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Research paper

Variation in xylem vulnerability to embolism in European beech from geographically marginal populations

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Climate change is expected to increase the frequency and intensity of droughts and heatwaves in Europe, leading to effects on forest growth and major forest dieback events due to hydraulic failure caused by xylem embolism. Inter-specific variability in embolism resistance has been studied in detail, but little is known about intra-specific variability, particularly in marginal populations. We evaluated 15 European beech populations, mostly from geographically marginal sites of the species distribution range, focusing particularly on populations from the dry southern margin. We found small, but significant differences in resistance to embolism between populations, with xylem pressures causing 50% loss of hydraulic conductivity ranging from −2.84 to −3.55 MPa. Significant phenotypic clines of increasing embolism resistance with increasing temperature and aridity were observed: the southernmost beech populations growing in a warmer drier climate and with lower habitat suitability have higher resistance to embolism than those from Northern Europe growing more favourable conditions. Previous studies have shown that there is little or no difference in embolism resistance between core populations, but our findings show that marginal populations have developed ways of protecting their xylem based on either evolution or plasticity.

Keywords: climatic niche, European beech, marginal population, phenotypic variation, xylem embolism resistance.

Introduction

It is widely accepted that the climate changes induced by human activity will increase the frequency and intensity of drought events (IPCC 2007), thereby exacerbating tree mortality worldwide (Allen et al. 2010). This will have important consequences for forest production and management in Europe, due to the expected changes in the distribution, composition and function of forests (Grady et al. 2011, Renton et al. 2012). With their long life-spans, trees cannot adapt rapidly to environmental changes, and forest tree species will have to cope with these changes within a single generation (Breda et al. 2006, Lindner et al. 2010). Beech (*Fagus sylvatica* L.) is an excellent model species for evaluations of the consequences of an increasing frequency and severity of drought events, because: (i) it is known to be drought-sensitive (Kramer et al. 2010) and (ii) it is thought that beech growing in its current natural range (low suitability) may be unable to adapt to future environmental conditions, leading to a major decrease in the productivity of beech stands and die-off in marginal southern areas (Lakatos and Molnar 2009, Bellard et al. 2012). There is, therefore, growing concern about the effects of climate change on the future survival and sustainability of beech ecosystems in Europe (Aranda et al. 2000, Geßler et al. 2007). This issue is of particular relevance in Southern Europe, because the beech populations most likely to be endangered by climate change are those at the southern limit of the species distribution (Jump et al. 2006, Benito-Garzón et al. 2013). However, these predictions could be altered by phenotypic variation of some traits, including those relating to drought resistance. For instance, the inclusion of phenotypic variation in tree growth and survival for the calibration of species distribution models greatly modifies projections of range shift under climate change (Benito Garzon et al. 2011, Valladares et al. 2014). Species distribution models have been widely used to predict species range, but it remains challenging to include or compare ecophysiological traits across species ranges (Laughlin et al. 2012, Violle et al. 2014). Increases in mortality at the drier margins of the range have already been observed in forest trees (*Populus tremuloides*) close to the southern and western distribution boundaries in the USA (Anderegg et al. 2015*a*). A global understanding of the ability of beech populations to cope with and adapt to drought stress is, therefore, crucial, for assessments of the future of beech forests as a major ecosystem in Europe.

Vulnerability to embolism is a key physiological trait determining the limits of drought tolerance across tree species (Choat et al. 2012). The embolism of xylem conduits by 'air-seeding' (Tyree and Zimmermann 2002) occurs as a consequence of the negative pressures required for water transport from the soil to the leaves (Maherali and Delucia 2000, Salleo et al. 2000, Ogasa et al. 2013). It breaks the water columns in the xylem, thereby reducing the capacity of the tree to transport water (Cochard et al. 2007, Lamy et al. 2011). This decrease in water transport efficiency may lead to tissue desiccation and, ultimately, the death of the tree (Anderegg et al. 2013, 2015*b*). The extent to which plants are resistant to embolism seems to depend primarily on intervessel pit structure (Lens et al. 2011). Tree species with shallower pit chambers, thicker pit membranes and smaller pores are generally more resistant to embolism. Within beech populations, shorter genotypes are likely to display better drought resistance, with a later decrease in leaf water potential and gas exchange (Tognetti et al. 1995). However, little is known about intra-specific variation in the hydraulic components of stress resistance in beech (e.g., Borghetti et al. 1993, Wortemann et al. 2011, Aranda et al. 2015), although differences in structural properties, water relations, leaf anatomy, gas exchange, stable isotopes and growth traits between populations from different seed sources have been reported (e.g., Peuke et al. 2006, Knutzen et al. 2015, Cocozza et al. 2016, Ježík et al. 2016).

Resistance to embolism (expressed as the xylem pressure inducing a 50% loss of conductivity, P_{50}) varies greatly between tree species. For example, Delzon et al. (2010) found that P_{50} ranged from −2.9 to −11.3 MPa in an evaluation of embolism resistance in 40 different coniferous tree species. Significant differences in embolism between species were also reported by Cochard et al. (2008) for 10 *Prunus* species and by Torres-Ruiz et al. (2017) for 4 *Cistus* species. However, several studies have also reported low levels of within-species variability for embolism resistance both within and between populations, under different water stress conditions (Matzner et al. 2001, Martínez-Vilalta et al. 2009, Lamy et al. 2011, Wortemann et al. 2011, Torres-Ruiz et al. 2013). Nevertheless, information about the genetic and phenotypic variability of embolism resistance within-species remains very scarce (Neufeld et al. 1992, Lamy et al. 2011). Only a few recent studies have assessed genetic variation in embolism resistance (Corcuera et al. 2011, Lamy et al. 2011, 2014, Wortemann et al. 2011, Aranda et al. 2015), but none of these studies considered populations at the margins of the distributions of the species concerned. Populations growing at marginal sites are generally subject to unsuitable conditions and have a lower chance of survival; they are, therefore, more likely to be subject to selection and to undergo genetic differentiation (Kreyling et al. 2014). Marginal populations may, therefore, constitute important gene pools, due to the evolutionary processes to which they have been subjected (Hampe and Petit 2005). Recent common garden studies on European beech have suggested that marginal populations may be more resistant to drought than populations from more central areas in the European range of this species (Rose et al. 2009, Eilmann et al. 2014, Thiel et al. 2014). Sagarin and Gaines (2002) suggested that, despite their frequently smaller size and lower level of variability than for populations from the core of the species distribution range, marginal populations may, potentially, be better adapted to future climate conditions.

