Am. J. Bot.* 87:1287–1299.
- Rahbek, C. 1995. The elevational gradient of species richness: a uniform pattern? *Ecography* 18:200–205.
- Rose, L., C. Leuschner, B. Köckemann and H. Buschmann. 2009. Are marginal beech (*Fagus sylvatica* L.) provenances a source for drought tolerant ecotypes? *Eur. J. For. Res.* 128:335–343.
- Sangsing, K., P. Kasemsap, S. Thanisawanyangkura, K. Sangkhasila, E. Gohet, P. Thaler and H. Cochard. 2004. Xylem embolism and stomatal regulation in two rubber clones (*Hevea brasiliensis* Muell. Arg.). *Trees Struct. Funct.* 18:109–114.
- Sparks, J.P. and R.A. Black. 1999. Regulation of water loss in populations of *Populus trichocarpa*: the role of stomatal control in preventing xylem cavitation. *Tree Physiol.* 19:453–459.
- Sperry, J. and U. Hacke. 2002. Desert shrub water relations with respect to soil characteristics and plant functional type. *Funct. Ecol.* 16:367–378.
- Sperry, J. and N. Saliendra. 1994. Intra- and inter-plant variation in xylem cavitation in *Betula occidentalis*. *Plant Cell Environ.* 17:1233–1241.
- Stickan, W. and X. Zhang. 1992. Seasonal changes in CO₂ and H₂O gas exchange of young European beech (*Fagus sylvatica* L.). *Trees Struct. Funct.* 6:96–102.

- Tyree, M. and F. Ewers. 1991. The hydraulic architecture of trees and other woody plants. *New Phytol.* 119:345–360.
- Tyree, M., H. Cochard, P. Cruiziat, B. Sinclair and T. Ameglio. 1993. Drought-induced leaf shedding in walnut – evidence for vulnerability segmentation. *Plant Cell Environ.* 16:879–882.
- Tyree, M., S. Davis and H. Cochard. 1994. Biophysical perspectives of xylem evolution: is there a tradeoff of hydraulic efficiency for vulnerability to dysfunction? *IAWA J.* 15:335–360.
- Tyree, M.T., B.M. Engelbrecht, G. Vargas and T.A. Kursar. 2003. Desiccation tolerance of five tropical seedlings in Panama. Relationship to a field assessment of drought performance. *Plant Physiol.* 132:1439–47.
- Vander Willigen, C. and N.W. Pammenter. 1998. Relationship between growth and xylem hydraulic characteristics of clones of *Eucalyptus* spp. at contrasting sites. *Tree Physiol.* 18:595–600.