The main objective of this study was to evaluate the in situ phenotypic variability of embolism resistance across 15 beech populations from different marginal sites of the species distribution in Europe, and to evaluate the relationship between embolism resistance and climate in these populations. We hypothesized that the southernmost populations, which experience more frequent and severe drought events in this area of low climatic suitability, would be more resistant to embolism than populations from Northern Europe, which inhabit a more suitable climate and are less frequently exposed to drought stress. We hypothesized that, if embolism resistance is somehow related to the suitability of the populations for the environment in which they find themselves, then species distribution may be modified by the capacity of marginal populations to cope with water deficit.

Materials and methods

Beech populations studied

The distribution of European beech extends from southern Scandinavia to northern Sicily, and from France and southern England in the west, to eastern Poland and south-western Kaliningrad District in Russia in the east (Bolte et al. 2007). In the northern parts of its distribution, beech populations occupy sites at low elevation (e.g., Denmark 0–150 m, Germany 30 m) whereas, in southern areas, it is found at elevations above 1000 m above sea level (a.s.l.) (e.g., Slovakia over 1200 m, Greece over 1300 m, Sicily over 1500 m, Serbia over 1600 m). Beech is a highly competitive tree species broadly tolerant to diverse soil chemical conditions (Rose et al. 2009). It grows fastest in moist soils on calcareous or volcanic rock beds (von Wuehlisch 2008). According to Paule (1995), the optimal habitats for beach have five clear months in which vegetative growth is possible, a mean annual temperature of 10 °C, a mean July temperature of ~18 °C and more than 1000 mm of precipitation per year. A threshold of 500 mm of precipitation per year (250 mm from May to September) is considered to be critical for the presence of beech (Bolte et al. 2007).

We studied 15 European beech populations from marginal and peripheral sites (Table 1; Figure 1). Those forest populations are at the edges of species ranges where conditions are less suitable for survival and could respond differently to environmental changes than populations growing at the core of the distribution range. They might constitute valuable forest genetic resources for enhancing the resilience of beech forests through Europe. Five of these populations were located in the northern part of the beech distribution range, the other 10 being found in a range of environmental conditions from south-eastern to south-western Europe. All trees have been sampled in situ in order to quantify the phenotypic variability of the hydraulic traits studied. Mean annual temperature ranged from 7.2 °C (Moncayo, Spain) to 12.3 °C (Ciron, France), and cumulative precipitation ranged from 537 mm (Jamy, Poland) to 986 mm per year (Banja Luka, Bosnia). These populations were located at various elevations, from 12 m (Stenderup Midtskov, Denmark) to 1449 m (Monti Nebrodi, Italy) a.s.l.

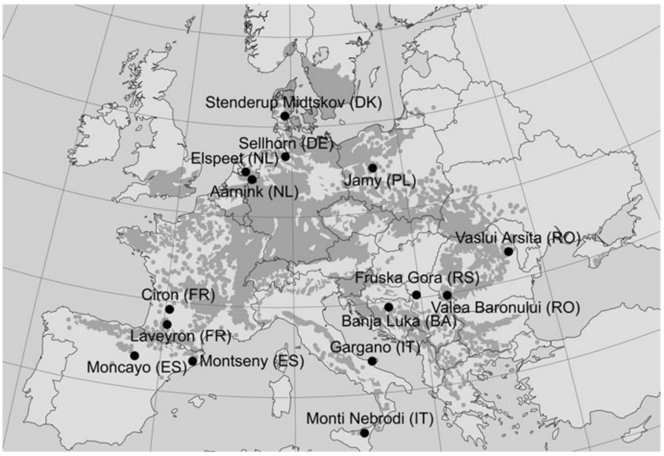

Figure 1. Map of Europe showing the distribution range of *Fagus sylvatica* (dark shaded area; after von Wuehlisch 2008) and the 15 marginal populations studied here (black dots).

Vulnerability to embolism

The P_{50} value of each beech population was determined by plotting embolism vulnerability curves obtained with the Cavitron technique (Cochard et al. 2005, Delzon et al. 2010). Briefly, 1- to 3-year-old branches were collected in the morning, from a sunny position in the upper third of the crown. The selected branches were 0.7–1.1 cm in diameter (not including the bark) and 35–40 cm long. For each population, we collected two branches per individual from at least 10 individuals. The collected samples were wrapped in wet paper and placed in sealed plastic bags for transportation. On their arrival at the laboratory, the branches were stored at 5 °C until processing, which took place within 10 days.

All measurements were performed at the high-throughput phenotyping platform for hydraulic traits (Caviplace, University of Bordeaux, Talence, France). One vulnerability curve per branch was obtained with the Cavitron. To this end, each branch was cut to the desired length (28 cm long) with a razor blade. Before mounting in the rotor chamber of the Cavitron, the samples were flushed at 1.5 bars for 20 min with an ionic solution of 10 mM KCl and 1 mM $CaCl_2$, to eliminate native embolisms. A Sorvall RC-5 C centrifuge (Sorvall RC-5 C, Thermo Fisher Scientific, Waltham, MA, USA) was used as the Cavitron rotor chamber. Spin speeds were adjusted and conductance measurements were made with CaviSoft 4.0 software (University of Bordeaux, Bordeaux, France). Measurements began at a xylem pressure of −0.8 MPa, to determine maximal hydraulic conductance (k_{max}), and the pressure was gradually decreased until the percentage loss of conductivity (PLC) reached at least 90%. During centrifugation, an ionic solution of 10 mM KCl and 1 mM $CaCl_2$ was injected into the samples for the measurement of hydraulic conductance (k) at each xylem pressure for the calculation of PLC (three to four measurements were made at each pressure step):

$$\mathrm{PLC} = 100 \times (1 - k/k_{\mathrm{max}})$$

A sigmoid function was fitted to the vulnerability curves to describe the relationship between PLC and xylem pressure (Pammenter and Vander Willigen 1998):

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

where P_{50} (MPa) is the xylem pressure inducing a 50% loss of hydraulic conductivity and s (% MPa^{-1}) is the slope of the curve.

In addition to P_{50}, we also determined the pressures inducing 12% (P_{12}) and 88% (P_{88}) losses of conductivity (Domec and Gartner 2001):

$$P_{12} = P_{50} + 50/\mathrm{slope}$$

$$P_{88} = P_{50} - 50/\mathrm{slope}$$

P_{12} estimates the xylem water potential at which embolism begins (Sparks and Black 1999), whereas P_{88} estimates the xylem water potential at which the xylem is no longer able to transport water ('full embolism point'). The xylem-specific hydraulic conductivity (k_s, $m^2\ MPa^{-1}\ s^{-1}$) was calculated by dividing the maximum hydraulic conductivity measured at low speed by the sapwood area of the sample.

Climate data

Climate data with a resolution of 30 s (corresponding to ~1 km) were downloaded from the WorldClim database (Hijmans et al. 2005). Climate was estimated by averaging climate data from 1950 to 2000. Future scenarios, for 2050, were estimated by averaging the predictions from 10 globally circulating models (BCC-CSM1-1, CCSM4, GISS-E2-R, HadGEM2-AO, IPSL-CM5A-LR, MIROC5, MIROC-ESM-CHEM, MIROC-ESM, MRI-CGCM3, NorESM1-M) for the representative concentration pathway 4.5 (rcp4.5), an intermediate climate change scenario with a mean temperature increase of 1.4 °C (IPCC, http://www.ipcc-data.org/, accessed in January 2015). We assessed the correlation between six climate variables and hydraulic traits: mean annual precipitation (MAP), MAP during the period of vegetative growth (April–September), mean annual air temperature (MAT), mean air temperature during the period of vegetative growth (April–September), maximum temperature of the warmest month (MTWM) and mean July air temperature. An aridity index (AI = MAP divided by mean annual potential evapotranspiration, http://www.cgiar-csi.org/data/global-aridity-and-pet-database) was also calculated and its correlation with the embolism resistance of populations was assessed.

Four of these variables were used to build the species distribution model: MAP, MTWM, mean temperature of the coldest month and MAT.

Modeling habitat suitability

Habitat suitability models correlate the probability of occurrence of a given species with the climatic conditions across its range. These models, therefore, predict the occurrence of the species concerned as a function of climate. We developed a habitat suitability model based on the current distribution of *F. sylvatica* (http://www.euforgen.org/distribution-maps/) presence/absence and projected the distribution of this species for the present climate and for the climatic conditions predicted for 2050. Among the three prevailing climate change scenarios, we have selected the RCP4.5, which is the most widely used and which is neither conservative (RCP2.6) nor extreme (RCP8.5). Then, we used the random forest algorithm, a non-parametric technique, to capture non-linear relationships between predictors, in combination with the automatic selection of tree predictors (random Forest R library; Breiman 2001, Liaw and Wiener 2002). The model was cross-validated by splitting the original data into training and evaluation subsets, making it possible to validate the model with independent data (Benito-Garzón et al. 2006). The random forest algorithm is a combination of automatic decision tree predictors operating in a three-step process: n ($n = 500$) groups of decision trees are bootstrapped from the original data, a regression is calculated for each group of trees and the final prediction is calculated as the mean value for all the fully grown trees (Breiman 2001). The goodness of fit of the habitat suitability model was estimated by determining the percentage of the variance explained by the model, and its generalization power was estimated by calculating Pearson's coefficient for the correlation between predictions, using the training data only and leaving the independent data out for validation.

The probability of occurrence in current climatic conditions, as predicted by the model, was extracted for each of the 15 populations, with the aim of comparing the mean P_{50} value of each population with the probability of occurrence predicted by the models. The probability of presence of the species was then transformed into binary maps (presence/absence) by maximizing True Skill Statistics (TSS; Allouche et al. 2006), which compares the prediction output with the real distribution of the species. The TSS is independent of prevalence and accounts for sensitivity and specificity (TSS = sensitivity + specificity − 1). The TSS ranges from −1 to 1, with positive values indicating good agreement between the real and predicted distributions. Sensitivity is defined as the proportion of presences correctly predicted by the model, whereas specificity is the proportion of absences correctly predicted by the model. We used this binary presence/absence map for this species to estimate whether the 15 populations would lie within or outside the suitable habitats predicted by the model for likely future climate conditions.

Statistical analysis

We assessed differences in embolism resistance between populations, by applying a general linear model (GLM) with a single effect (that of population), followed by a Tukey test for the comparison of means. We performed the analyses with both all samples and the 2-year-old branches only (87% of the samples) and found no difference (same P-value and population ranking). Moreover, we did not detect any correlation between xylem-specific hydraulic conductivity and embolism resistance ($r = 0.1$; $P = 0.19$). Both results provide sound evidence that P_{50} measurements were not biased by native embolism as a consequence of past embolism events and the analyses were therefore performed with all samples. Pearson's correlation analysis was performed at the individual level, to investigate the relationship between P_{50}, P_{12}, P_{88}, slope, k_s and geographic and climatic variables. We checked that the assumptions of homogeneous variance and normal distribution held for all hydraulic traits before carrying out the analysis. All analyses were performed with SAS Studio 3.1 (SAS Institute Inc., Cary, NC, USA). Correlations were considered to be significant if $P < 0.05$. The coefficient of variation (CV %) was calculated within (CV_{intra}) and between populations (CV_{inter}).

Results

Variability of hydraulic traits

For all populations, embolism vulnerability curves had a typical sigmoid shape, with P_{12} values consistently below −2 MPa (Figure 2; see Table S1 available as Supplementary Data at *Tree Physiology* Online). Significant differences in embolism resistance were observed between populations ($F = 5.16$; $P < 0.0001$; Figure 3; see Table S2 available as Supplementary Data at *Tree Physiology* Online), with mean P_{50} values ranging from −2.84 MPa for the most vulnerable population (Stenderup Midtskov, Denmark) to −3.55 MPa for the most resistant population (Laveyron, France), and a CV_{inter} of 8.9% (Figure 2). Intrapopulation CVs ranged from 5.7% (Monti Nebrodi, Italy) to 13.9% (Vaslui Arsita, Romania), with a mean value of 8.8%.

Significant differences between populations were also observed for k_s ($F = 8.42$; $P < 0.0001$), P_{12} ($F = 3.08$; $P = 0.0003$) and P_{88} ($F = 7.89$; $P < 0.0001$; see Table S2 available as Supplementary Data at *Tree Physiology* Online). Mean k_s values ranged from 3.5×10^{-4} (Gargano, Italy) to 16.1×10^{-4} (Banja Luka, Bosnia and Herzegovina; Table S1 available as Supplementary Data at *Tree Physiology* Online). Intrapopulation CVs for k_s ranged from 14.7% (Laveyron, France) to 59.5% (Gargano, Italy), with a mean value of 40.7%, and were similar to the CV_{inter} (37.8%).

Correlation between hydraulic traits and climate

The significant positive correlation between P_{50} and latitude (Pearson's $r = 0.334$; $P < 0.0001$) indicates that the southernmost beech populations are more resistant to embolism than those from the northern part of the distribution range (Table 2; Figure 4). Significant relationships were also observed between P_{50} and annual mean air temperature (Pearson's $r = -0.285$; $P = 0.0002$), P_{50} and AI (Pearson's $r = 0.259$; $P = 0.0008$), and P_{50} and the MTWM (Pearson's $r = -0.311$; $P = 0.0003$), demonstrating the greater resistance to embolism of populations from warmer and drier environments. Pertinent relationships were also observed between P_{50} and mean air temperature during the growing season (April–September) (Pearson's $r = -0.343$; $P < 0.0001$) and between P_{50} and mean July air temperature (Pearson's $r = -0.351$; $P < 0.0001$).

Like P_{50}, P_{88} was found to be significantly correlated with mean annual temperature (Pearson's $r = -0.268$; $P = 0.0005$), mean air temperature during the period of vegetative growth (April–September) (Pearson's $r = -0.393$; $P < 0.0001$), MTWM (Pearson's $r = -0.371$; $P < 0.0001$), mean July air

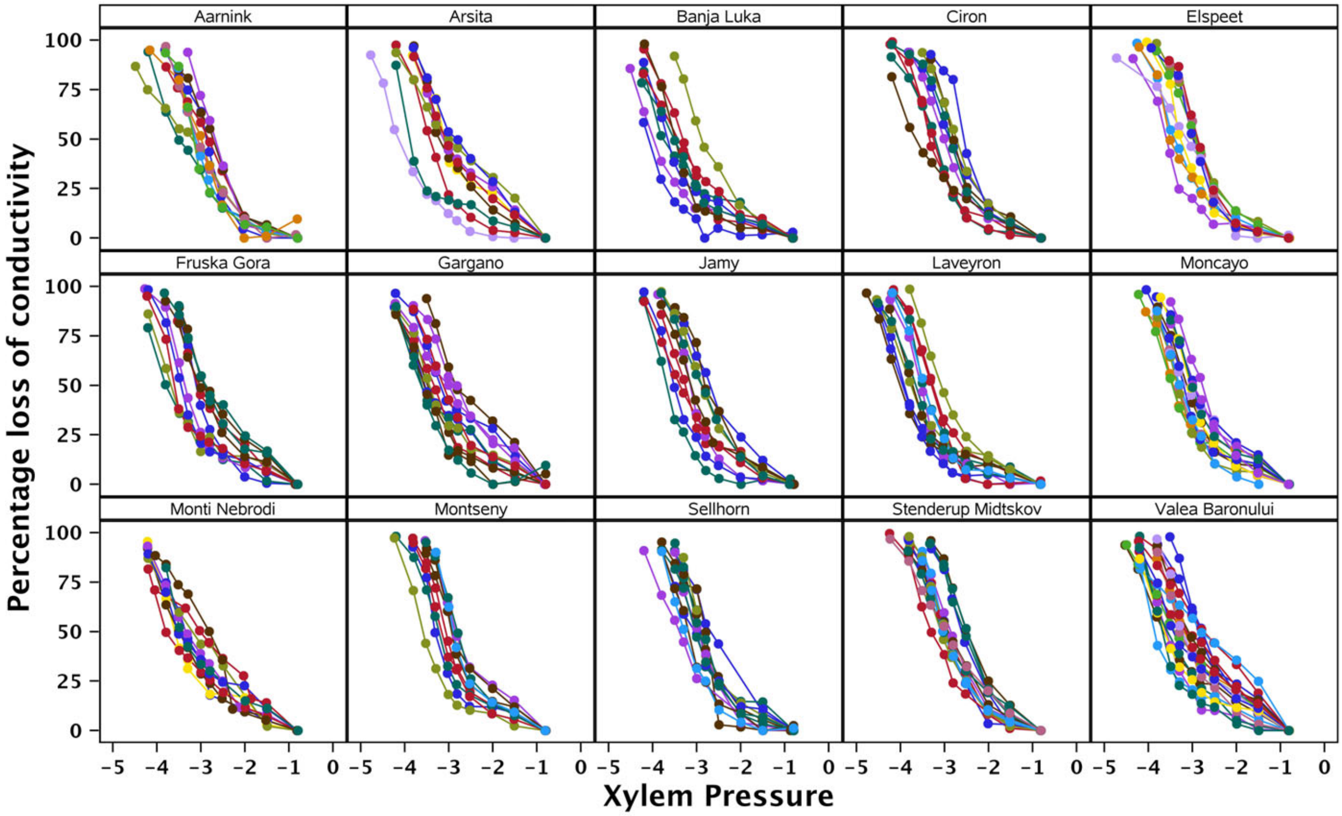

Figure 2. Vulnerability curves for at least 10 individual trees of *F. sylvatica*. Each colour represent a tree and each point represents mean value of percentage loss of hydraulic conductivity over at least three measurements of hydraulic conductance.

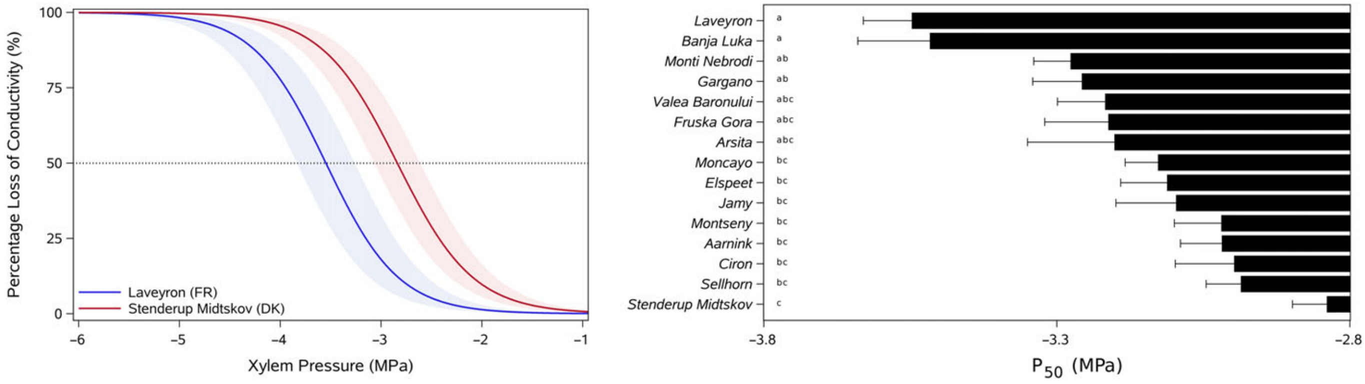

Figure 3. The left panel shows the mean vulnerability curves of the European beech populations most resistant to embolism (Laveyron, France; P_{50} = −3.55 MPa) and the vulnerable to embolism (Stenderup Midtskov, Denmark; P_{50} = −2.84 MPa). The shaded band represents the standard deviation (left panel). The right panel shows the variation of P_{50} (xylem pressure inducing a 50% loss of hydraulic conductance) between the European beech populations studied (n = 15 per population). The error bars represent the standard deviation. Different letters indicate significant differences between populations at $\alpha = 0.05$ (right panel).

temperature (Pearson's r = −0.455; $P < 0.0001$) and AI (Pearson's r = 0.250; P = 0.0013). P_{88} was also correlated with the latitude (Pearson's r = 0.426; $P < 0.0001$), longitude (Pearson's r = −0.308; $P < 0.0001$) and altitude of the beech populations studied (Pearson's r = −0.225; P = 0.0037). In terms of hydraulic efficiency, k_s was significantly correlated with the latitude and altitude of the population, and, to a lesser extent, with MAP. Thus, beech populations from southern Europe and higher altitudes had lower xylem-specific hydraulic conductivity. Similarly, lower values of k_s were generally recorded in beech populations from sites with lower MAP values.

By contrast, neither P_{50} nor P_{88} was correlated with xylem-specific hydraulic conductivity (k_s) (Table 2) or with cumulative annual precipitation of the various marginal sites. P_{12} was not correlated with any of the environmental variables studied.

Is resistance to embolism related to the climatic niche of the species?

The niche model yielded good results in terms of the goodness of fit (89.20% of the total variance was explained by the four climatic variables selected) and generalization power (Pearson's coefficient calculated with independent data = 0.90). We used a threshold of 0.5, which maximizes TSS (TSS = 0.89), to transform the probability of occurrence of the species into a binary map of presence/absence of the species (habitat suitability values of 0.5 or more were considered to indicate that the species was present. Values below 0.5 were considered to indicate that the species was absent).

The area suitable for *F. sylvatica* is projected to contract in the regions inhabited by the southern and eastern marginal populations and to expand northwards by 2050 (Figure 5a and b). Only limited areas in the central part of the current distribution of the species are likely to remain suitable for this species in 2050 (Figure 5). The differences between the areas considered suitable for *F. sylvatica* at the moment and those projected to be suitable in 2050 suggest that most of the populations from the southernmost margin sampled here will be located outside the area considered climatically suitable for this species in 2050 (Figure 5c, blue areas).

Like the comparison between P_{50} and climatic values, a comparison of the probability of occurrence (Figure 6) in current conditions and P_{50} provides a representation of the relationship of P_{50} to climatic gradients across the range of this species. The populations most resistant to embolism (more negative P_{50} values) are those growing in the least suitable climates (Pearson's coefficient = 0.62; P-value = 0.01; Figure 6). The correlation between the differences in habitat suitability between 2050 and present conditions projected by the model with the P_{50} for each populations show a negative non-significant relationship (Pearson's coefficient = −0.38: P-value = 0.16; Figure 6a). Only three populations showed an increase in habitat suitability in the future in relation with the present (Figure 6b).

Discussion

The intra-specific variability of embolism resistance has been investigated in diverse species over the last 10 years (Wortemann et al. 2011, David-Schwartz et al. 2016), but marginal populations have been studied only rarely (e.g., Borghetti et al. 1993, Tognetti et al. 1995, Lopez et al. 2016). We found significant differences in embolism resistance between in situ beech populations from various marginal sites across Europe, with maximal between-population differences of 0.7 MPa for P_{50} and 0.8 MPa for P_{88}. The significant correlations between embolism resistance and both latitude and AI indicate that beech populations located in southern Europe, which experience higher water deficits, are more resistant to embolism than those located in northern Europe, where drought is less frequent and milder. Modeling also showed that populations with lower habitat suitability values were more resistant to embolism than those with higher habitat suitability values. Together, these results

Table 2. Correlation between hydraulic, geographic and climate variables for the 15 beech populations studied. The values shown are Pearson correlation coefficients (r) estimated at the individual level. Values in bold indicate significant correlations (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$).

Variable	k_s	Slope	Long	Lat	Alt.	MAP	MAP_{VP}	MAT	MAT_{VP}	MTWM	JulyMT	AI
P_{12}	−0.006	0.049	0.039	0.035	0.027	0.060	0.005	0.041	0.012	0.011	0.017	0.019
P_{50}	−0.103	0.139	−0.101	**0.334*****	−0.121	−0.104	−0.063	**−0.285*****	**−0.343*****	**−0.311*****	**−0.351*****	**0.259*****
P_{88}	0.044	**0.640*****	**−0.308*****	**0.426*****	**−0.225****	0.055	0.100	**−0.268*****	**−0.393*****	**−0.371*****	**−0.455*****	**0.333*****
Slope	**0.204****	–	**−0.408*****	**0.285*****	**−0.222****	**0.253****	**0.261*****	−0.065	**−0.213****	**−0.212***	**−0.307*****	**0.242****
k_s	–	–	−0.005	**0.348*****	**−0.435*****	**0.168***	**0.313*****	−0.055	0.026	−0.134	−0.063	0.116

P_{12}, xylem water potential at which embolism begins (MPa); P_{50}, xylem pressure causing a 50% loss of hydraulic conductivity (MPa); P_{88}, xylem water potential at critical embolism level (MPa); k_s, xylem-specific hydraulic conductivity ($m^2\ m^{-1}\ MPa^{-1}\ s^{-1}$); MAP, mean annual precipitation (mm); MAP_{VP}, mean annual precipitation during the period of vegetative growth (April–September) (mm); MAT, mean annual air temperature (°C); MAT_{VP}, mean air temperature during the period of vegetative growth (April–September) (°C); MTWM, maximum temperature of the warmest month (°C); JulyMT, mean air temperature in July (°C); AI, aridity index.

suggest that southern marginal populations have developed ways of protecting the xylem, through evolution and/or plasticity, in response to water scarcity.

In situ phenotypic differentiation of embolism resistance

The mean P_{50} value obtained in our study ($P_{50} = -3.16$ MPa) is similar to those previously reported for European beech (Herbette et al. 2010, Wortemann et al. 2011, Aranda et al. 2015, Schuldt et al. 2015). However, Herbette et al. (2010) reported a higher phenotypic variability between populations than that reported here, with a maximum difference of 1.4 MPa between five in situ beech populations growing in northern and southern France. These phenotypic differences in hydraulic traits between natural populations may be due to genetic variation and/or phenotypic plasticity. However, no clear association was found between genetic variation and the variation of hydraulic traits for beech populations of different geographic origins in Italy (Borghetti et al. 1993) and Germany (Hajek et al. 2016). Moreover, Herbette et al. (2010) considered environmental factors to play a major role in the variation of embolism resistance between in situ beech populations. This conclusion was supported by the results of a study on beech showing an absence of significant genetic differentiation for this trait between 17 populations grown in common garden experiments (Wortemann et al. 2011), which reported P_{50} values ranging from −2.8 to −3.2 MPa. Interestingly, studies of the same provenances grown at another planting site revealed significant differences between planting sites, highlighting the importance of phenotypic plasticity in embolism resistance in beech. A predominant role for plasticity in the variability of P_{50} between populations is also suggested by the significant but very low level of genetic variation reported for this trait between six populations (maximum difference of 0.3 MPa, Aranda et al. 2015).

The in situ phenotypic variability between beech populations observed here, therefore, probably reflects phenotypic plasticity rather than genetic variations, as reported in other species (Corcuera et al. 2011, Lamy et al. 2014). Limited genetic differentiation between populations for P_{50} has indeed been found for conifer species (Corcuera et al. 2011, Lamy et al. 2011, Sáenz-Romero et al. 2013). For example, Lamy et al. (2011) reported a very narrow range of embolism resistance (0.18 MPa) in six *Pinus pinaster* populations grown in a provenance trial. In their studies of the variability of functional traits in combined in situ and common garden experiments, Bresson et al. (2011) demonstrated that genetic variation had a lesser effect than variations in natural conditions in beech. Nevertheless, we cannot rule out the possibility that there is genetic variation for embolism resistance in beech, because this has never been investigated in marginal populations and, according to genetic theory, these geographically marginal populations would be expected to display greater genetic differentiation. Finally, CV_{intra} values

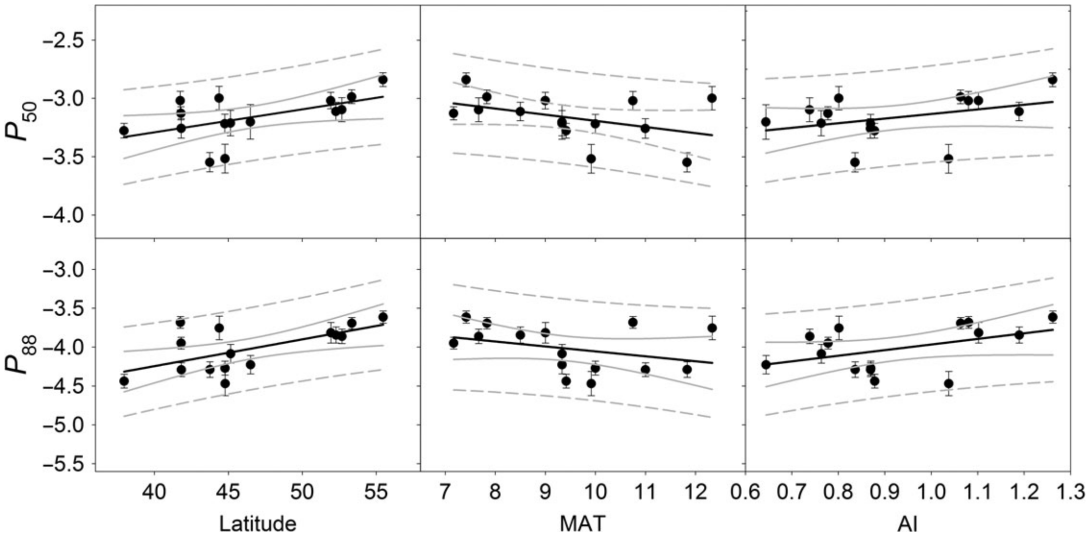

Figure 4. Mean P_{50} (in MPa, xylem pressure inducing a 50% loss of hydraulic conductance; top panels) and P_{88} (in MPa, xylem pressure inducing an 88% loss of hydraulic conductance; bottom panels) values for the various European beech populations studied, according to latitude, mean annual air temperature (MAT) and aridity index (AI). Black lines correspond to linear regressions. Solid grey and dashed grey lines indicate 95% confidence and prediction intervals, respectively. The error bars represent the standard errors.

were generally equal to or greater than CV_{inter} values in this study, suggesting the existence of high levels of genetic variation within populations, as already suggested by other studies on this species based on quantitative traits (Hajek et al. 2016) and on izoenzymes and other molecular markers (Comps et al. 1990, Gömöry et al. 1992, Borghetti et al. 1993, Demesure et al. 1996, Csilléry et al. 2014). Bontemps et al. (2016), who specifically studied a marginal European beech population, reported considerable genetic diversity for important ecophysiological traits regarding drought adaptation.

Relationships between embolism resistance and current and future climates

The embolism resistance measured in beech populations in situ was significantly correlated with AI and latitude, in particular, and, more generally, with habitat suitability, which reflects the complex relationship between climate variables across the species range. This finding is consistent with those of Bolte et al. (2016), who reported significant relationships between the drought resistance of young beech populations and precipitation patterns during the growing season at the site of origin of the population. Similarly, Schuldt et al. (2015) showed a linear intraspecific increase in embolism resistance with increasing drought stress across beech populations growing in north-western Germany. Tognetti et al. (1997) also found that *Pinus halepensis* seedlings from xeric provenances were more resistant to desiccation and potentially more suitable for establishment on sites increasingly prone to drought. Greater embolism resistance has also been reported for Douglas fir (*Pseudotsuga menziesii*) individuals from populations growing in areas with higher maximum temperatures than for those from mesic populations (Kavanagh et al. 1999). However, this is not a general pattern across species. Martínez-Vilalta et al. (2009) reported that P_{50} was unrelated to climate aridity in natural populations of Scots pine. Lamy et al. (2014) also found no significant relationship between P_{50} and AI in *P. pinaster* populations grown in dry and wet provenance-progeny trials, and in natural stands 'in situ'. In all these cases in which no relationship between resistance to embolism and single climatic variables was detected, our combined approach of comparing the climatic suitability of the species (based on complex relationships between several climatic variables) with resistance to embolism across populations would make it easier to determine whether any relationship between climate and resistance to embolism actually existed. The relationship between resistance to embolism and future habitat suitability is, however, more controversial. Our results show that those populations showing lower resistance to embolism would have a decrease in their potential suitability based on average climate, which would make the survival of these marginal populations difficult in the future.

In our study, the increased embolism resistance observed with increasing aridity could be explained by changes in pit membrane properties. Whereas several studies found that pit anatomical traits such as the torus overlap explains variability in conifers P_{50} between and within conifer species (Delzon et al. 2010, Bouche et al. 2014), measurements that link the intervessel pit membrane thickness with P_{50} remain scarce in angiosperms. However, recent studies showed that pit membrane thickness is potentially the hydraulically most relevant anatomical feature that explains variation in embolism resistance across woody angiosperms (Jansen et al. 2009, Li et al. 2016). This pit anatomical feature and its variability need to be assessed at the

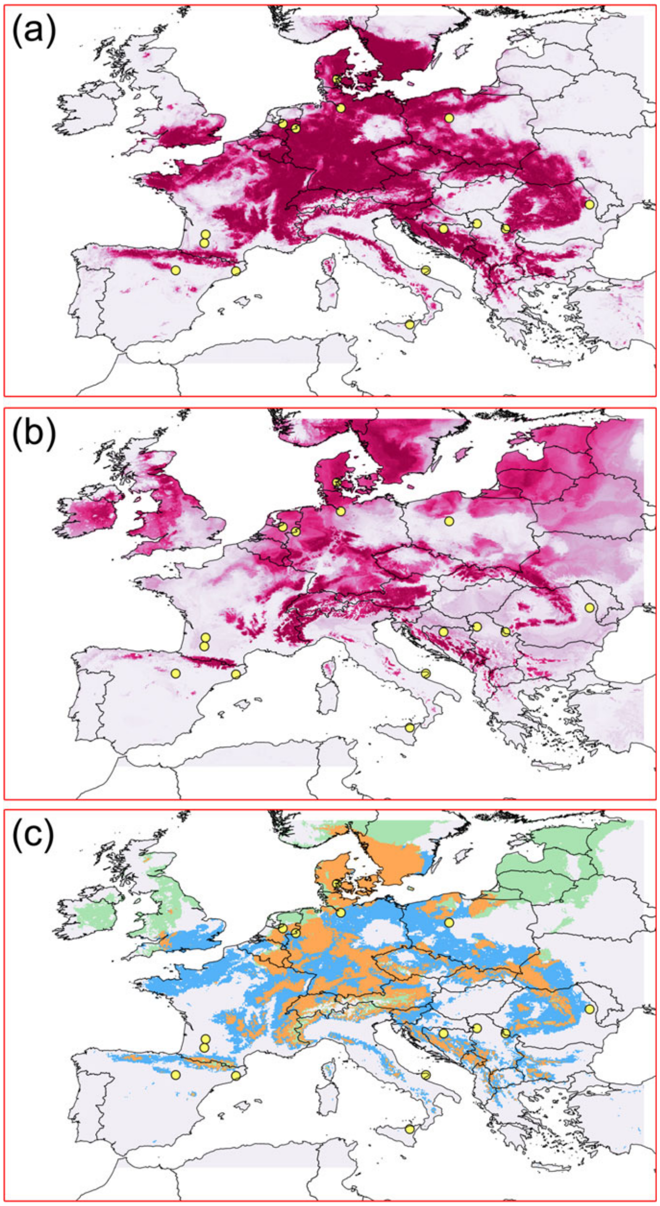

Figure 5. Habitat suitability of *F. sylvatica* for the current climate (a), the climate projected for 2050 (b), and differences between present and future habitat suitability (c) showing areas in which no change in habitat suitability (orange), a loss of habitat suitability (blue) or a gain of habitat suitability (green) is predicted for 2050. The populations studied are plotted in yellow.

intra-specific level in future studies. Xylem-specific hydraulic conductivity also declined with decreasing mean annual precipitation in the present study. The main cause of this decline may be a decrease in vessel size. A previous study evaluating the phenotypic responses of several functional traits to different environmental variables found that increasing aridity significantly affected hydraulic architecture in 28 *Eucalyptus* species from Australia. As aridity increased, vessel diameters narrowed and vessel density increased, leading to a decrease in theoretical hydraulic conductivity (Pfautsch et al. 2016). It would, therefore, be interesting to study hydraulic and anatomical traits together, to gain greater insight into the response of beech trees to water shortage. For other physiological and morphological traits, significant phenotypic clines have been already reported for beech populations growing in situ (Bresson et al. 2011), with leaf phenology traits displaying the strongest responses to environmental conditions. In their studies of the sensitivity of leaf phenology gradients to temperature along elevation gradients, Vitasse et al. (2009) found that beech was the least sensitive to temperature of the seven species they studied. However, the phenotypic variability reported for leaf phenology was much greater than that described here for embolism resistance and hydraulic conductivity. Tognetti et al. (1995) also reported an absence of difference in leaf-specific hydraulic conductivity between beech populations from Sicily and Abetone in northern Italy.

Growth declines in beech populations growing at the rear edge of their natural distribution in Europe have been observed during summer droughts by dendroecological studies (Peñuelas and Boada 2003, Jump et al. 2006). More generally, marginal populations of deciduous tree species exhibited a global growth decline in the Mediterranean basin, and this trend was more pronounced in beech populations (Dorado-Liñán et al. 2017). Those marginal populations also had higher mortality rates (Benito-Garzón et al. 2013). In our study, southern beech populations had lower P_{50} values than beech populations from the northern part of the distribution. Thus, even populations with high levels of drought resistance may not cope successfully with new climates in the southern part of the species range. This finding is consistent with the results reported by Cavin ad Jump (2017), showing that, despite their particularly high levels of drought resistance, range-edge beech populations have lower recovery capacities and relative resilience in situations in which growth is affected. An increase in aridity is predicted for the near future in southern Europe (Vautard et al. 2014), which is home to the southernmost populations of many temperate trees, including beech. Our approach combining estimations of the area in which climate is suitable and the drought resistance of marginal populations will be valuable for the future management of these populations. However, the conclusions drawn here may require adjustment at a later stage, when reliable measurements of leaf and fine root xylem vulnerability will be available to be incorporated into our proposed approach. In addition, key mechanistic traits linked to survival under several droughts such as cuticular transpiration and stomatal leakiness urgently need to be investigated if we are to understand tree population responses to severe drought (Brodribb et al. 2014, Blackman et al. 2016, Martin-StPaul et al. 2017). Our approach can identify populations at climatic risk for which even the highest level of drought resistance observed across the range would be insufficient to deal with future climate change (rcp4.5). It can also facilitate the development of programmes for translocated populations from one area to another, to compensate for climate

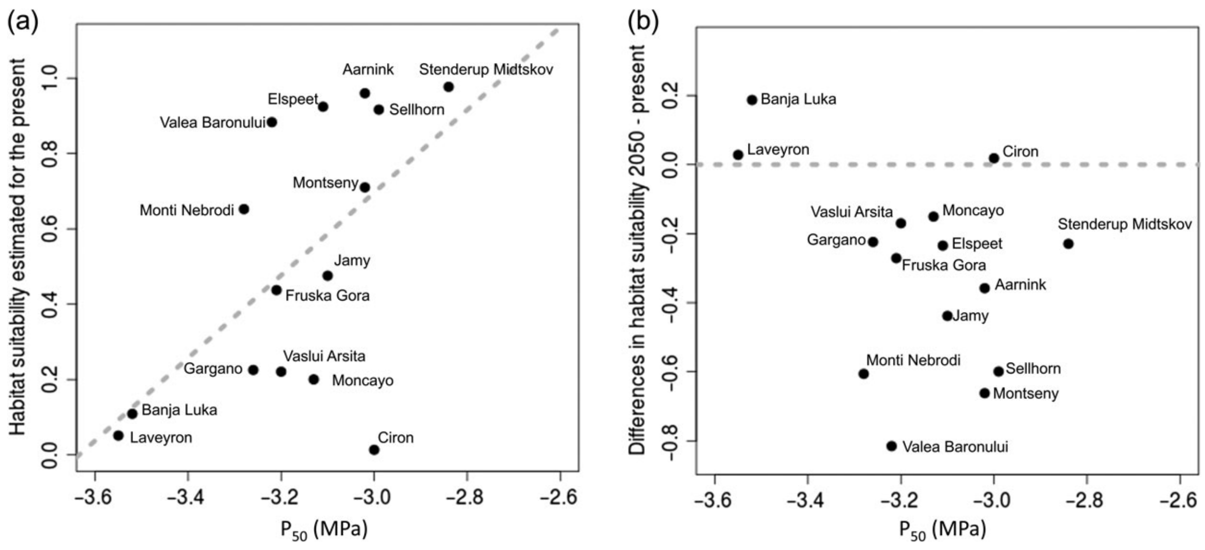

Figure 6. (a) Correlation between estimated present habitat suitability values and the P_{50} of beech populations measured in the field. Pearson's coefficient = 0.62; *P*-value = 0.01. (b) Correlation between the differences in habitat suitability between 2050 (rcp4.5) and the present conditions and the P_{50} of beech populations measured in the field. The dotted zero line indicates no differences in habitat suitability between the future and the present climatic conditions; negative values of habitat suitability indicate populations for which suitability is projected to decrease in 2050 and positive values of habitat suitability indicate populations for which suitability is projected to increase in 2050. Pearson coefficient = −0.38; *P*-value = 0.16.

Table 1. Geographic and climatic data for the 15 beech populations sampled across Europe. MAT, mean annual air temperature (°C) for 1950–2000; AP, annual sum of precipitation (mm) for 1950–2000; MAT_{VP}, MAT during the period of vegetative growth (April–September) (°C) from 1950 to 2000; AP_{VP}, sum of precipitation during the period of vegetative growth (April–September) (mm) from 1950–2000.

Population	Country	Longitude (E deg. min)	Latitude (N deg. min)	Altitude (m a.s.l.)	MAT (°C)	AP (mm)	MAT_{VP} (°C)	AP_{VP} (mm)
Aarnink	The Netherlands	06.73	51.93	40	9.0	785	13.8	405
Vaslui Arsita	Romania	27.67	46.50	189	9.3	544	16.5	363
Banja Luka	Bosnia	17.27	44.78	380	9.9	986	16.2	524
Ciron	France	00.30	44.38	26	12.3	807	17.0	385
Elspeet	The Netherlands	05.82	52.28	59	8.5	804	13.0	404
Fruska Gora	Serbia	19.63	45.15	353	9.3	699	15.7	402
Gargano	Italy	16.00	41.82	788	11.0	634	15.8	271
Jamy	Poland	17.67	52.68	106	7.7	537	14.2	337
Laveyron	France	00.22	43.75	151	11.8	822	16.5	400
Moncayo	Spain	−01.82	41.80	1190	7.2	716	12.0	368
Monti Nebrodi	Italy	14.85	37.95	1449	9.4	657	14.2	194
Montseny	Spain	02.47	41.75	986	10.8	898	15.0	458
Sellhorn	Germany	09.93	53.35	90	7.8	754	13.0	406
Stenderup Midtskov	Denmark	09.65	55.47	12	7.4	717	12.0	352
Valea Baronului	Romania	21.68	44.77	301	10.0	690	16.5	408

change (Richardson et al. 2009, Hewit et al. 2011, Neff and Larson 2014). For trees, the possibility of moving populations from southern to northern locations has been studied, as a means of improving the productivity of future forests (Pedlar et al. 2012, Benito-Garzón and Fernández-Manjarrés 2015). In the last decade, the use of locally adapted tree species and populations from xeric environments resembling climate projections for the future has also been considered (Broadmeadow et al. 2005, Bolte et al. 2009). However, as the higher levels of embolism resistance found in marginal southern populations are probably due to environmental variables, the movement of these populations northwards would not enhance the survival of northern populations, resulting in a loss of diversity within-species. Attempts to manage populations for the future will require the consideration of multiple traits, including drought resistance. Our results could facilitate the design of new assisted migration scenarios for the development of 'neo-native' forests (Millar et al. 2007).

Conclusion

The in situ phenotypic differentiation of embolism resistance described here is relatively large (almost 1 MPa between populations) and probably results from phenotypic plasticity, even if we cannot exclude the role of genetic variation for embolism resistance in marginal beech populations. Yet, the genetic differentiation induced by local adaptation under extreme selective drought pressure at the xeric margins of the range (Hampe and Petit 2005) may also be valuable for adaptation to new environments. Therefore, common garden experiments that include marginal beech populations should be installed in the future to better understand the determinism of the phenotypic differentiation observed here (Vitasse et al. 2010). In any case, our findings suggest that the potential of beech to acclimate to diverse environmental conditions should not be neglected in studies of the impact of predicted climate change (Stojnić et al. 2015).

Supplementary Data

Supplementary Data for this article are available at *Tree Physiology* Online.

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Conflict of interest

None declared.

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